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THE GENERA OF BERBERIDACEAE, LARDIZABALACEAE, AND MENISPERMACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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BERBERIDACEAE A. L. de Jussieu, Gen. Pl. 286. 1789, "Berberides," nom. cons.

(BARBERRY FAMILY)

Perennial, rhizomatous herbs or shrubs [to small trees], often with perulate vegetative buds; plants glabrous or hairs unicellular [or uniseriate, sometimes glandular], occasionally glaucous. Leaves mostly petiolate, exstipulate (or substipulate), cauline and alternate (in *Berberis* some reduced to spines, the others fasciculate), or ± opposite (*Podophyllum*), or radical (*Jeffersonia*), simple or variously divided, pinnately or ternately compound, palmately (or pinnately) veined; stomata ranunculaceous. Inflorescences 1 to many flowered, terminal or axillary, usually bracteate, scapiform, racemose, cymose, umbelliform (or paniculiform). Flowers regular, hypogynous, often calyculate, bisexual. Perianth usually 3(–5)-merous, aposepalous and apopetalous, usually multiseriate (some-

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times partly acyclic). Sepals often petaloid, usually 6 (4 to many) in 2 (1–4) series. Petals usually 6 (–9) [4] in 2 (3) series, sometimes glandular or nectariferous. Stamens usually as many as and opposite the petals (or stamens twice as many or more), equal, appearing as 1 or 2 series; filaments sometimes expanded; anthers 2-locular at anthesis, the pollen sacs lateral to ± introrse [or extrorse?], longitudinally dehiscent, sometimes forming narrow valves hinged laterally or at the apex; pollen mostly 3-colpate (spiny in *Diphylleia*). Gynoecium 1-carpellate; stigma various; style present or absent; ovary superior, 1-locular, usually ± gibbous; placenta solitary, parietal or subbasal; ovules anatropous, 2-integumented, mostly ± ascending, the micropyle down, the raphe usually above. Fruit few (1) to many seeded, fleshy or dry, nonfollicular, indehiscent or irregularly ruptured (or transversely [obliquely] loculicidal). Seeds oblong, straight to slightly curved (or ± spherical or disciform-subhemispheric), sometimes arillate; endosperm present; embryo ± straight, usually small (elongate in *Berberis*). (Including Podophyllaceae DC. and *Nandina* Thunb.; excluding *Glaucidium* Sieb. & Zucc. and *Hydrastis* Ellis.) TYPE GENUS: *Berberis* L.

About 10 or 12 genera, variously estimated to include 300 to perhaps over 600 species (*Berberis*, ca. 500 species, *Mahonia*, ca. 100; cf. Ahrendt), mostly in the Northern Hemisphere. The herbaceous species probably amount to fewer than 50. One species in each of five genera is indigenous in the eastern United States; three other genera are indigenous in the western United States. With the exception of *Berberis*, which is represented in both Eurasia and South America, the American genera lack close counterparts in Europe but exhibit strong affinities with vicarious taxa in eastern Asia (Gray), where they also are distributed in deciduous woodlands. At least one species of *Berberis* has been naturalized in our area. One or two other taxa are to be looked for as possible escapes from cultivation.

The conformation of the leaves and, especially, the venation patterns are diverse, but at the generic level more or less palmate venation is frequent, even in the leaflets of pinnately divided leaves. The most conspicuous morphological tendencies uniting Berberidaceae include the calyculate flowers; the multiseriate, deciduous, more or less imbricate perianth; the stamens opposite the petals; and the peculiar, valvelike dehiscence of the anthers of many taxa. The solitary, unicarpellate, nonfollicular gynoecium is a unifying characteristic. The petals in some respects resemble staminodia but are situated in the position of the corolla and are often glandular or nectariferous. The tendency for a multiseriate perianth with more than one series of sepals and of petals places the stamens opposite the petals and the petals opposite the sepals. Sometimes, however, the insertion appears to be slightly acyclic or spiral (see Schmidt) or the stamens may seem to be uniseriate. The opposition of stamens and petals as it occurs in Berberidaceae and Menispermaceae contrasts with the theoretically dissimilar situation in Primulaceae, Rhamnaceae, etc. (Bentham; see also developmental stages in Payer). In *Berberis*, *Mahonia*, and *Ranzania*, the stamens are tactile, bending inward when touched (Chaveaud, Dop, Kumazawa, and Müller). Initially the anthers are 4-locular and more or less introrse or simply lateral. Later, their orientation may be obscured by somewhat unequal development or by the various modes of dehiscence of the anther wall. In all cases, the anthers are longitudinally dehiscent and more or less 2-locular at anthesis. All of the tissue on the outer side of a locule may function as a single vertical, abaxially hinged valve, as in *Podophyllum*, or as two opposing, laterally hinged valves, as in *Nandina*. In *Ranzania* all of the outer wall of tissue forms an apically hinged valve, while in the remaining genera only a portion of the wall forms a similar but narrower valve (see Kumazawa).

The monomeric nature of the gynoecium (see Eckardt) has been challenged (Chapman, Eames), but the arguments against the older interpretation do not seem always to be convincing. In some clearly teratological examples (*Podophyllum*), more than one ovary of similar structure is formed in the same flower. Although the basic morphology of the gynoecium appears more or less uniform, some of the characteristics of maturation become important taxonomically.

The limits of the higher systematic units of the family are unclear when based exclusively on either floral or vegetative morphology. Subfamily Berberidoideae (including *Mahonia* and *Nandina*) is woody, and the rachis of the imparipinnate (rarely trifoliolate) leaves is either jointed and somewhat swollen at the insertion of the leaflets (or secondary rachises) or, in *Berberis*, the simple leaves are articulated, usually near the base. Subfamily Podophylloideae is herbaceous, usually with scarious ground-level bracts and with scattered vascular bundles in the aerial stems (Agardh, Brown, Harvey-Gibson & Horsman, Metcalf & Chalk). The leaves are simple (sometimes two-parted) and palmately veined or are bi- or trifoliolate or ternately decompound (pinnately compound in *Bongardia*); the rachis of the leaves is not jointed as in Berberidoideae. Although the venation sometimes is obscure and may vary in a single species and among the leaflets on a single leaf, the tendency for palmate or ternate venation is more conspicuous in Podophylloideae than in Berberidoideae. Close morphological relationships among some taxa are clearly evident, but the overlapping of major characteristics seems to prevent the separation of the genera into tribes. For points of view and arrangements of the genera see Heintze, Janchen, Kumazawa, Miyaji, and Tischler.

About 40 named alkaloids have been identified in about eight genera of Berberidaceae (see Willaman & Schubert); of these, about half (20) are reported only for Berberidaceae. Others are reported also for Menispermaceae (9), Ranunculaceae (7), Rutaceae (4), Leguminosae (3); Annonaceae, Monimiaceae, and Papaveraceae (2 each); Aristolochiaceae, Compositae, Lauraceae, Magnoliaceae, and Solanaceae (1 each). Phylogenetic interest naturally focuses on the examples where chemical as well as morphological similarities are noted. *Hydrastis* and *Glaucidium* are vegetatively similar to some Berberidaceae, but on the basis of floral structure are better referred to Ranunculaceae. Other superficial similarities recall some Papaveraceae and Fumariaceae. The insertion of perianth parts and stamens in Berberidaceae suggests alliance with Menispermaceae and with Lardizabalaceae where the stamens also tend to be opposite the petals. Although phylogenetic relationships among these families are implied, the degree of the relationships is difficult to estimate. In the above instances, it is the solitary, monomeric nature of the gynoecium that clearly distinguishes Berberidaceae. The fruits are neither follicles (in the sense that they do not open longitudinally through the placenta), achenes, nor drupes.

The range of chromosome numbers in the family seems fairly well explored at the generic level, with reports of $2n = 10, 12, 14, 16, 28$, and 56.

The useful properties of some taxa are discussed by Baillon and by Gray; see also genera in *The Merck Index*, ed. 7., 1960, for medicinal and poisonous properties. In some species, the roots or rhizomes and foliage are believed poisonous but the ripe fruits are considered edible (Fernald & Kinsey). No part of the plants should be considered entirely safe for eating, since the family is rich in alkaloids and contains some potentially poisonous compounds. Many taxa are desirable garden plants (cf. *Berberis*).

Some of the exceptional characteristics of taxa not covered in the family description are as follows: in *Achlys* DC., inflorescence spicate, flowers in tight clusters of two or three, perianth absent, stamens several, fruits one-seeded; in *Epimedium* L., petals long-saccate; in *Leontice* L., stipules leafy; in *Leontice* and *Bongardia* C. A. Mey., fruits ± inflated, scarious, and gaping; in *Ranzania* T. Ito, pollen 6–12-rugate; in *Vancouveria* C. Morr. & Decne., filaments ± connivent.

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KEY TO THE GENERA OF BERBERIDACEAE

General characters: *plants woody or herbaceous perennials; leaves exstipulate, mostly alternate; flowers often calyculate, bisexual, hypogynous, regular; perianth usually of more than 2 series, ± cyclic, mostly 3-merous, fugacious; petals mostly as many (or twice as many) as sepals and opposite the stamens (or stamens twice as many as petals); anthers longitudinally dehiscent, often forming 2 apically hinged valves; gynoecium of a solitary 1-locular carpel; placenta parietal or subbasal; fruit mostly fleshy (rarely loculicidal or ruptured by the young seeds), usually with more than 1 seed.*

A. Plants woody; leaves variously articulated above the base.

- B. Leaves pinnately decompound; inflorescences paniculiform; petals whitish, without distinct glands; anthers longitudinally dehiscent. .... 1. *Nandina.*
- B. Leaves simple, usually fascicled in the axil of a simple or branched cauline spine; petals yellowish, usually with a pair of adaxial glands; anthers opening by 2 apically hinged valves. .... 2. *Berberis.*

A. Plants herbaceous, rhizomatous; leaves not articulated.

- C. Flowers solitary on scapes; leaves all radical, 2-foliolate; petals white, usually twice as many as sepals; fruit transversely loculicidal; seeds with a laciniate aril. .... 5. *Jeffersonia.*
- C. Flowers 1 or more, borne on leaf-bearing stems; petals usually as many as sepals.
  - D. Leaves ternately (or apparently pinnately) compound, the leaflets variously veined and lobed; inflorescences racemose; flowers ± greenish to purplish, the petals ± truncate and glandular; seeds globular, mostly paired, on stout funiculi, soon bursting the ovary wall. .... 6. *Caulophyllum.*

D. Leaves simple, palmately veined and lobed; petals white (or pinkish), rounded and without glands; seeds several in a fleshy fruit.
 E. Flowers solitary, usually subtended by 2 ± opposite (rarely alternate), several-lobed leaves; stamens usually twice as many as petals; anthers longitudinally dehiscent. . . 3. *Podophyllum*.
 E. Flowers in umbelliform cymes, usually subtended by 2 distinctly 2-cleft, alternate leaves; stamens as many as petals; anthers with 2 apically hinged valves. . . . . 4. *Diphylleia*.

Subfam. BERBERIDOIDEAE

1. **Nandina** Thunberg, Nov. Gen. Pl. 1: 14. 1781.

Evergreen, glabrous shrubs with upright branches, to 2 m. tall. Leaves odd-pinnately decompound, the rachises swollen and articulated both at the insertion of the secondary branches and of the numerous pinnately veined, often reddish, ± sessile, ovate or lanceolate leaflets; petioles persistent, enlarged basally, substipulate and ± clasping. Inflorescences terminal (and axillary), many flowered, paniculiform, determinate, bracteate, the rachises ± scabrous. Perianth multiseriate, mostly 3-merous, the segments coriaceous to scarious and smaller below, ± petaloid and larger above; the lowest 3 segments usually most durable and regularly or irregularly inserted; receptacle elongated. Sepals in about 4 series. Petals in 2 or 3 series, whitish and without distinct glands, ± merging with the sepals. Stamens ± in 1 series; anthers elongate, subsessile, slightly exceeded by the broad connective, longitudinally dehiscent; pollen 3-colpate. Stigma ± 3-lobed; style persistent; placenta parietal; ovules 2 (3 or 4). Fruit globular, coriaceous, usually red and 2-seeded, indehiscent. Seeds ± horizontally oriented, ± disciform, concave-convex with hollow faces adjacent. TYPE SPECIES: *N. domestica* Thunb. (Name derived from a portion of the Chinese for "plant from the south.")

A single species, *Nandina domestica*, heavenly bamboo, $2n = 20$, with many horticultural forms, native to China and perhaps Japan, occurring to an altitude of about 1200 m. An attractive shrub, it is commonly cultivated in the Southeast, where it freely reproduces by seeds in some gardens. It has been found growing without cultivation in Durham County, North Carolina, and should be looked for in other areas as a garden escape.

Although usually classified with Podophylloideae, *Nandina* seems to have no immediate relationship to those herbaceous genera and is here placed with the Berberidoideae because of its woody habit and articulated leaves. The decompound leaves, the graduated multiseriate calyx that more or less merges with the corolla, the anthers without apically hinged valves, the lower chromosome number, and the peculiar seeds distinguish *Nandina* from the *Berberis-Mahonia* complex. The genus sometimes has been considered a separate family, Nandinaceae, but this seems unnecessary. Furthermore, a legitimate family name is not available, since Nandinaceae Horaninow (1834) included the type of Berberidaceae, and Nandinaceae Nakai is a later homonym.

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2. **Berberis** Linnaeus, Sp. Pl. 1: 330. 1753; Gen. Pl. ed. 5. 153. 1754.

Evergreen or deciduous, usually spiny shrubs to 2.5 [6] m. tall, with arching branches and yellow inner bark and wood. Leaves simple, ± spatulate, articulated usually near the base, usually ± fasciculate on 1 or more short shoots in the axil of a stout, simple or branched spine [or spine rarely foliaceous or absent]; venation ± pinnately [or palmately] reticulate. Inflorescences axillary, few (1) to many flowered, racemose to subumbellate, terminating short, bracteate shoots. Flowers calyculate; perianth ± yellowish [to reddish orange]. Sepals usually 6, 2[1–4]-seriate, ± petaloid. Petals mostly 6, 2-seriate, usually each with a pair of adaxial glandular regions. Stamens 6; filaments tactile [sometimes ± toothed]; anthers with 2 valves hinged at the apex; pollen 3-colpate. Stigma orbiculate, ± umbilicate; style ± absent [or present]; placenta subbasal; ovules 2–9, erect. Fruit ± oblong, indehiscent, fleshy. Seeds 1–9[–15], without arils; embryo long. (Excluding *Mahonia* Nutt., nom. cons.) LECTOTYPE SPECIES: *B. vulgaris* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 127. 1913. (Name Medieval Latin, apparently from *berbêrys*, presumably the Arabic name of the fruit.) — BARBERRY, BERBERRY.

Perhaps 175 to nearly 500 species, mostly in Asia and South America, poorly represented in North Africa, Europe, and North America. Infrageneric relationships are poorly understood and seem complicated by numerous, presumably interspecific, hybrids. Twenty-one sections were recognized by Schneider, 32 sections by Ahrendt, and 15 series by Rehder. In our area, one species is indigenous, one is naturalized, and one or two others may have escaped from cultivation.

In *Berberis canadensis* Mill. (§ *Sinenses* Schneid.; ser. *Sinenses* Rehd.; § *Canadenses* Ahrendt), American or Allegheny barberry, $2n = 28$, occurring in the mountains of West Virginia and Virginia, southward to

Georgia, and sporadic westward to Missouri (absent from Canada), the leaves tend to be remotely dentate, the petals are apically notched, and the few-flowered racemes often are subumbelliform. In the southwestern United States *B. Fendleri* Gray is somewhat similar. *Berberis* × *Rehderiana* Schneid., of horticulture, is said to be a hybrid between the two. *Berberis Thunbergii* DC. (§ *Sinenses* Schneid.; ser. *Sinenses* Rehd.; § *Tschonoskyanae* Schneid. [cf. Ahrendt]), Japanese barberry, $2n = 28$, naturalized in our area and in much of the eastern United States, is distinguished by its more or less entire leaves, its solitary flowers (or few-flowered umbels), and its immunity to wheat rust. The European *B. vulgaris* L. (§ *Berberis*; § *Vulgares* Schneid.; ser. *Vulgares* Rehd.), $2n = 28$, common barberry, resembling *B. canadensis* but tending to have denticulate leaves, entire petals, and many-flowered racemes, should be looked for in our area, since it is widely naturalized in the Northeastern and the Midwestern States. *Berberis ottawaensis* Schneid. is said to be a hybrid between *B. Thunbergii* and *B. vulgaris*, and *Berberis declinata* Schrad. one between *B. canadensis* and *B. vulgaris*.

The cauline spines of *Berberis*, no doubt the equivalent of leaves, are nearly ubiquitous (sometimes absent), usually obvious, stout, nonarticulated, and variable within the species and also on some plants. In some instances, a fully expanded but nonarticulated leaf is formed, rather than a spine, and in others the spines are soft and soon deteriorate. In any event, the spines, which subtend lateral branches, are distinct in appearance from the scales usually associated with vegetative buds and from the comparable scales also found in some species of *Mahonia*. The simple leaf of *Berberis* seems like a reduction of the more complicated leaves of *Mahonia*, yet the seedling leaves of *Mahonia* probably also are simple. In some taxa of *Berberis* the articulation of the leaves is either subbasal, or midway on the narrowed, petiole-like base of the blade, or distal on a distinct petiole at the base of the expanded blade; and in one (or more) South American species the apparently simple leaves have double articulations, one subbasal and one distal on the petiole.

The separate generic status of *Mahonia* (*Berberis* subg. *Mahonia* Gray and subg. *Trilicina* Gray), which seems to differ consistently from *Berberis* only in its compound leaves (see Ahrendt), is likely to remain debatable. *Mahonia*, however, does not have cauline spines, and the distributional pattern is somewhat more restricted than in *Berberis*. There can be no doubt that *Berberis* and *Mahonia* have much in common, including similar and somewhat unusual pollen, chromosome number, tactile stamens, and susceptibility to wheat rust. The question is whether it is better to treat these two groups of species as separate genera or as an inclusive genus, *Berberis*, with two subgenera. Close affinities between particular species of *Mahonia* and of *Berberis*, which might suggest normal recent pathways of genetic exchange, have not been pointed out, unless this is implied by the several taxa described under × *Mahoberberis* Schneid. (see Ahrendt, Jensen, Levan, Melander & Eade, Vaarama, Wyman). These presumed intergeneric hybrids, with dimorphic leaves, would seem to bridge the gap between *Mahonia* and *Berberis*, but thus far, only hybrids involving *M. aquifolium* (Pursh) Nutt. are available. The leaves of the elongated shoots of the hybrids tend to be simple and more or less sessile with coarsely spiny margins and are weakly articulated above the insertion on the stem; these leaves seem to be homologous with the prevalent spines of *Berberis*. The leaves of the shorter shoots tend to be trifoliolate, with the rachis articulated at the insertion of the leaflets, the margins of which are less coarsely dentate. The hybrid plants seem to bloom reluctantly and the flowers appear to be sterile. Information regarding the synthesis of hybrids under controlled conditions does not seem to be available.

Chromosome numbers of $2n = 28$ and 56 are reported for *Berberis* and $2n = 28$ for both *Mahonia* and × *Mahoberberis*. Most species are ornamental, but their cultivation is prohibited unless they are known to be either immune or highly resistant to black stem-rust of wheat (see Fulling). The fruits often are considered edible (Fernald & Kinsey) but should be sampled with caution, since potentially toxic substances occur in the family. In the Southeast, *B. Thunbergii*, *B. Julianae* Schneid., and *Mahonia Bealei* (Fort.) Carr. are commonly cultivated.

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Subfam. PODOPHYLLOIDEAE Lindl.

3. **Podophyllum** Linnaeus, Sp. Pl. **1**: 505. 1753; Gen. Pl. ed. 5. 223. 1754.

Herbaceous, rhizomatous perennials to about 50 cm. tall. Solitary leaves ± orbicular, palmately veined, 5–9-lobed, ± centrally peltate, long-petiolate; cauline leaves usually 2 (1–3), ± marginally peltate, 3–7-lobed, short-petiolate, usually subopposite (or alternate), subtending a single flower (rarely 2); juvenile leaves ± quadrate. Hairs unicellular. Inflorescence terminal, of a single, pedunculate, calyculate, ± 3-merous flower. Sepals 6, 2-seriate. Petals 6 or 9, in 2 or 3 series, white (pink). Stamens 12–18 (or more), usually twice as many as petals [or 6 and opposite the petals]; anthers longitudinally dehiscent. Gynoecium normally unicarpellate and solitary (or sometimes of 2–8 free ovaries); stigma convoluted; style indefinite or absent; placenta parietal; ovules numerous. Fruit ± ovate, to 5 cm. long, yellow to reddish orange or purplish, indehiscent, filled with the many seeds and the pulpy placenta, the latter forming ± discreet arils, each inclosing a seed. Seedling cotyledons connate at the base. (Excluding *Dysosma* Woodson.) LECTOTYPE SPECIES: *P. peltatum* L.; typified by the removal of *P. diphyllum* L. to *Jeffersonia* Bart.; see Persoon, Syn. Pl. **1**: 418. 1805. (Name from Greek, *podos*, foot, and *phyllon*, leaf; contraction of *Anapodophyllum* Tourn.) — MAY-APPLE, MANDRAKE.

One species in the woodlands and meadows of eastern North America and one (or more) species in Asia. *Podophyllum peltatum*, $2n = 12$, occurs from Florida to Texas, northward to Minnesota, Ontario, and Quebec. The early spring plants are conspicuous, with the terminal solitary flower bud characteristically placed between more or less paired, reflexed, furled leaves. The arrangement of the leaves and the position of the flower are variable (Foerste, Halsted, Harris, Holm, Wadmond); in exceptional instances the flowering stems lack leaves. The flowers are unusual in having twice as many stamens as petals; occasionally, the flowers have extra or irregularly inserted petals or two or more separate gynoecia (Clute). Eames insists that the normal fruits are the equivalent of three carpels and are only falsely monomeric (see also Chapman). The fruits usually are yellow but sometimes also orange-tinged or reddish; plants with reddish fruits seem to have pinkish petals (Raymond, Steyermark). The rhizomes, which sometimes cause dermatitis when handled, and other parts of the plants, including the green fruits, are bitter and may contain dangerous amounts of "podophyllin," a mixture of potentially poisonous compounds. The ripe fruits, however, are considered edible and sometimes are preserved (Fernald & Kinsey, Muenscher, and Pammel).

In Asia, *Podophyllum emodi* Wall. ex Hook. & Thoms., $2n = 12$, with pink (or white) petals, as many stamens as petals, and reddish fruits, and occurring to an altitude of 4500 m., has the characteristic vernal appearance of the American species, but the cauline leaves (occasionally there are three) are more often alternate and usually are distinctly ternately parted.

The cotyledons of *Podophyllum* are broadly oval or ovate and fused into an elongate, tubular, petiole-like base. During the first growing-season the epicotyl is undeveloped or retarded so that the cotyledons are the only photosynthetic organs. Later, the plumule bursts through the base of the cotyledonary tube, producing first a few bracts and then a peltate leaf with a long petiole (Holm, Dickson, Lubbock). The conformation of the flowering stems in some respects recalls superficially some Ranunculaceae (*Glaucidium, Hydrastis*), some Papaveraceae (*Hylomecon, Stylophorum*); in our flora, *Podophyllum* vegetatively resembles *Diphylleia.* The relationship of *Podophyllum* to the one or two species of *Dysosma* Woodson, of Asia, is uncertain (see Kumazawa). In *D. pleiantha* (Hance) Woodson (*Podophyllum pleianthum* Hance), the leaves are of a distinctive texture and usually with distinctively toothed margin; the several pendent, usually dark flowers are arranged in an extra-axillary umbel; and the rhizome seems to resemble that of *Diphylleia.* In another taxon of *Dysosma*, the leaves appear to be more or less square and centrally peltate.

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4. **Diphylleia** Michaux, Fl. Bor.-Am. 1: 203. *pls. 19, 20*. 1803.

Perennial herbs, to 1 m. tall, from a characteristically jointed rhizome. Solitary leaves reticulately palmately veined, reniform-orbiculate, 2-cleft, to 70 cm. broad, ± centrally peltate, long-petiolate; cauline leaves similar, usually 2, marginally peltate, distinctly alternate. Hairs unicellular. Inflorescence long-peduncled, many flowered, cymose, umbelliform. Flowers 3-merous, noncalyculate. Sepals 6, 2-seriate. Petals 6, 2-seriate, white. Stamens 6; anthers dehiscent by 2 apically hinged valves; pollen conspicuously spiny, ? irregularly aperturate. Style indistinct; placenta parietal; ovules 5 or 6, inserted near the base of the placenta. Fruit ± gibbous, indehiscent, to 1 cm. broad, blue and glaucous. Seeds 2–4, oblong, slightly curved. TYPE SPECIES: *D. cymosa* Michx. (Name from Greek, *dis*, double or twice, and *phyllon*, leaf.) — UMBRELLA-LEAF.

One species along mountain streams in our area from about 1000 to 1700 m. altitude and one or two species in Asia. *Diphylleia cymosa*, $2n = 12$, is distributed in the higher altitudes of northern Georgia, eastern Tennessee, western North Carolina, and adjacent Virginia. The leaves and the inflorescences are sparsely pubescent. In the Asiatic *D. Grayi* F. S. Schmidt, $2n = 12$, the margins of the leaves usually are somewhat less incised, and the pedicels are especially pubescent. The latter taxon, sometimes given varietal status under *D. cymosa*, although that combination seems not to have been formalized, is considered by Li to be a separate species distributed in Japan and Sakhalin, while the Chinese plants, occurring to about 3700 m. altitude in Hupeh, Szechuan, and Yunnan, are referred to *D. sinensis* Li. In the Japanese material, the uppermost leaf tends to be more or less sessile. *Diphylleia* has been attributed, without the citation of specimens, to the Amur region of Manchuria-Siberia (see Kumazawa, Li). The distribution is given in the *Flora of the USSR*, however, as Japan and Sakhalin only.

Diphylleia resembles *Podophyllum* and *Dysosma* but is distinguished by the two cleft leaves; the long-peduncled, umbelliform inflorescence; the white petals; the anthers with two uplifting valves; and the spiny pollen.

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5. **Jeffersonia** Barton, Trans. Am. Philos. Soc. **3**: 342. *1 pl.* 1793.

Low, acaulescent, glabrous herbs to about 50 cm. tall, from short rhizomes with fibrous, matted roots. Leaves few, radical, subtended by bracts, long-petiolate, the blade deeply 2-parted or 2-foliolate, the parts ± palmately veined [or leaves undivided and ± reniform]. Inflorescence scapiform with a solitary flower (rarely subtended by a linear bract). Perianth 4(3–5)-merous, 3-seriate, often ± acyclic. Sepals 4 (3–5), petaloid, 1-seriate. Petals 8 (9), ± 2-seriate, white [or lavender]. Stamens 8; anthers dehiscent by 2 narrow valves hinged at the apex. Stigma ± 2-lobed; style ± distinct; placenta parietal, the ovules many, indefinite. Fruit ± clavate, ± tuberculate, incompletely transversely [or obliquely] loculicidally dehiscent near the summit, the margins of the stoma becoming extended and ± revolute. Seeds many, oblong; aril laciniate, attached at the upper side of the hilum. TYPE SPECIES: *J. binata* Barton = *J. diphylla* (L.) Pers. (Named in honor of Thomas Jefferson, 1743–1826, Secretary of State under George Washington and third President of the United States, without "reference to his political character or to his reputation for general science, and for literature," but for his knowledge of natural history, especially botany and zoology.) — TWINLEAF, RHEUMATISM ROOT.

One species in eastern Asia and one in eastern North America, usually in rich deciduous woods. *Jeffersonia diphylla*, $2n = 12$, occurs from Alabama and Tennessee northward to Iowa, Ontario, New York, and Virginia, often in calcareous soil. Frequently there is a minute apiculation at the terminus of the petiole between the two leaflets. The dehiscence of the odd fruits is more or less horizontal. The Asiatic *J. dubia* (Maxim.) Benth. & Hook. ex Baker & Moore (*Plagiorhegma dubium* Maxim.), $2n = 12$, has undivided, slightly apiculate, cordate-reniform leaves, lavender petals, and somewhat obliquely dehiscent fruits.

The unusual features of *Jeffersonia* are the acaulescent habit, flowers with half as many sepals as either petals or stamens, and the definite loculicidal dehiscence of the fruits. Sometimes the insertion of the perianth segments is not quite regular. Both species superficially resemble *Sanguinaria canadensis* L., of the Papaveraceae. The asymmetrical leaflets of *J. diphylla* recall the lateral leaflets of *Achlys*.

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6. **Caulophyllum** Michaux, Fl. Bor.-Am. **1**: 204. *pl. 21*. 1803.

Herbaceous, glabrous, rhizomatous perennials. Leaves usually 2 (3), cauline, alternate, the lower 1 (2) ternately (to biternately) or apparently pinnately compound but ± sessile and easily mistaken for 3 leaves (i.e., the common petiole mostly obscure or absent); leaflets 9 or more, variable in shape, the terminal ones ± obovate, ternately lobed or divided, and ± palmately veined; the lateral leaflets sometimes lanceolate and pinnately veined; the uppermost leaf ± similar but smaller. Inflorescence terminal (often with a smaller one axillary), bracteate, several flowered, ± racemose or paniculiform. Flowers yellowish green to purplish, calyculate, 3-merous. Sepals 6, 2-seriate, petaloid. Petals 6, ± uniseriate, small, ±

truncated, glandular. Stamens 6; anthers dehiscent by 2 uplifting valves. Stigma minute, ± introrsely decurrent; style subulate; placenta subbasal; ovules usually 2, on stout funiculi. Fruit soon ruptured by the enlarging seeds, small, thin walled, evanescent. Seeds usually paired, about 1 cm. broad, ± spherical, fleshy, glaucous and blue (easily mistaken for fruits), elevated on conspicuous stout funiculi, and somewhat persistent; endosperm ± spherical, hard, inconspicuously umbilicate ventrally; embryo vertical, central, cylindrical, with radical below. Seedling cotyledons hypogeal. TYPE SPECIES: *C. thalictroides* (L.) Michx. (*Leontice thalictroides* L.). (Name from Greek, *caulos*, stem, and *phyllon*, leaf, in recognition of the peculiar continuity of the stem and leaf.) — BLUE COHOSH, PAPOOSE-ROOT.

One species distributed in eastern North America and another in eastern Asia. *Caulophyllum thalictroides* (*Leontice* subg. *Caulophyllum* Gray; § *Caulophyllum* Prantl), $2n = 16$, occurs in moist deciduous woodlands from New Brunswick and Nova Scotia to Manitoba, and southward, to an altitude of over 1000 m., in the mountains of North and South Carolina, Tennessee, Alabama, and Georgia. The rhizomes contain the alkaloid methylcytisine and perhaps glucosides. The herbage also is bitter, and children should be warned against eating the prominent berry-like seeds. Handling of the plants may cause dermatitis or irritation of mucous surfaces (Muenscher). The roasted endosperm has been suggested as a possible coffee substitute (Gray).

The Asiatic *Caulophyllum robustum* Maxim., $2n = 16$, usually seeming to be more vigorous or larger than our species, occurs to an altitude of about 3500 m. The mostly narrower leaflets more often are pinnately veined.

The unusual leaves, the peculiarly colored flowers, the truncated and glandular petals, and the unique maturation of the seeds are the salient characteristics of *Caulophyllum*. The leaflets and flowers somewhat recall those of *Ranzania japonica* (T. Ito) T. Ito, $2n = 14$, of eastern Asia. Some floral similarities have been noted between *Caulophyllum* and the Eurasian *Leontice* L., having ternately decompound leaves, and *Bongardia* (*Leontice* § *Bongardia* Prantl), having imparipinnate leaves. The seeds in these two, however, do not exceed the finally gaping and scarious ovaries.

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LARDIZABALACEAE Decaisne, Arch. Mus. Hist. Nat. Paris 1: 185. 1839, "Lardizabaleae," nom. cons.

(LARDIZABALA FAMILY)

About five genera in Asia and two in western South America, probably totaling less than 50 species. One species of *Akebia*, a garden escape, is established in several of the eastern United States.

Among the more common characteristics of the family are the scandent [rarely arborescent], woody habit and perulate buds; the multiple articulation of the alternate, usually palmately [rarely pinnately] compound leaves; the regular, cyclic, trimerous structure of the functionally unisexual [rarely bisexual], hypogynous flowers; and aposepaly, apetaly [or petals reduced], and apocarpy. All or half of the [sometimes monadelphous] stamens are opposite the perianth segments. Although not well exemplified by *Akebia*, the flowers of Lardizabalaceae tend to have two series of sepals and two of petals, so that a sepal subtends a petal, which, in turn, subtends a stamen or staminodium. This pattern also is characteristic of Menispermaceae and Berberidaceae, but contrasts with, for example, Papaveraceae and Fumariaceae, which have only a single series of sepals and conspicuous petals that are not so regularly opposed to as many stamens. Lardizabalaceae are distinguished from Berberidaceae in having unisexual flowers, extrorse anthers, and gynoecia of three or more free carpels. From Menispermaceae they are distinguished in being primarily monoecious [rarely dioecious or bisexual], in having more than a single seed per carpel, and in lacking a bony endocarp. Especially significant in Lardizabalaceae is the submarginal or laminal distribution of the ovules along the ovary wall rather than the restriction of the ovules to a single parietal or subbasal placenta. The fruits of Lardizabalaceae usually are fleshy and more or less follicular [or sometimes baccate] and are considered edible (see Fernald & Kinsey). The plants usually are glabrous [rarely with simple hairs]. Exceptional taxa are *Decaisnea* Hook. f. & Thoms., a hardy, upright shrub or small tree with pinnately compound leaves and bisexual flowers; and *Lardizabala* Ruiz & Pavon, nomenclatural type of the family, which is dioecious. The reported chromosome numbers are $2n = 28$, 30, and 32. Only a few species are cultivated for ornament. In general, the family seems allied with Berberidaceae, Menispermaceae, and Sargentodoxaceae Stapf ex Hutchinson.

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1. **Akebia** Decaisne, Arch. Mus. Hist. Nat. Paris **1**: 195. 1839.

Twining, glabrous, deciduous or evergreen, woody vines. Leaves alternate or ± fascicled on short shoots, exstipulate, palmately compound, about 5[3]-foliolate; petioles long, articulated near the base and at the insertion of the petiolules, the latter articulated at the base of the ± elliptical or obovate, ± emarginate, usually minutely apiculate leaflets; blades ± pinnately veined but often with 3 prominent veins from below. Plants monoecious; inflorescences axillary, unisexual or bisexual, bracteate, pedunculate, racemose, or ± subumbelliform. Flowers pedicellate, regular, aposepalous, 3-merous, the sepals usually 3 (6), ± petaloid, brownish or purplish, apetalous, functionally unisexual, hypogynous, apocarpous. ♂ flowers several to many, distal on the raceme (sometimes a few also below); stamens usually 6, free, equal; filaments short; anthers elongate, extrorse, longitudinally dehiscent; pollen mostly 3-colpate; gynoecium rudimentary. ♀ flowers larger, solitary or few; stamens rudimentary; gynoecium of 3–12 free carpels; stigmas ± broad, truncated; style obscure; ovary unilocular; placentae 2, laminal; ovules many, ± orthotropous. Fruits follicular, many seeded, dehiscent along the suture, placenta ± pulpy. Seeds ± arillate?, endosperm present; embryo small. (*Rajania* Houtt. non L.) LECTOTYPE SPECIES: *A. quinata* (Houtt.) Decne.; see A. Rehder, Bibl. Cult. Trees Shrubs 166. 1949. (Name derived from the Japanese word for the plant.)

About four species native to eastern Asia. In our area *Akebia quinata*, $2n = 32$, occasionally grown for ornament, apparently is established and growing without cultivation in Madison County, North Carolina. Several authors warn that, if extensively naturalized, this species could become a nuisance by forming dense mats over other vegetation. The number of leaflets sometimes is variable, the terminal one, with slightly longer petiolule, usually somewhat larger. The clusters of slightly fragrant flowers are striking in appearance with their unusual color and velvety texture. The color has been likened to that of raw liver, sometimes appearing maroon; or the sepals of the staminate flowers appear rosy purple and those of the carpellate flowers purplish brown (Anderson). The unusual oblong fruits, to 8 cm. long, seldom seen in cultivation unless the plants are cross-pollinated, are glaucous, purple-violet. When the fruits ripen and open, the seeds are displayed in an elongated, gelatinous pulp derived from the inner portion of the ovary wall. The fruits and roots sometimes are used medicinally in China (Hu).

Another species, *A. trifoliata* (Thunb.) Koidz., $2n = 32$, usually with 3-foliolate leaves and paler sepals and fruits, sometimes also is cultivated. *Akebia* × *pentaphylla* (Mak.) Mak. is said to be a hybrid between this and *A. quinata*.

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MENISPERMACEAE A. L. de Jussieu, Gen. Pl. 284. 1789, "Menisperma," nom. cons.

(MOONSEED FAMILY)

Perennial herbaceous vines, woody at least at base [sometimes from tubers, rarely erect shrubs or small trees], sometimes with colorless, bitter juice. Leaves variable, alternate, simple [rarely 3-foliolate], usually exstipulate, the blades mostly palmately [to pinnately] veined, the margin entire to palmately lobed, sometimes peltate, deciduous or evergreen; the petiole sometimes swollen distally and/or basally. Hairs 1- or 2-celled (or multicellular-uniseriate) [sometimes glandular]. Plants mostly dioecious (? sometimes polygamous or flowers tending to be bisexual). Inflorescences variable, commonly supra-axillary, bracteate, usually of many [rarely solitary] flowers, racemose to paniculiform or umbelliform, ± determinate, sometimes concentrated at ends of branches. Flowers mostly small, usually unisexual, usually ± regular (irregular), hypogynous, usually 3(2 or 1)[4 or 6]-merous, greenish, yellowish to whitish, sometimes ± calyculate, the perianth cyclic (to ± acyclic), usually deciduous, aposepalous, apopetalous (sympetalous or apetalous). Sepals 4–9 (or 1) [to many], often in 3-merous cycles, ± 2(3)[or more]-seriate. Petals 6–8 (or 1 or absent), mostly ± 2-seriate. Stamens usually 6 (3, 4) to many [40] in ♂ flowers, often opposite and as many as the petals (or indefinite); filaments free [monadelphous], sometimes embraced by the petals, or anthers sessile on an androphore; anthers 4(? 2)-locular, becoming ± 1(2)-locular at anthesis; pollen mostly prolate (oblate) and 3-colpate (colporate); staminodia often opposite the petals in ♀ flowers. Gynoecium of 3–6 (or 1) [–32] free [to ?partially connivent] carpels, usually in 1 series, often on a gynophore; stigmas various, subulate to laciniate; styles usually short; ovary unilocular, ± gibbous; ovules 1 (or 2), usually inserted ± medially on the solitary parietal placenta, 2-integumented, ± anatropous, descending, the micropyle up (apotropous); gynoecium mostly absent (or rudimentary) in ♂ flowers. Fruits drupes, 1–5 per flower, ± fleshy and indehiscent; endocarp bony, characteristically curved and sculptured, usually laterally compressed; seeds solitary; endosperm present [sometimes ± ruminated or absent]; embryo ± curved, folded or ± cochleate [to straight], molded around a variously shaped ventral intrusion of the endocarp (condyle); cotyledons narrow, ± appressed and fleshy (or foliaceous and laterally displaced) [sometimes unequal]. TYPE GENUS: *Menispermum* L.

Perhaps 80 genera and 370 species of tropical and subtropical regions. Four genera and five species are indigenous to the continental United States; four species, representing two tribes, occur in our area.

Among the characteristics uniting most Menispermaceae are the perennial, mostly woody, dioecious, scandent habit; the simple leaves of variable conformation, the blade often with palmate venation and the petiole sometimes swollen distally and sometimes also basally; the perianth tending to have two series of sepals (sometimes also calyculate) and two series of petals (these often reduced or thickened, sometimes involute or absent) tending to be shorter than the sepals and with each opposite a stamen or staminodium; the apocarpous gynoecium, mostly of more than a solitary carpel, the ovules (usually solitary) medially attached with the micropyle up; and the fleshy, indehiscent fruits with bony endocarp and solitary, usually strongly curved, folded, or somewhat coiled seeds.

The vascular bundles of young stems are separated by broad medullary rays. The wood is distinctive, with secondary thickening from fascicular or extrafascicular cambia, sometimes forming concentric or eccentric rings of bundles, resulting in many cambia and alternating layers of xylem and phloem (see Metcalf & Chalk and Esau). Within a taxon, the leaves often vary from entire to lobed, nonpeltate to peltate. The matching of the dioecious materials and the determination of sterile specimens often is difficult. Correlations between taxa resembling one another in the anatomical structure of the swollen portion of the petiole (which differs from the remainder of the petiole) and taxa resembling one another in fruit and seed characters have not been found (Rudolph, fide Metcalf & Chalk). Most of the hairs that seem to be unicellular probably are bicellular, the basal cell inconspicuous. The lack of tubers in our species should be verified.

The (anatropous) ovules at first seem more or less straight and vertical, the micropyle up. During the maturation of the endocarp or stone, the placental region seems to buckle inward towards the seed, leaving a notch or hollow exteriorly and forming inwardly an intrusion, or condyle (Miers), of various proportions around which the seed and the embryo are curved. The condyle in tribe Menispermeae is seen superficially as a depression (nearly orbicular in *Menispermum*, excentric in *Cocculus*, or narrowly obovate in *Cissampelos*) on the broad faces of the laterally compressed endocarps bordered adaxially by a notch or indentation on the margin of the endocarp. Internally the condyle may be hollow, perforated, or reduced to a narrow, partial partition of the seed.

Although the shape of the fruits may be nearly spherical, abaxial deformation of the endocarp often is accompanied by extreme abaxial enlargement of the pericarp, so that the final position of the style (and the apex of the seed) is subbasal in tribe Menispermeae. Abaxially, a median-longitudinal line or crest is characteristic of many endocarps; adaxially the crest often is obscured by the condyle. Insight into the form of the closed condyles of tribe Menispermeae may be provided by the broad, open concavity of the endocarp of *Calycocarpum* (tribe Tinosporeae) with its conspicuous median adaxial crest.

Menispermaceae, distinguished by habit, dioecism, position of micropyle, drupaceous fruits, and curved seeds, resemble Berberidaceae and Lardizabalaceae in the insertion of perianth (petals often reduced) and androecium, and in the apocarpous gynoecia. Flowers of Berberidaceae, however, are bisexual, and the solitary carpels usually develop more than one seed, attached to a single parietal or subbasal placenta, apparently with the micropyles down. In Lardizabalaceae, the plants usually are monoecious (otherwise dioecious), the flowers unisexual, the ovules submarginal in more than one vertical row, and the leaflets of the compound leaves articulated with the rachis.

The family customarily has been divided largely on characteristics of the fruits (endocarp) and seeds (endosperm and embryo). Originally six (later seven) tribes were recognized by Miers, five tribes by Hooker & Thomson, four series by Baillon, four tribes by Prantl, and, most recently, eight tribes by Diels. In each case, the genera were rearranged to some extent. In Diels's treatment, the three largest tribes (comprising over 80% of the species and of the genera) are Triclisieae Diels (14 genera, 96 species), lacking endosperm; Tinosporeae Hook. & Thoms. (41 genera, 78 species), having endosperm and thin, laterally displaced foliaceous cotyledons; and Menispermeae (Cocculeae Hook. & Thoms.) (16 genera, 140 species), having endosperm and appressed, nonfoliaceous cotyledons.

Menispermaceae in our area are but the fringes of a large, complex family. When classified according to conformation of endocarps and embryos, *Cocculus* (*q.v.*), *Menispermum*, and *Cissampelos* (all of tribe Menispermeae), seem relatively similar, while *Calycocarpum* (tribe Tinosporeae), seems remote. A classification based upon floral morphology, however, would lessen the apparent isolation of *Calycocarpum* and emphasize the distinctness of *Cissampelos* (*q.v.*), with its strongly dimorphic flowers.

About 90 named alkaloids have been identified in about 29 genera of Menispermaceae (see Willaman & Schubert); of these, about three-fourths (ca. 68) are reported for Menispermaceae only. Others occur also in Berberidaceae (9), Fumariaceae (6), Rutaceae (6), Ranunculaceae (5), Lauraceae (5), Monimiaceae (3); Papaveraceae, Magnoliaceae, Annonaceae, and Buxaceae (2 each); and Aristolochiaceae and Hernandiaceae (1 each).

The poisonous and medicinal properties of Menispermaceae are discussed by Baillon. Commercial curare (Intocostrin), for medicinal use, is prepared from a species of *Chondodendron* (Merck Index, ed. 7. 1960). Portions of some taxa are used for aboriginal poisons and sometimes, with potentially dangerous consequences, for fish poisons, pesticides, or bitter flavorings. Only a few species of the family are cultivated for ornament.

Chromosome numbers of $2n = 18, 20, 24, 26, 38, 48, 50, 52, 54$, and 78 have been reported from among about ten genera.

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KEY TO THE GENERA OF MENISPERMACEAE

General characters (see *Cissampelos*): *dioecious vines, woody at base; leaves exstipulate, alternate, petiolate, palmately veined, entire to lobed; flowers unisexual, hypogynous, usually regular (irregular), often calyculate; sepals 2(or more)-seriate (or 1); petals reduced, ± 2-seriate (or 1, sympetalous, or absent); stamens free, often opposite and embraced by the petals (or anthers sessile on an androphore); anthers longitudinally (or horizontally) dehiscent; gynoecium apocarpous, of (1) 3–6 carpels; ovules usually solitary (or 2), the micropyle up; fruits drupaceous, the endocarp bony, characteristically shaped, often sculptured; 1-seeded; embryo usually curved or folded.*

A. Plant bearing only ♀ flowers.
  B. Perianth of 1 sepal opposite 1 petal; gynoecium of 1 pubescent carpel; peduncles unbranched, several in the axil of a broad bract; fruit red, pubescent, the style subbasal; stone orbicular, laterally compressed, sculptured (subtropical Florida). .... 4. *Cissampelos*.
  B. Perianth of 6 or more segments; gynoecium of 3 or 6 glabrous carpels; peduncles branched, minutely bracteate.
    C. Petals apparently absent; sepals glabrate, usually each subtending two short, unequal staminodia; carpels 3, stigmas irregularly laciniate, extrorsely radiate; gynophore inconspicuous; fruits black, the style apical; stone ± smooth, broadly cup shaped and adaxially toothed. .... 1. *Calycocarpum*.
    C. Petals present, shorter than the sepals; fruits with style subbasal; stone sculptured, laterally compressed.
      D. Carpels 3, stigmas extrorsely dilated and convolute; gynophore mostly longer than broad; sepals glabrate; fruits glaucous, blue-black, sessile on the 2–3 mm. long gynophore; stone crescent shaped. .... 3. *Menispermum*.
      D. Carpels 6, stigmas subulate; gynophore broader than long;

sepals coarsely pubescent; fruits red, short-stipitate on an inconspicuous gynophore; stone appearing coiled. . . 2. *Cocculus.*

A. Plant bearing only ♂ flowers.

E. Anthers 4, sessile on a short androphore, the dehiscence horizontal; sepals 4, coarsely pubescent; corolla sympetalous. . . . . 4. *Cissampelos.*

E. Anthers 6 to many, filaments free; sepals more than 4.

F. Stamens 12 or more; sepals glabrous or glabrate.

G. Anthers included, introrse, oblong, 2-locular at anthesis, the dehiscence vertical. . . . . 1. *Calycocarpum.*

G. Anthers exserted, ± apical, 4-lobed, erect, ± 1-locular at anthesis, the dehiscence ± confluent apically. 3. *Menispermum.*

F. Stamens 6, anthers included, ± apical, 4-lobed, nodding inward, ± 1-locular at anthesis, dehiscence ± confluent apically; each filament embraced by a petal; sepals coarsely pubescent. . . . . 2. *Cocculus.*

Tribe TINOSPOREAE Hook. f. & Thoms.

1. **Calycocarpum** Nuttall ex Gray, Gen. Pl. U. S. 1: 75. *pl. 30.* 1848.

Leaves thin, deciduous, not peltate, usually 5(7)-veined, 3–5–7-lobed; petiole often longer than blade. Hairs mostly multicellular-uniseriate. Flowers regular, ± calyculate with 1–3 small sepal-like bracts. Sepals 6, ± petaloid, 2-seriate, ± equal, glabrate. ♂ flowers: petals absent; stamens about 12, arrangement ± indefinite, not enfolded by perianth segments; filaments free; anthers included, ± introrse, attached subapically, 2-locular at anthesis, longitudinally dehiscent; pollen prolate, 3-colpate (colporate). ♀ flowers: petals apparently absent; staminodia 12, narrow, short, thick, unequal, 2 opposed above each sepal (the lower staminodia probably equivalent to petals); gynophore inconspicuous; carpels 3 (4); stigma extrorsely reflexed, irregularly laciniate, conspicuous; style short; ovules apparently solitary. Fruits 1–3 per flower, black, ± ovoid, ca. 25 mm. long, the style apical, the gynophore inconspicuous; endocarp large (to ca. 20 mm. long, 15 mm. wide), ovoid-cup-shaped, ± smooth abaxially, broadly concave adaxially and toothed, ± mucronate apically; embryo broadly curved, the cotyledons foliaceous, laterally displaced. TYPE SPECIES: *C. Lyonii* (Pursh) Gray. (Name from Greek, *calyx*, a cup, and *carpos*, fruit.) — CUPSEED, LYONIA-VINE.

Monotypic, distributed in rich or alluvial soils, in thickets, woods, or river banks, from northwestern Florida and western Georgia, northward to Tennessee, Kentucky, and southern Illinois, and westward to eastern Kansas (?), eastern Oklahoma, and Texas.

The thin, nonpeltate leaves with petioles at least as long as the blades are notable. The blades, to ca. 25 cm. long and wide and usually with five or more veins, are deeply three or more lobed to near the center of the blade with the lobes narrowed basally. The flowers of both sexes seem to be apetalous. In the staminate, the included, introrse, finally two-locular anthers are distinctive. In the carpellate, two reduced staminodia are opposed above each sepal; the lower series of staminodia, apparently

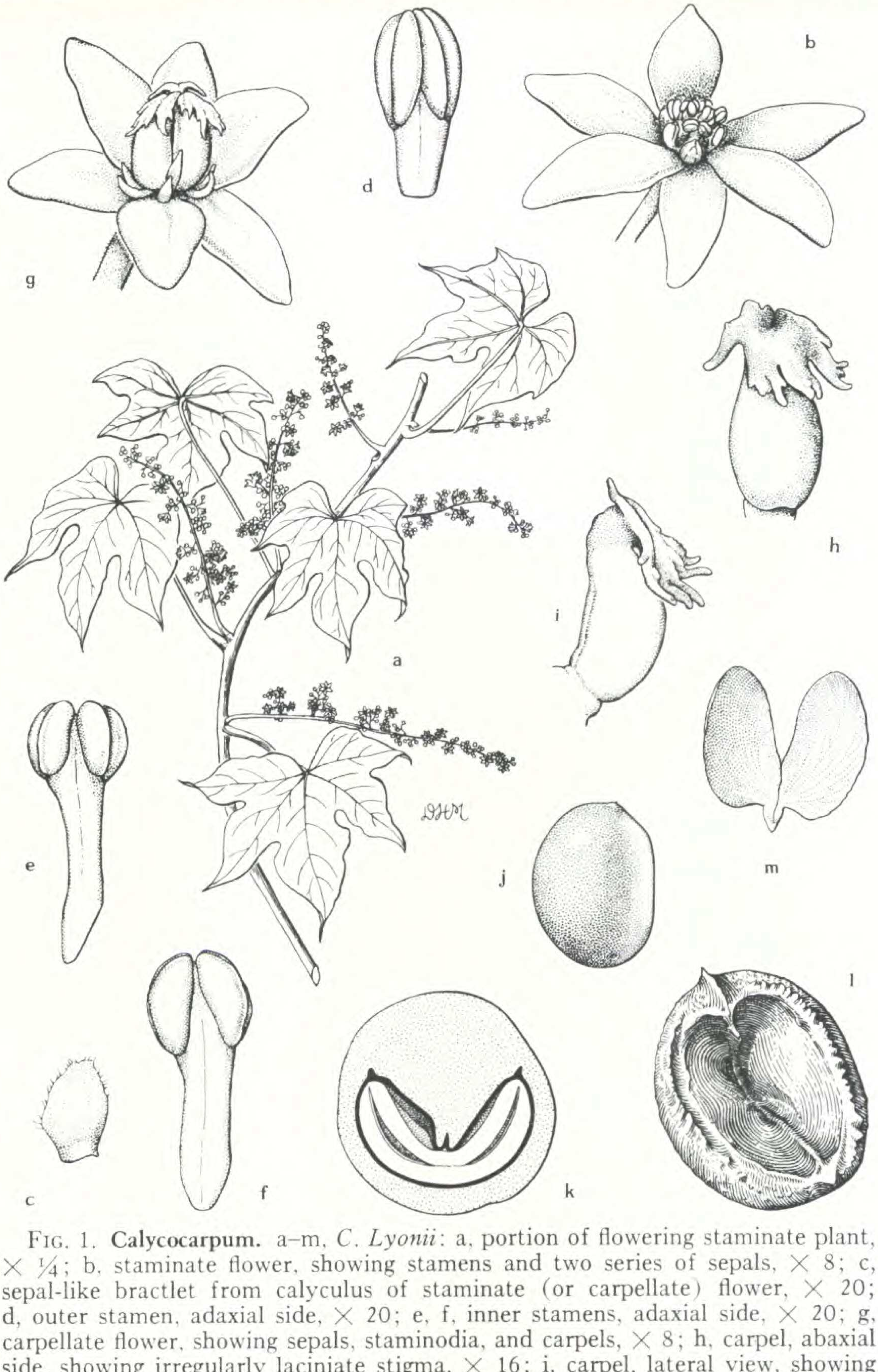

FIG. 1. **Calycocarpum.** a–m, *C. Lyonii*: a, portion of flowering staminate plant, × ¼; b, staminate flower, showing stamens and two series of sepals, × 8; c, sepal-like bractlet from calyculus of staminate (or carpellate) flower, × 20; d, outer stamen, adaxial side, × 20; e, f, inner stamens, adaxial side, × 20; g, carpellate flower, showing sepals, staminodia, and carpels, × 8; h, carpel, abaxial side, showing irregularly laciniate stigma, × 16; i, carpel, lateral view, showing stigma and short gynophore; j, mature drupe, showing terminal stigma-style, × 1; k, semidiagrammatic cross section of fruit, showing foliaceous cotyledons of embryo surrounded by endosperm (white), bony endocarp (black), and fleshy fruit wall, × 2; l, endocarp, adaxial side, × 2; m, embryo, × 2.

missed by Gray, were called petals by Miers and Diels. In texture and appearance, these organs resemble staminodia more than petals, but are in the appropriate position for petals. Unlike other Menispermaceae in our area, the style remains apical in the fruit, and the ovoid endocarps are smooth and not laterally compressed. While the embryo is not so tightly curved as in tribe Menispermeae, it is broadly so, conforming to the wide, open adaxial depression of the condyle.

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2. **Cocculus** A. P. de Candolle, Syst. Nat. **1**: 515. 1817 ("1818"), nom. cons.

Leaves ± coriaceous, the blades mostly longer than the petioles, non-peltate, prominently 3-veined (often with a finer submarginal vein at either side), deltoid to ovate, sometimes 3- or 5-lobed, often apically mucronulate, basally oblique to cordate. Hairs 1- or 2-celled. Flowers ± regular, calyculate with 1–3 small sepal-like bracts. Sepals 6, ± pubescent, 2-seriate, the inner 3 larger, the margins ± fimbriate to erose. Petals 6, ± 2-seriate, shorter than the inner sepals, ± fleshy [bifid], each embracing a stamen or staminodium. ♂ flowers: stamens 6, free, included, usually nodding inward; anthers 4-lobed, appearing terminal, ± 1-locular at anthesis, dehiscence ± apically confluent; pollen prolate, 3-colpate (?colporate). ♀ flowers: staminodia 6, ± linear; gynophore distinct, broader than long; carpels 6, in 1 series; stigma ± subulate, terete, turned outward, grooved along the upper surface; style short. Fruits 3–5 per flower, red [purple], glabrous, short-stipitate (–1 mm.), the style subbasal, the gynophore inconspicuous (less than 1 mm. long); endocarp sculptured, appearing coiled, laterally compressed, shallowly notched adaxially, the radicular end slightly projecting; embryo ± coiled, the cotyledons appressed, narrow (but wider than the radicle). LECTOTYPE SPECIES: *C. hirsutus* (L.) Diels (*Menispermum hirsutum* L.), typ. cons.; see Rickett & Stafleu, Taxon **8**: 271. 1959, and Int. Code Bot. Nomencl. 1961: 259. (Name from Greek, diminutive of *coccos*, berry; originally applied to "Cocculus indicus" [*Menispermum Cocculus* L. = *Anamirta Cocculus* (L.) Wight & Arn.]) — SNAILSEED, MOONSEED.

About 11 species, mostly of warmer regions, eight in the Old World, two in North America, and one in Hawaii; the conserved type species is native to Africa.

Cocculus carolinus (L.) DC. (*Menispermum carolinum* L., *Cebatha carolina* (L.) Britt., *Epibaterium carolinum* (L.) Britt.), coralbeads, Carolina moonseed, $2n = 78$, is distributed in woods, thickets, and fields from Florida to Texas northward to Kansas, Indiana, Virginia, and North Carolina, and in Mexico, from Coahuila to Tamaulipas. The nonpeltate leaves with three prominent veins, the blades to ca. 14 cm. long and wide; the pubescent sepals; the included stamens, each embraced by a petal;

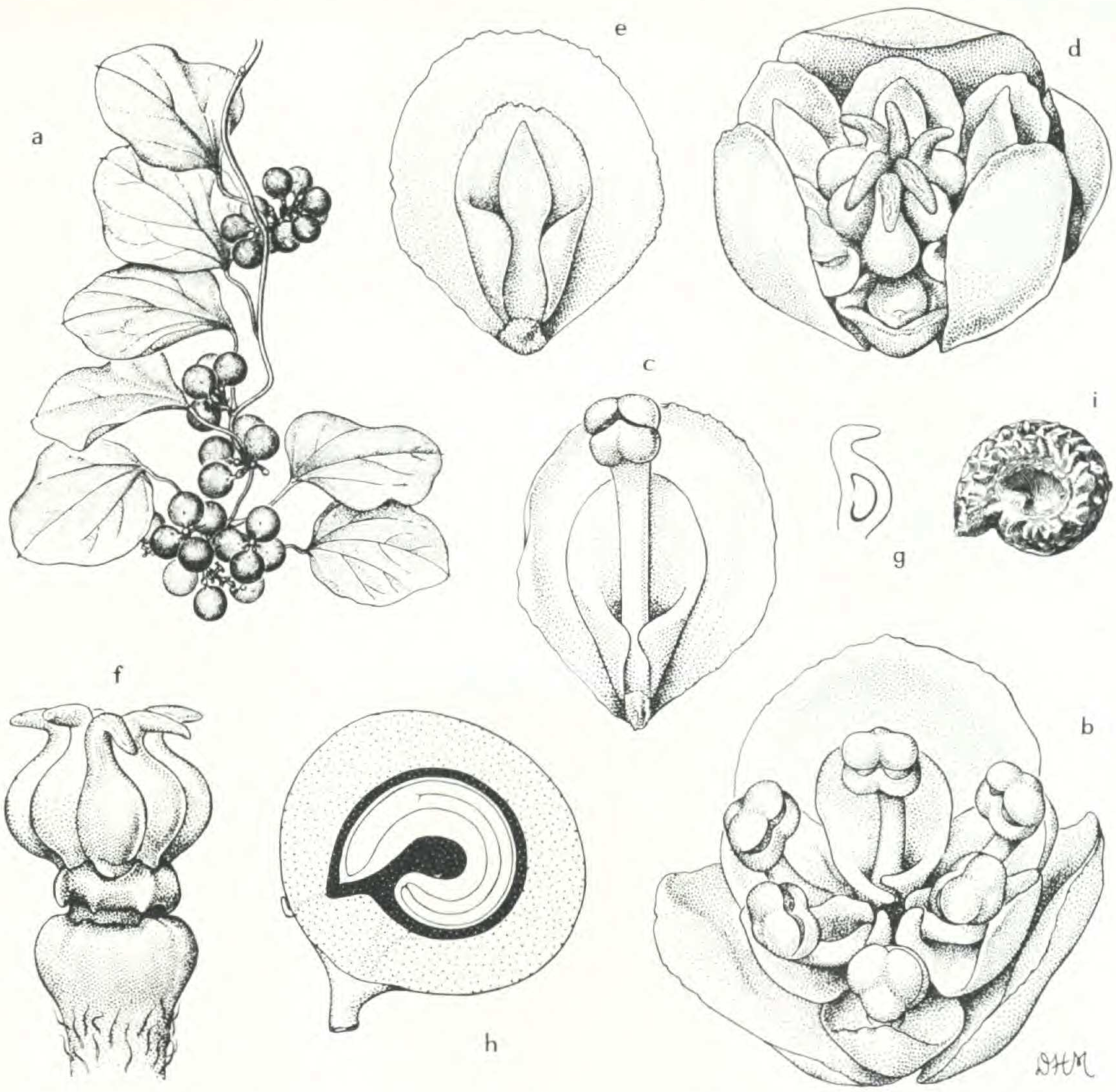

FIG. 2. **Cocculus.** a–i, *C. carolinus*: a, pendent branch with fruit, × ½; b, staminate flower, showing inner sepals, two series of petals and stamens, the short outer sepals not visible, × 15; c, inner sepal, clasping petal, and stamen, showing dehiscence of anther, × 15; d, carpellate flower, outer sepal in foreground removed to show inner sepals, two series of petals, staminodia, and carpels, × 15; e, inner sepal, clasping petal, and staminodium, × 15; f, carpellate flower, with perianth and staminodia removed to show receptacle, gynophore, and gynoecium of gibbous carpels with reflexed, subulate stigmas, × 15; g, diagrammatic vertical section of carpel, showing attachment of ovule, the micropyle up, × 10; h, diagrammatic vertical section of fruit, showing stipitate base, subbasal stigma-style, coiled embryo surrounded by endosperm (white), bony endocarp (dark), and fleshy fruit wall, × 4; i, subhelical sculptured endocarp, showing central depression of condyle, the micropyle to the lower left, × 3.

the short, broad gynophore; and the glabrous, short-stipitate, red fruits with somewhat coiled endocarp are distinctive. The closest affinities may lie with some portion of the complex involving *C. trilobus* (Thunb.) DC., of eastern Asia, although in the latter the petals are ligulate and bifurcate and the fruits dark purple.

West of our area, *Cocculus diversifolius* DC., having leaves with short petioles and often narrow, oblong blades with revolute margins, and dark purple fruits, occurs in Texas and Arizona, and southward, in Mexico, to Oaxaca.

While the taxa of *Cocculus* primarily are scandent (resembling *Menispermum*), *C. laurifolius* DC., $2n = 26$, of Southeast Asia, sometimes cultivated in the warmer parts of the United States, is an upright shrub or small tree with glossy leaves. In Socotra, *C. Balfourii* Schweinf., also shrubby, is conspicuous for its extra- or supra-axillary, flattened, sometimes branched cladodes on which are borne the flowers and fruits. *Cocculus* and *Menispermum* were placed in subtribe Menisperminae (Cocculinae Hook. & Thoms.) by Diels, but Miers(see p. 114. 1871) separated them, placing *Cocculus* in his tribe "Platygoneae."

Chromosome numbers of $2n = 18, 20, 22, 26, 38, 50, 52$, and 78 are reported.

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3. **Menispermum** Linnaeus, Sp. Pl. **1**: 340. 1753; Gen. Pl. ed. 5. 158. 1754.

Leaves ± coriaceous (or thin), usually ± peltate (nonpeltate); blade usually 5(or more)-veined, cordate, or deltoid to reniform in outline, shallowly to deeply ± 5–7(3–9)-lobed or pointed (or unlobed), often apically mucronulate, the petioles at least as long as the blades. Hairs 1- or 2-celled. Flowers ± regular and calyculate with 1 or 2 small sepal-like bracts; insertion of perianth and stamens or staminodia sometimes ± acyclic. Sepals 6 (4–10), entire to ± erose, ± 2-seriate. Petals 6–9, ± fleshy, the margins ± involute, often nearly equalling the sepals. ♂ flowers: stamens (9) 12–24, exserted, filaments erect, sometimes ± embraced by the petals; anthers 4-lobed, appearing terminal, ± 1-locular at anthesis, the dehiscence ± apically confluent; pollen prolate, 3-colpate. ♀ flowers: petals not embracing the staminodia, spatulate, somewhat larger than in ♂ flowers; staminodia (4) 6–12, ± filiform, variously inserted or 1-seriate and opposite the petals, the rudimentary anthers introrse; gynophore distinct, longer than broad; carpels 3; stigmas extrorsely dilated, ± convolute; style short, reflexed. Fruits 1 or 2 per flower, black, glaucous, nonstipitate, the style subbasal, the gynophore 2–3 mm. long; endocarp sculptured, broadly crescent shaped, laterally compressed, conspicuously notched adaxially; embryo broadly crescent shaped, the cotyledons appressed, narrow, no wider than the radicle. LECTOTYPE SPECIES: *M. canadense* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 131. 1913. (Name from Greek, *mene*, moon, and *sperma*, seed.) — MOONSEED.

One species of eastern Asia and one of thickets, woods, stream banks, and hedgerows in eastern North America. Many species originally described in *Menispermum* now are placed in other genera.

Menispermum canadense L., $2n = 52$, is distributed from southeastern Manitoba to Quebec, southward to western North Carolina, northern Georgia, northwestern Florida, ?Alabama, Tennessee, Arkansas, and Oklahoma. The leaf blades tend to be peltate, rather thin, mostly with five or more veins, and the petioles at least as long as the blades. Among other distinguishing characteristics are the glabrate sepals, the exserted stamens, the relatively long gynophore, and the nonstipitate, black fruits. Plants referred to *M. mexicana* Rose, occurring disjunctly in Nuevo León, Mexico, with leaves varying from peltate to nonpeltate, probably are conspecific with *M. canadense.* Our species somewhat resembles *Cocculus carolinus* vegetatively, but the leaves of the latter are nonpeltate and tend to have only three prominent veins. In eastern China and Japan, *M. dahuricum* DC., $2n = 52–54$, resembles our species, but the leaves seem more strongly peltate. The fruits, looking like grapes, are bitter and probably poisonous.

The taxonomy of *Menispermum* has been complicated by lack of agreement on the proximity of *Cocculus* and *Cissampelos*, but is simplified to the extent that the name of the tribe and subtribe must be formed on the root *Menisperm-*. Miers, placing *Cocculus* in another tribe, divided the Menispermeae ("Leptogoneae") into subtribes Menisperminae and Cissampelineae (see *Cissampelos*). Tribe Cocculeae of Hooker & Thomson and of Diels included both *Menispermum* and *Cocculus*. In addition to the differences in floral structure, the stones and embryos of *Menispermum* are broadly crescent shaped, while those of *Cocculus* appear somewhat coiled.

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4. **Cissampelos** Linnaeus, Sp. Pl. 2: 1031. 1753; Gen. Pl. ed. 5. 455. 1754.

Leaves ± coriaceous, ± broadly reniform (to ovate or suborbicular), often apically emarginate, mucronulate [sometimes peltate], usually with 5 or more veins. Hairs 1- or 2-celled. Flowers minute, symmetrically dimorphic; perianth pubescent [glabrous], not calyculate. ♂ flowers: regular; sepals 4, valvate; corolla sympetalous [? or of 2–4 free petals]; anthers about 4 [? to 8 or more], extrorse, included, uniseriate, sessile on a short, central, columnar androphore, ± 1-locular at anthesis, the dehiscence horizontal; pollen ± oblate, 3-colpate. ♀ flowers: irregular; sepal 1; petal 1 [sometimes divided], opposite the sepal; staminodia absent; gynoecium of a solitary carpel; stigma 3-parted; style short, erect; ovary pubescent [glabrous]; ovules 2, the placenta toward the perianth. Fruit red, pubescent [glabrous], nonstipitate, the style subbasal; endocarp sculptured, ± orbicular, laterally compressed, minutely notched adaxially; embryo ± conduplicate, the cotyledons appressed, narrow, no wider than the radicle. LECTOTYPE SPECIES: *C. Pareira* L.; see Britton & Millspaugh, Bahama Fl. 142. 1920. (Name from Greek, *cissos,* ivy [*Hedera*], and *ampelos*, grape [*Vitis*].)

Number of species uncertain, perhaps 20 to nearly 70, widely distributed in warmer regions.

Pantropical and perhaps the most widely distributed taxon of Menispermaceae (cf. Diels), *Cissampelos Pareira*, $2n = 24$, is known in our area from Dade County, Florida. The plants are reported to be high climbing. The leaf blades seem to be nonpeltate, somewhat reniform, with five or more veins, and the petioles at least as long as the blades; in other areas the blades sometimes are ovate and peltate. The carpellate flowers are borne in the axils of usually broad, relatively large bracts resembling small, thin, leaves on peculiar inflorescence branches. Several flowers, each on a separate, stout, upright, unbranched peduncle, these apparently arranged in two parallel ranks, are clustered in the axil of each bract. The bracts are variable in size but often equal or exceed the flowers and, later, the pubescent, red fruits; bractlets seem to be absent. The stones are nearly orbicular, with only a minute adaxial indentation; externally, the condyle appears obovate, and the embryo is strongly folded or horseshoe shaped. The staminate flowers are borne in very finely branched inflorescences with a few bracts and bractlets of various sizes; many of the filiform pedicels are ebracteate. The number of locules in the anthers before anthesis is not apparent.

Floral dimorphism is especially conspicuous in *Cissampelos*, with the regular, sympetalous staminate flowers having a symmetrical androphore, and the irregular carpellate flowers composed of a solitary sepal, petal, and carpel. The general shape and sculpturing of the endocarps seem relatively similar to those of *Cocculus,* and especially *Menispermum*, but the floral morphology is distinctive; consequently, the systematic position of *Cissampelos* seems somewhat unclear. Miers placed *Cissampelos* (along with four other genera) in the subtribe Cissampelineae ("Cissampelideae"), one of his two subtribes under Menispermeae ("Leptogoneae"), approximating the later treatment of Diels who, however, divided the Menispermeae ("Cocculeae") into three subtribes. Hooker & Thomson placed *Cissampelos* in their tribe Cissampelideae.

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