

THE GENERA OF THE PRIMULES OF THE SOUTHEASTERN UNITED STATES *

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THE FAMILIES Theophrastaceae, Myrsinaceae and Primulaceae which compose the order Primulales are almost universally agreed to be rather closely related. Both Theophrastaceae and Myrsinaceae are woody tropical groups (with few exceptions), while the Primulaceae are primarily of temperate distribution and are herbaceous, apparently approaching the Myrsinaceae most closely through a few woody species of *Lysimachia*. All three groups are held together, however, by the mostly pentamerous and sympetalous flowers; by the androecium of an outer, antesealous whorl of staminodia (which may be lacking) and an inner, antepetalous whorl of stamens; by the similar pollen; by the unilocular ovary with free-central placentation; and by the bitegumented ovules.

Although in the Englerian sequence of families the Primulales are placed immediately following the Ericales and Diapensiales, the free-central placentation has led various botanists to associate the Primulales with the Caryophyllales (Centrospermae). Cronquist (Bull. Jard. Bot. Bruxelles 27: 25, 26. 1957) has pointed out, however, that difficulties attend the derivation of the woody and tropical Myrsinaceae from the predominantly herbaceous Caryophyllales. "A resort to woody members of the Caryophyllales such as some of the Phytolaccaceae, as possible near-ancestors of the Primulales tends to vitiate the significance of the free-central placentation as an indicator of relationship between the Primulales and Caryophyllales, inasmuch as the genera of the Phytolaccaceae with united carpels have axile placentation. If the Primulales are indeed related to the Caryophyllales it must be through a woody common ancestor with axile placentation or even with separate carpels, and the free-central placentation has been independently achieved in both groups. On the basis of present evidence the Guttiferales meet the qualifications of a possible ancestor of the Primulales at least as well as do any of the Caryophyllales."

Although the Plumbaginaceae are sometimes included in the Primulales, several lines of evidence indicate that the apparent similarities to this group are probably parallel developments. The Plumbaginaceae seem to be treated best as a separate order Plumbaginales, related to but distinct from the Caryophyllales, although they have been placed with this group by Friedrich (Studien über die natürliche Verwandtschaft der Plumbaginales und Centrospermae. Phyt. Austria 6: 220-263. 1956).

The familial and generic treatments below follow the general scheme out-

* Previously published papers in this series include the genera of the woody Ranales (Jour. Arnold Arb. 39: 296-346. 1958), the Nymphaeaceae and Ceratophyllaceae (40: 94-112. 1959), and the Empetraceae and Diapensiaceae (40: 161-171. 1959).

lined in the first paper of this series of studies prepared for a biologically oriented generic flora of the southeastern United States. It may be called to attention again, however, that the area is bounded by and includes North Carolina and Tennessee, Arkansas and Louisiana; that the descriptions are based primarily upon the species occurring within this area, with any supplementary material added for clarity being included in brackets; that the abbreviations used for periodicals follow the useful principles of Schwarten and Rickett (Bull. Torrey Bot. Club 76: 277–300. 1958); and that all references which we have not seen are marked by an asterisk.

This work on the flora of the southeastern United States, which is being conducted as a joint project of the Gray Herbarium and the Arnold Arboretum, has been made possible through the kind support of George R. Cooley and through a grant from the National Science Foundation. The treatments below were prepared originally by the first author in 1957 while he was associated with the Gray Herbarium and the Arnold Arboretum; they have been edited by the second author as a result of the development of a standard format for these studies and have been modified by him through the incorporation of additional material which has been located since that time. In all of this work on the southeastern United States we are greatly indebted to many of our colleagues and friends for their interest and assistance. In connection with the Primulales we are further indebted to George R. Cooley, for temperature data in connection with the effects of the low temperatures in Florida in 1957–1958 (see *Rapanea*), and to Richard A. Eaton, for his assistance in obtaining living specimens of *Hottonia* for illustration. As in the previous papers in this series, the illustrations are the careful work of Dorothy H. Marsh.

THEOPHRASTACEAE (JOEWOOD FAMILY)

Shrubs and trees differing from the Myrsinaceae in the biseriate androecium, the outer (antesepalous) whorl staminodial, and by anatomical features, including the absence of secretory elements and the presence of long strands of sclerenchymatous tissue beneath the leaf epidermis. The presence of broad rays in the wood apparently is correlated with the highly dissected nature of the vascular system of the axis. The relationship of these two families is worthy of further anatomical investigation. The fruit of the Myrsinaceae is a 1–few-seeded drupe, usually small and dark brown or black, while that of the Theophrastaceae is usually a large yellow or orange berry, only rarely a 1-seeded drupe. TYPE GENUS: *Theophrasta* L.

A family of four genera, differing in the form and disposition of the staminodia, and about 60 species distributed in the American tropics and Hawaii. Represented with us by a single indigenous species of *Jacquinia*.

Clavija longifolia (Jacq.) Mez is sometimes cultivated as an ornamental in the South. Native to Venezuela and Colombia, it is a shrub of *Mahonia*-like habit, attaining a height of 3–5 m. It has large oblong-spatulate to lanceolate, leathery, spinose-toothed leaves and drooping racemes of fragrant, orange or saffron flowers with glandular staminodia.

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1. *Jacquinia* L. Amoen. Acad. 5: 388. 1760, "*Jaquinia*"; L. Sp. Pl. ed. 2. 1: 271. 1762, "*Jaquinia*"; Jacq. Select. Stirp. Am. Hist. 53. 1763; L. Gen. Pl. ed. 6. 101. 1764.

Shrubs or small trees with alternate, simple, persistent, exstipulate leaves without resin ducts. Flowers complete, hypogynous, actinomorphic, 5-merous, gamopetalous. Androecium biseriate: fertile stamens 5, epipetalous at the base of the corolla tube in a single whorl opposite the corolla lobes, the anthers extrorse; staminodia 5, alternating, forming the outer series, petaloid, adnate near the base of the corolla lobes. Gynoecium derived from 5 carpels but appearing simple: ovary unilocular with a central free placenta and several anatropous 2-integumented ovules embedded in the mucilaginous matrix filling the ovary cavity; style and stigma 1. Fruit a dry berry. Seeds few, with well developed embryo and copious endosperm. TYPE SPECIES: *Jacquinia ruscifolia* Jacq. (= *J. aculeata* (L.) Mez). (Generic name in honor of Nicolaus Joseph Jacquin, 1727–1817, distinguished Austrian botanist, sent by Emperor Francis I to the West Indies to procure plants for the Imperial Garden at Schoenbrunn, of which he later became director.) — JOEWOOD, CUDJOEWOOD.

A tropical American genus of about 25–30 species, of which a single one, *Jacquinia keyensis* Mez (*J. armillaris* sensu Chapm. non Jacq.), occurs in our area. Our plant is a compact, symmetrical shrub or small tree with a round-topped crown of yellowish green foliage, attaining a height of about 5 meters. It is characteristically a strand species, distributed in our area in dry coastal hammocks of southern peninsular Florida, on calcareous rock of the Everglade Keys and the Florida Keys, and beyond our region in the Bahamas and Hispaniola. The obovate or cuneate-spatulate coriaceous leaves, usually notched at the apex, have entire, revolute margins and are often clustered at the ends of the brittle, sclerose-tomentose twigs. The very fragrant yellowish or straw-colored flowers are produced in racemes at the ends of the twigs, primarily in winter. The fruits are borne on erect or ascending, bracteate pedicels and are pointed with the base of the persistent style.

Jacquinia armillaris Jacq. (*J. Barbasco* Mez), a native of the West Indies, is sometimes cultivated in Florida as an ornamental. Resembling *J. keyensis* in foliage, this species has white flowers with scarious-margined, non-ciliate sepals and red fruits.

REFERENCE:

SARGENT, C. S. *Jacquinia*. Silva N. Am. 5: 155–158. pl. 242. 1893.

MYRSINACEAE (MYRSINE FAMILY)

Shrubs or trees, mostly with alternate, simple, entire, exstipulate, glandular-punctate leaves, in ours persistent. Flowers 4–6-merous, regular, usually hypogynous, complete or polygamo-dioecious, variously disposed, often clustered on scaly spurs or in panicles or cymes. Calyx shorter than the corolla, the sepals imbricate, connate at the base, persistent. Corolla rotate or short-salverform, the lobes united at the base or sometimes distinct. Stamens distinct, in a single whorl adnate to the corolla tube opposite the lobes, the anthers [transversely or] longitudinally dehiscent; staminodia absent. Pistil 1, derived from 4–6 carpels but appearing simple: ovary 1-loculed, bearing few to many semi-anatropous or semi-campylotropous ovules buried in a fleshy-proliferated axile or basally attached free central placenta filling the ovary cavity. Fruit in ours a 1-seeded drupe, usually dark colored, the seed with a cylindrical embryo and copious endosperm. (Including Ardisiaceae.)

A relatively large family of about 32 genera and approximately 1000 species widely distributed in the tropics and subtropics; two indigenous species in our area, representing two of the largest genera, both of subfam. MYRSINOIDEAE Pax, characterized by the superior ovary and the 1-seeded fruits.

The Myrsinaceae and the Theophrastaceae are distinguished from the Primulaceae by their woody habit, the indehiscent 1–few-seeded drupaceous or berry-like fruits and the fleshy or pulpy, sometimes mucilaginous placenta surrounding or embedding the ovules. The Myrsinaceae differ from the Theophrastaceae by the absence of staminodia and by anatomical features enumerated under the latter family.

The pollen grains of the Myrsinaceae are usually 3(–5)-colpor(oid)ate, suboblate to prolate, more or less similar to those of Primulaceae and Theophrastaceae.

The family is of limited economic importance. It is the source of several ornamental shrubs.

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KEY TO THE GENERA OF MYRSINACEAE

- Ovules multiseriate (Tribe ARDISIEAE); inflorescences terminal, manifestly paniculate, the pedicels slender, longer than the flowers or fruit; flowers conspicuous, the corolla lobes reflexed; style slender; stigma entire. 1. *Ardisia*.
 Ovules in a single circumferential series (Tribe MYRSINEAE); inflorescences ap-

pearing as congested cymes scattered along the twigs on scaly spurs, the pedicels 1–2 mm. in length, shorter than the flower or fruit; flowers inconspicuous, the corolla lobes erect or spreading; style short; stigma lobed.
 2. *Rapanea*.

Tribe ARDISIEAE A. DC.

1. *Ardisia* Swartz, Prodr. Veg. Ind. Occ. 48. 1788, nom. cons.

Shrubs or small trees, the flowers of our species conspicuous, in terminal panicles, the pedicels slender, articulate at the base, the corolla rotate, 5 (rarely 4–6)-parted, the lobes convolute in the bud or sometimes one wholly exterior, recurved at anthesis. Stamens distinct, erect, connivent in a column around the style; anthers sagittate at the base, pointed at the apex, dehiscent by slits, the filaments equalling the anthers in length. Style linear, exceeding the anthers; stigma entire. Fruit a drupe, the endocarp longitudinally ribbed, bony. (Including *Icacorea* Aubl. 1775, nom. rejic.) TYPE SPECIES: *Ardisia tinifolia* Swartz. (Name from Greek *ardis*, point, apparently referring to the apiculate-tipped stamens of some species.) — MARLBERRY, MARBLEBERRY, CHERRY.

A large genus of about 250 species, mostly tropical. Represented with us by a single indigenous species of subgenus ARDISIA (subg. *Pickeringia* (Nutt.) Mez). *Ardisia escallonioides* Cham. & Schlecht. (*A. Pickeringia* Nutt., *Icacorea paniculata* (Nutt.) Sudw.) is a common small tree of coastal hammocks of southern Florida, extending northward along about two-thirds of the east coast of the peninsula and about one-half of the west, and occurring inland to some extent in moist hammocks and in the hammocks and pinelands of the Everglade Keys and Florida Keys. Beyond our area it is most abundant in the Bahamas, Cuba and Hispaniola, less frequent in Mexico and Central America. In Florida the marlberry commonly grows in the shade of other trees, the small crown of leaves often elevated to 3 m. or more. The white, purple-streaked, fragrant flowers appear in abundance in paniculate clusters at the ends of the leafy twigs, usually about November. The globose, shining, black fruits, about 7–8 mm. in diameter, mature more or less throughout the year. The long, linear styles are often persistent in fruit.

Ardisia polycephala Wall. (subg. TINUS (Burm.) Mez), native to Burma, has been reported to occur in hammocks and around old homesteads in southern Florida as an escape from cultivation. This species has axillary clusters of white or pinkish flowers with contorted corolla lobes and slender-tipped anthers. The nearly black fruits are about 1 cm. in diameter. Although persisting, this shrub does not appear to spread to any significant extent.

Ardisia crenata Sims (*A. crispa* sensu A. DC. and many others, not *A. crispa* (Thunb.) A. DC.), of subg. CRISPARDISIA Mez, and *A. japonica* (Hornsted) Blume, of subg. BLADHIA (Thunb.) Mez, both natives of eastern Asia, are used rather extensively as horticultural ornamentals for their foliage and showy red berries.

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Tribe MYRSINEAE Pax

2. *Rapanea* Aubl. Hist. Pl. Guiane Franç. 1: 121. pl. 46. 1775.

Shrubs or small trees, the flowers small, inconspicuous, congested-umbellate, on short, scaly axillary spurs scattered along the twigs, the pedicels short. Corolla spreading or rotate, 5-parted, the tube short. Stamens with ovate-oblong anthers, nearly sessile. Style obsolete, shorter than the stamens; stigma lobed. TYPE SPECIES: *Rapanea guianensis* Aubl. (Name derived from a native name for the plant in French Guiana.)

About 140 species of tropical and subtropical distribution in both hemispheres. *Rapanea guianensis* (*Myrsine Rapanea* Roem. & Schult., *Myrsine floridana* A. DC.) occurs in coastal hammocks of southern peninsular Florida as far north as Volusia County on the east coast and Levy County on the west, in hammock "islands" in the Everglades, on the Everglade Keys and the Florida Keys. It is distributed through tropical America to southern Brazil and Bolivia, being most common in the West Indies, less frequent or rare in Mexico. The flowers and fruits are borne on short spurs along the branches, as in species of *Myrica*, and fruiting specimens bear a very close superficial resemblance to *M. inodora* Bartr., even the foliage being comparable. The globose fruits are dark blue or black in color and at maturity are about 4 mm. in diameter, capped by the persistent sessile stigma. The oblong-obovate leaves, 4-10 cm. long, are mostly clustered at the ends of the branchlets.

The unusually cold winter of 1957-1958 provided various examples of the effects of low temperatures on tropical and subtropical genera. *Rapanea guianensis* which was seen in abundance in April 1958 in Gulf Hammock, near Chassahowitzka, Citrus County, not far from the apparent northern limit of the species on the west coast of Florida, had been killed to the ground by the cold of the winter (temperatures of 15° F. reported locally) but was sending out abundant sprouts from the bases of the plants. Severe winters such as this undoubtedly are one of the primary factors involved in determining the northern limit of this species.

PRIMULACEAE (PRIMROSE FAMILY)

Annual, winter-annual or perennial herbs [or very rarely shrubs] with alternate, opposite or whorled simple leaves and regular, complete, hypogynous or (in *Samolus*) perigynous, 4-8-merous flowers. Stamens as many as the gamopetalous corolla lobes, epipetalous, inserted opposite the lobes on or at the base of the tube, sometimes with as many alternating stami-

nodia, the filaments sometimes connate, the anthers introrse, longitudinally dehiscent. Pistil 1, compound (as indicated by the valves of the ovary); ovary 1-locular with a free-central placenta arising from the base and bearing several to many amphitropous or anatropous ovules; style 1, glabrous; stigma terminal, usually slightly dilated. Fruit a valvate or circumscissile capsule [or rarely indehiscent]. Seeds several to many, with a small embryo in fleshy albumen.

A family of about 20 genera and approximately 500 species, widely distributed in the Northern Hemisphere, occurring on all continents but most abundant in the north-temperate regions.

The Primulaceae are distinguished by their predominantly herbaceous habit, gamopetalous corollas, epipetalous stamens in a single whorl opposite the corolla lobes, free-central placentation and valvate or circumscissile capsules with numerous seeds.

Vascular evidence indicates that the unilocular condition of the ovary of the Primulaceae, with free-central placentation, is of a derivation similar to that of the Caryophyllaceae; the primulaceous flower is descended from an ancestor having a plurilocular ovary with axile placentation. Several modern systematists have suggested that the primitive condition may well be found among the Centrospermae. However, evidence from the remainder of the plant has not yet been adequately considered.

Generic relationships within the Primulaceae are not clear. Consequently, several different tribal arrangements exist for the family. Objections have recently been raised to the alliance (on the basis of the reflexed corolla lobes) of *Dodecatheon* with *Cyclamen* and the resultant separation of these genera from *Primula*. *Dodecatheon* has been considered on anatomical grounds to approximate more closely the original primulaceous flower than any of the other family representatives, but evidence based upon chromosome numbers raises some question in this regard. *Lysimachia* has also been suggested as the most primitive genus of the family and that nearest the Myrsinaceae, for some species of sect. *Apodanthera* (cf. *L. solanoides* Hand.-Mazz.) are lignescent, with indehiscent or hardly dehiscent capsules, and subsessile, upright anthers which open by terminal pores. There has been no recent study of the problem of generic relationships within the Primulaceae taking into consideration evidence from all available sources.

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machia vulgaris, *Anagallis arvensis*, *Primula vulgaris* and *Samolus Valerandii*.]

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KEY TO THE GENERA OF PRIMULACEAE

- A. Terrestrial or marsh plants with entire or merely toothed leaves; flowers solitary, umbellate or racemose.
 - B. Ovary wholly free from the calyx.
 - C. Scapose; flowers in involucrate umbels.
 - D. Low, rosulate annuals with pubescent leaves; corolla inconspicuous, the lobes erect or spreading at anthesis; calyx accrescent, the lobes green, not ridged, the tube whitish and prominently ridged; stamens distinct, included. 1. *Androsace*.
 - D. Perennials with broad, glabrous or glabrate leaves; corolla conspicuous, the lobes reflexed at anthesis; calyx herbaceous, not ridged, the lobes and tube similar in texture; filaments connate below, the anthers forming an exerted cone. 2. *Dodecatheon*.
 - C. Caulescent; flowers solitary in the leaf axils or in racemes.
 - E. Stem with scale-like alternate leaves below and a single whorl of thin, lanceolate leaves at the summit, subtending the pedunculate, 6–8 (mostly 7)-merous flowers; corolla white. 4. *Trientalis*.
 - E. Stem leafy throughout, leaves alternate, opposite or whorled; flowers 4–6-merous.
 - F. Capsule valvate; corolla yellow; perennials with opposite or whorled leaves; flowers 5–6-merous. 5. *Lysimachia*.
 - F. Capsule circumscissile; corolla scarlet, blue or white; annuals with alternate or opposite leaves; flowers 4–5-merous. 6. *Anagallis*.
 - B. Ovary partially inferior, adnate to the calyx tube; inflorescence racemose, the pedicels bracteate or ebracteate. 7. *Samolus*.

- A. Aquatic plants with pectinately dissected leaves; flowers in whorls on the conspicuously inflated, floating peduncles. 3. *Hottonia*.

1. *Androsace* L. Sp. Pl. 1: 141. 1753; Gen. Pl. ed. 5. 69. 1754.

Small, scapose, pubescent annuals [biennials or perennials, these scapose or caespitose]. Leaves ovate-lanceolate, sparingly denticulate [or quite various]. Scapes 1-many, the inflorescence a simple umbel [or scapes single-flowered]; flowers involucrate, borne on unequal pedicels. Calyx accrescent, the whitish tube broadly ridged, the 5 lobes green and not ridged. Corolla small, white, marcescent, included within the calyx, the lobes obtuse, shorter than the tube [or in perennials surpassing the calyx and conspicuous]. Stamens 5, the anthers oval to oblong, the short filaments attached at or below the middle of the corolla tube. Style short, the stigma capitate-dis-coid, the ovary superior, ovoid to globose. Capsule valvate to the middle, coriaceous above, membranaceous below. Seeds many, small, blackish. TYPE SPECIES: *Androsace carnea* L. (A name applied by Pliny to some unknown plant.)

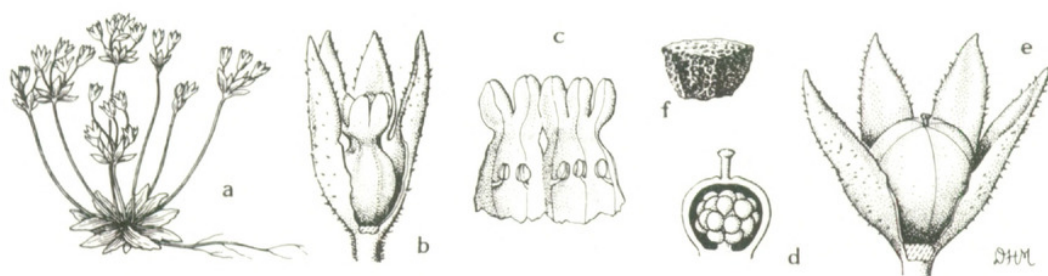


FIG. 1. *Androsace*. a-f, *A. occidentalis* Pursh var. *occidentalis*: a, habit, $\times \frac{1}{2}$; b, flower with one sepal removed, $\times 5$; c, corolla opened to show stamens, $\times 5$; d, pistil, semi-diagrammatic, the ovary in vertical section, $\times 10$; e, mature fruit and calyx, one sepal removed, $\times 5$; f, seed, $\times 10$.

About 85-90 species, chiefly of the mountainous and boreal-arctic regions of Eurasia, but with six species and six varieties, all of sect. *CHAMAEJASME* Koch (sensu Handel-Mazzetti), in North America. The genus barely enters our range in Washington County, Arkansas, where *Androsace occidentalis* Pursh var. *occidentalis* has been collected. This variety with erect or somewhat spreading calyx lobes and erect to arched-ascending pedicels, has a wide range, primarily in the western United States (Mississippi, Missouri, and Arkansas river valleys, foothills of the Rocky Mountains in Colorado, Utah and Montana and into southwestern British Columbia, and also in the mountains of New Mexico and Arizona) in dry sands, gravels and rocky woods. Var. *arizonica* (Gray) St. John, with spreading to arched-reflexed calyx lobes and filiform pedicels, is restricted to the mountains of southeastern Arizona.

The marcescent corollas, often exhibiting a narrow constriction of the tube below the lobes, are inconspicuous in the annual species and are not

used taxonomically in this group; here the primary characters are those of calyx and capsule.

Chromosome numbers of $2n = 20$, and 72 have been reported for two Old World species.

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2. *Dodecatheon* L. Sp. Pl. 1: 144. 1753; Gen. Pl. ed. 5. 71. 1754.

Scapose perennial herbs chiefly of calcareous soils. Leaves lanceolate or oblanceolate, entire, the inflorescence a naked scape bearing a simple, involucrate umbel, the pedicels erect in bud, somewhat recurved or arched at anthesis, erect in fruit. Calyx 5-lobed, the lobes equalling or longer than the tube, reflexed at anthesis, erect in fruit. Corolla white or purplish, 5-parted, the tube short, the lobes oblong, erect in bud, reflexed at anthesis. Stamens 5, erect, the filaments short, separate or united into a tube, the anthers basifixed, much longer than the filaments, connivent around the style, the connective prominent, smooth. Stigma slightly if at all dilated, exserted beyond the stamens; style filiform; ovary ovoid, equaling the filaments at anthesis. Capsule ovoid or cylindric-conical, much longer than the calyx, thick-walled, valvate; seeds numerous, spherical or ovoid, ours without membranaceous edges, reticulate, anatropous. TYPE SPECIES: *Dodecatheon Meadia* L. (The name from the Greek *dodeca*, twelve, and *theos*, god, given by Pliny to another plant, probably the primrose, which was allegedly under the care of the twelve superior gods.) — SHOOTING-STARS, AMERICAN COWSLIPS, MEADIAS.

A North American genus of about 15 species, mostly western. Section DODECATHEON, to which our species belongs, differs from sections PURPUREO-TUBULOSA Knuth and CAPITULUM H. J. Thompson by a combination of characters, including the nondilated stigma, valvate capsule (as opposed to operculate), the yellow (rarely dark), separate or united filaments and the seeds without membranaceous margins. There are also developmental differences in the seedlings of the three sections: the first true roots in sect. DODECATHEON develop from the hypocotyl just below ground level, well below the cotyledons; in sect. PURPUREO-TUBULOSA from a subterranean carrot-shaped caudex; and in sect. CAPITULUM from the aerial hypocotyl at the base of the cotyledons.

Dodecatheon Meadia has been variously treated taxonomically. Fassett recognized 5 varieties, some of dubious taxonomic significance, based primarily on quantitative characters of stamen-tube, calyx-lobe and capsule dimensions. Thompson has more recently recognized only three units:

subsp. *Meadia* ($2n = 88$), subsp. *brachycarpum* (Small) Knuth and subsp. *membranaceum* Knuth, the first two of which occur within our area.

Subspecies *brachycarpum* (var. *brachycarpum* (Small) Fassett) (Virginia to northern Georgia, Tennessee, Missouri, Oklahoma and Texas) is characterized by small flowers and fruits. Throughout its range it is sympatric with subsp. *Meadia* with which it intergrades wherever the two come into contact. The latter, however, occurs northward to Wisconsin well into the area of glaciation. Within glaciated territory morphological variation in this species is unimodal, while outside this area variation is bimodal, suggesting the presence of two populations. Populations within glaciated territory are, however, more variable as to flower color than those of unglaciated areas.

The third, subsp. *membranaceum* (var. *Frenchii* Vasey), is restricted in distribution to southern Illinois, adjacent Kentucky and the driftless area of Wisconsin. Characteristically a plant of overhanging, wet or dripping cliffs, where it grows in dense shade, it is characterized morphologically by the abrupt contraction of the leaf blade into the petiole. It occurs within the extensive range of subsp. *Meadia*, which has considerably thicker, noncordate blades. Specimens of the two subspecies have occasionally been found growing within a few feet of one another, although they are easily distinguished morphologically. Ecological experiments, including reciprocal transplantation in the field, as well as greenhouse observations, indicate no change in leaf form as a result of varying light intensities and support the genetical and morphological distinctness of the two taxa.

With the exception of var. *Frenchii* Vasey (subsp. *membranaceum*), the five varieties of *Dodecatheon Meadia* recognized by Fassett on morphological grounds do not occupy different environments. Based primarily on quantitative characters of stamen-tube, calyx-lobe and capsule dimensions, these varieties are of dubious taxonomic significance. Solution of the problems of variation in this complex would appear to require genetic studies.

The taxonomic characters utilized in this group vary considerably. Collectors should record corolla color in the field and such other characters as may be obscured in pressing. The varying shape of the connective and the connation of the filaments have been found to be unreliable as taxonomic characters but no one has suggested the cause of such variation. The red color at the base of the leaves of *D. Meadia* is not lost in herbarium material; in pressing this color consistently disappears from the leaves of *D. radicum* Greene (*D. amethystinum* Fassett), a species of the East but one apparently not represented in our area. Fruit-texture and -color are reported to be reliable both in the field and in the laboratory.

Although insects have occasionally been observed to visit the flowers of *Dodecatheon*, their role in pollination is unknown. The structure of the flower suggests that self-pollination is frequent, if it is not the primary means of pollination. The observations of collectors in this respect would be helpful. The flower buds are at first erect, but, during anthesis when the sepals and petals are reflexed, the pedicels arch outward and downward,

placing the flowers in a nodding position. The erect anthers surrounding the exerted style are thus inverted and, upon dehiscence along their connivent surfaces, a certain amount of pollen falls upon the stigma. In fruit the pedicels reassume an erect position.

The reported chromosome numbers form a polyploid series ($2n = 44, 66, 88, 132$).

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3. *Hottonia* L. *Sp. Pl.* 1: 149. 1753; *Gen. Pl.* ed. 5. 72. 1754.

Aquatic herbs with pectinate leaves scattered along the rooting and floating stem and crowded in a whorl beneath the cluster of conspicuous, inflated aerial peduncles; the pedicellate flowers and subtending sepaloïd bracts whorled at the constricted nodes, forming interrupted racemes. Calyx of 5 herbaceous, linear-oblong sepals. Corolla white, 5-lobed, the lobes as long as or shorter than the tube. Stamens 5, the filaments short, adnate near the center of the corolla tube; pollen 3-colporoidate. Stigma minutely clavate; style linear; ovary subglobose. Capsule obpyriform to subglobose, membranaceous, 5-valved, the valves sometimes coherent at base and apex; seeds numerous, small, oblong-oval, longitudinally rugose, anatropous. TYPE SPECIES: *Hottonia palustris* L. (The name in honor of Petrus Hotton, 1648–1709, Dutch botanist and professor at Leiden.) — FEATHERFALL, WATER-VIOLET.

Two species, the Eurasian *Hottonia palustris*, and *H. inflata* Ell. of the eastern United States. *Hottonia inflata* is widespread, but of sporadic occurrence, from Florida to Texas and north to New England, New York, Ohio, Indiana, southern Illinois and Missouri. In most areas it is considered rare, although it sometimes occurs in abundance. In New England the species is a winter annual, with the seeds germinating in autumn and the

seedlings growing rapidly. Although growth is retarded during the winter months, the plants survive protracted periods beneath a cover of ice. By May the plants reach the surface of the water and the inflated peduncles develop. The flowers appear from late May to mid-June. After flowering, the old plants shed the pectinate leaves and decay as the seeds ripen.



FIG. 2. *Hottonia*. a-g, *H. inflata*: a, flowering and fruiting plant, $\times \frac{1}{4}$; b, flower with bract, $\times 5$; c, corolla, opened to show stamens, $\times 5$; d, pistil, semi-diagrammatic, the ovary in vertical section, $\times 5$; e, mature fruit, $\times 5$; f, pedicel and placenta from a large fruit near base of inflorescence, after dehiscence of fruit, $\times 5$; g, seed, $\times 15$.

Structural and functional dimorphism is reported for *Hottonia palustris* ($2n = 20$) from the British Isles. Pollen grains of the long-styled flowers differ in size as compared with those of short-styled flowers by a proportion of 14 to 9, respectively. (Cf. *Pontederia*.) The significance of the size differences is unknown. Pollination experiments with short-styled flowers indicate that the species is at least partially self-fertile when artificially pollinated. Manual cross-pollination of short-styled flowers with pollen from a long-styled individual of a different source also effects seed production, with a considerably larger proportion of fruit and seed set than in the former instance, suggesting that the heterostylous condition is of functional significance in promoting cross-pollination. In contrast, *Hottonia inflata* exhibits neither heterostyly nor other structural dimorphism. Although the style is quite short, at anthesis the stigma reaches the included anthers and is often seen to be covered with pollen from the same flower, suggesting that self-pollination frequently occurs in this species.

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4. *Trientalis* L. Sp. Pl. 1: 344. 1753; Gen. Pl. ed. 5. 161. 1754.

Low, nearly smooth, rhizomatous, perennial herbs of woodlands and peaty slopes, spreading by slender, elongate stolons. Stems simple, erect, bearing several inconspicuous alternate bracts and a conspicuous whorl of lanceolate, acuminate, thin-textured, veiny leaves at the summit and a few axillary, slenderly pedunculate, star-shaped, delicate white flowers. Flowers (6)7(8)-merous. Calyx deeply parted, the lobes linear-lanceolate. Corolla deeply parted, rotate, the lobes ovate-elliptic, pointed, coherent at the base as a short, nearly obsolete tube. Stamens with slender filaments, united basally in a short ring on the base of the corolla, the anthers oblong, basifixed, revolutely coiled in anthesis. Stigma only slightly dilated; style filiform, equalling the filaments; ovary globose, about equalling the corolla tube at anthesis. Capsule globose, valvate to the base, the valves recurved, exposing the several grayish-granular seeds persisting temporarily upon the erect placenta. TYPE SPECIES: *Trientalis europaea* L. (The name from the Latin *triens*, one-third of a foot, alluding to the height of the plant.) — STARFLOWER, CHICKWEED-WINTERGREEN.

Three species of the North Temperate Zone, only one barely entering our area in northeastern Tennessee. *Trientalis borealis* Raf. (*T. americana* Pursh) is distributed from Labrador to Saskatchewan, south to Newfoundland, Nova Scotia, New England, Virginia, West Virginia, Tennessee, Ohio, Illinois and Minnesota. It occurs in shady woodlands southward and on peaty slopes northward, ascending to subalpine regions. *Trientalis latifolia* Hook. occurs in the montane and subalpine regions of Pacific North America from western California into British Columbia. *Trientalis europaea* L. var. *europaea* ($2n = \text{ca. } 112 \text{ or } 160$) is primarily Eurasian; var. *arctica* (Hook.) Ledeb. enters North America from western Siberia, extending from the Bering Strait and the Aleutians to the mountains of Oregon. Similar in habit, these species differ in the shape of leaves and corolla lobes. *Trientalis* is closely related to *Lysimachia*.

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5. *Lysimachia* L. Sp. Pl. 1: 146. 1753; Gen. Pl. ed. 5. 72. 1754.

Rhizomatous, caulescent, perennial herbs [or rarely shrubs] of decumbent or repent habit and with simple, opposite or whorled (sometimes glandular-punctate) entire leaves. Flowers 5, 6(7)-merous, variously disposed. Calyx herbaceous, of 5 deeply parted imbricate or valvate lobes. Corolla yellow [or white] rotate or somewhat campanulate, of 5 deeply parted, convolute or individually supervolute lobes and a short tube, sometimes with as many alternating staminodia. Filaments of the fertile stamens nearly distinct or united at the base, the 2-loculed anthers basifixed or somewhat versatile. Stigma terminal; style linear; ovary ovoid to globose. Capsule 5-valved, the seeds few to many, oblong, orbicular or angular, sometimes winged, the embryo in evident endosperm. [$2n = 18, 20, 24, 28, 30, 36, 60$, in species beyond our range.] (Including *Steironema* Raf.) TYPE SPECIES: *Lysimachia vulgaris* L. (Named, according to tradition, for King Lysimachus of Thrace, who, when confronted by an enraged bull, waved a loosestrife before it and quieted it; or from the Greek *lysis*, a release, and *mache*, strife, alluding to ancient lore which attributed to the plants the power of conciliation in animals.) — LOOSESTRIFE.

A genus of about 160 species in seven subgenera, of wide distribution, especially in the northern hemisphere (with the largest number of species in eastern India, northern Burma and southern China). Fourteen species, in two subgenera, occur in our area. At various times most of the subgenera have been considered to be independent genera, but on a world-wide basis there seems to be no positive evidence for such separation.

Subgenus SELEUCIA Bigelow (*Steironema* Raf.), with evident staminodia, erose or apiculate corolla lobes supervolute in bud (each inclosing a stamen), and epunctate leaves, includes five species of temperate America north of Mexico, all in our area. The continental-ranging *L. ciliata* L. is closely related to *L. tonsa* (Wood) Knuth, of the southern Appalachians. *Lysimachia radicans* Hook., primarily of the lower Mississippi embayment but with stations in Virginia, approaches *L. lanceolata* Walt., centered in the eastern United States and with two intergrading subspecies, *lanceolata* (including *L. heterophylla* Michx.) and *hybrida* (Michx.) J. D. Ray (var. *hybrida* (Michx.) Gray). Especially distinctive is *L. quadriflora* Sims, mostly of the north-central states but with stations in at least Georgia and Arkansas in our area.

Subgenus LYSIMACHIA (subg. *Cassandra* Bigelow), characterized by absence of staminodia, imbricate corolla lobes with entire margins, and punctate leaves, is a large and complex group centering in southeastern Asia, with only five indigenous American species. Section NUMMULARIA (Gilib.) Klatt includes the repent, very floriferous, but usually sterile and apparently apomictic, *L. Nummularia* L. ($2n = 36$), introduced from Europe, and, to the north of our area, *L. punctata* L. ($2n = 30$), also of European origin. Section LYSIMACHIA (sect. *Lysimastrum* Endl.) is composed of only the distinctive *L. Fraseri* Duby, of the mountains of North Carolina, Georgia, Tennessee and Alabama, the European *L. vulgaris* ($2n = 28$), nat-

uralized in the northern United States and Canada, and *L. salicifolia* F. Muell., of Australia. Section TRIDYNIA (Raf.) Gray includes the widespread *L. quadrifolia* L., primarily of woodlands, its close relative *L. asperulifolia* Poir., restricted to the Carolina coastal plain, *L. Loomsii* Torrey, with a similar distribution in the Carolinas and Georgia, and *L. terrestris* (L.) BSP., of wide northern distribution and unique in producing axillary bulblets. The fertile *L. × producta* (Gray) Fern. and the sterile *L. × commixta* Fern. are the putative hybrids of this last with *L. quadrifolia* and with *L. thyrsiflora* (subg. NAUMBURGIA), respectively.

Recently evaluated on a morphological basis, some of our species of *Lysimachia* are well marked and easily identified; others are believed to hybridize to a greater or lesser extent and present patterns of variation which are often difficult to interpret. Cytological and genetic investigations would appear to be a source of useful information on the relationships among the variable species.

The generic status sometimes accorded subgenus SELEUCIA (as *Steironema* Raf.) is based in part upon the presence of staminodia. Variouslly interpreted as sterile filaments and as mere nonvascular excrescences, in the two species studied anatomically these structures as primordia show vascular traces, but there is no further development of the vascular tissue. The floral anatomy of all of the species thus far examined is fundamentally the same, and, except for the presence of staminodia, species of *Steironema* fall naturally into the genus *Lysimachia*.

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6. **Anagallis** L. Sp. Pl. 1: 148. 1753; Gen. Pl. ed. 5. 73. 1754.

Low, erect, spreading or procumbent annual herbs with alternate or opposite entire leaves and peduncled or nearly sessile flowers solitary in the leaf axils; plants of sandy fields, low grounds, damp sands and mud. Corolla (4)5-lobed, conspicuous (rotate with almost no tube) and deciduous, or inconspicuous (the urceolate or globular tube equalling the lobes) and often marcescent at summit of the capsule. Stamens (4)5, the filaments bearded or glabrous, adnate at the base or near the middle of the corolla tube. Ovary ovoid, the style linear, the stigma minutely capitate; capsule membranaceous, globose, circumscissile near the middle, the seeds numerous, angular. (Including *Centunculus* L., *Micropyxis* Duby.) TYPE SPECIES: *Anagallis arvensis* L. (The ancient Greek name, probably from *ana*, again, and *agallein*, to delight in, alluding to the habit of the flowers of opening again in the sunlight after having closed in cloudy weather.) — PIMPERNEL, SCARLET PIMPERNEL, POOR MAN'S WEATHER GLASS.

About 24 species, mostly native to the Mediterranean region, Africa and South America, three widely distributed. The three species known from the United States, representing two of three subgenera, occur within our area.

Subgenus ANAGALLIS, including plants with conspicuous, nearly rotate corollas and opposite or whorled leaves, is represented in our area by *Anagallis arvensis* L. ($2n = 40$), native to the European-Mediterranean region but now a widespread weed on nearly every large land mass. The species includes three subspecies, two of which are known from the United States. Subspecies *arvensis* (subsp. *phoenicea* (Scop.) Vollmann) includes plants with scarlet, salmon, white, lilac, or blue corollas, with relatively large lobes, and comparatively smooth margins, fringed with numerous

gland-tipped, 3-celled trichomes. Subspecies *coerulea* (Schreb.) Vollmann (subsp. *foemina* (Mill.) Schinz & Thellung) comprises plants with blue flowers with narrower and smaller corolla lobes which are denticulate-margined and only sparsely glandular with 4-celled hairs. Both scarlet and blue forms of subsp. *arvensis* are well known in the United States. Subspecies *coerulea*, apparently less common, occurs at least in Illinois and Texas and may be expected within our area. Corolla color, rarely indicated, is difficult to determine in dried materials and should be noted by the collector. All blue-flowered plants should be examined carefully while fresh for the small, but important, distinguishing details. The corollas of both subspecies have a purple center produced by cells with purple sap in which small, blue, spicular crystals are aggregated.

Both subsp. *arvensis* and subsp. *coerulea* have been studied in considerable detail. The color variants of subsp. *arvensis* form an interfertile series which shows Mendelian segregation in the hybrids. Subsp. *coerulea* is partially isolated genetically and produces sterile F_1 hybrids with all except the salmon form of subsp. *arvensis*. The F_1 offspring of this last cross have pink flowers and are fully fertile. Segregation for flower color and other characters occurs in the F_2 .

The relationship to these of the third, subsp. *gentianeae* (Beck) Domac, requires further study. As delimited by Domac (1956), the subspecies includes plants with gentian-blue flowers, the petals of which are almost intermediate between those of the other two subspecies in shape, size and margin, and which are densely beset with 3-celled trichomes like those of subsp. *arvensis*. Trichomes of the stamen-filaments are 8–10 (mostly 9)-celled while those of subsp. *arvensis* are 5–8-celled and those of subsp. *coerulea* are 11–12-celled. Although all of the specimens cited by Domac were from Yugoslavia, the distribution is probably much wider.

Anagallis arvensis is an obligate long-day plant, continuing in vegetative growth indefinitely with less than the critical 12-hour light period. Cross-pollination in this species is by Hymenoptera and Diptera. The flowers are also adapted to self-pollination, however, and are fully self-fertile.

Subgenus CENTUNCULUS (L.) P. Taylor, primarily a group of tropical Africa and one traditionally treated as a genus, includes species which combine characters of erect habit, alternate leaves, terminal inflorescences, small, pale flowers, subpersistent corollas and glandular ovaries. In the widespread *A. minima* (L.) Krause (*Centunculus minimus* L.) ($2n = 22$) the corolla is very short and the stamens are connate and adnate to the corolla for about half their total length. The pantropical *A. pumila* Sw. (*Micropyxis pumila* (Sw.) Duby; *Centunculus pentandrus* R. Br.), composed of three varieties, is represented with us by var. *pumila*, confined to low grounds of peninsular Florida. The corolla is longer and the stamens are connate and adnate less than a quarter of their total length (except in *A. pumila* var. *djalonis* (A. Chev.) P. Taylor, of tropical Africa), as in the remainder of the subgenus and genus. Inasmuch as the adnation is merely a matter of degree and varies within a single species, the retention of *Centunculus* as a genus seems unjustified.

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7. *Samolus* L. Sp. Pl. 1: 171. 1753; Gen. Pl. ed. 5. 78. 1754.

Caulescent or subscapose, somewhat succulent, glabrous, perennial herbs with alternate, simple, entire leaves, typically of wet situations in sand, sandy loam or muck, occurring also in salt marshes and on almost bare, eroded limestone. Inflorescences racemose, the wiry pedicels with or without bracts. Calyx herbaceous, campanulate, the 5 triangular lobes acute or acutish, equal to or longer than the adherent tube. Corolla white or pinkish, 5-lobed, the tube shorter or longer than the lobes, the throat sometimes glandular-pubescent. Stamens 5, included, sometimes with alternating staminodia. Stigma terminal, sometimes capitate; style linear; ovary ovoid, half-inferior. Capsule subglobose, the 5 valves thick-textured above, thinner below; seeds small, numerous, angular. (Including *Samodia* Baudo ex Small.) TYPE SPECIES: *S. Valerandii* L. (The name probably of Celtic origin, said to refer to curative properties of the genus in diseases of cattle and swine.) — WATER-PIMPERNEL, MARSH-PIMPERNEL, BROOKWEED.

About ten species, four in North America, the others in the extratropical regions of the southern hemisphere; represented with us by at least two species.

The American representative of the nearly cosmopolitan *Samolus Valerandii* complex, the white-flowered *S. parviflorus* Raf. (*S. floribundus* HBK.), of shallow water and wet soils, is widespread from British Columbia, southern Ontario and Quebec and New Brunswick, southward throughout the United States into Mexico, Cuba and Hispaniola. What is apparently the same species also occurs in southern Brazil, Uruguay, Paraguay, Bolivia, Argentina and Chile. The pedicels are bracteate and the corollas bear staminodia alternate with the stamens. Varying considerably in habit and variously treated taxonomically, the American plant is, in general, more widely and diffusely branched than *S. Valerandii*, with lateral instead of ascending pedicels and setaceous instead of linear-lanceolate bracts. Only the European plant has been investigated cytologically; the $2n$ chromosome number has been reported to be ca. 24 and ca. 36. The pollen grains are 3-colporoidate and subprolate. The development of the embryo has been followed in considerable detail.

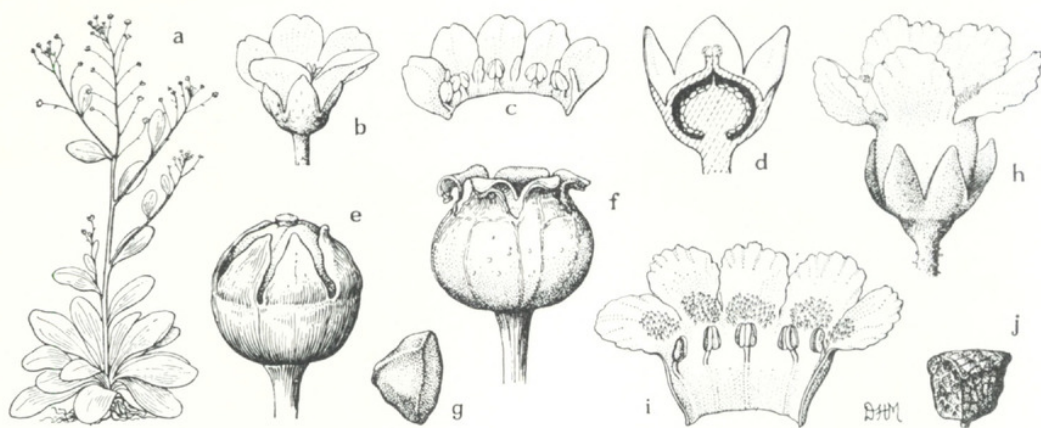


FIG. 3. *Samolus*. a-g, *S. parviflorus*: a, habit, $\times \frac{1}{4}$; b, flower, $\times 5$; c, corolla opened to show stamens and staminodia, $\times 5$; d, flower with corolla removed, the pistil in vertical section, $\times 10$; e, mature fruit before dehiscence, $\times 10$; f, fruit after dehiscence, $\times 10$; g, seed, $\times 20$. h-j, *S. ebracteatus*: h, flower, $\times 4$; i, corolla opened to show stamens and patches of glandular hairs, $\times 4$; j, seed, $\times 20$.

The pink-flowered *Samolus ebracteatus* HBK., lacking floral bracts and staminodia, grows equally well in sand or sandy loam or on almost bare limestone. Thus considerable variation exists in the extent of development of the stem-system and in leaf-shape, flower-size and the form of the inflorescence. Distributed in the West Indies, Florida, Oklahoma, Texas and Mexico, the species is restricted in our area to the southern tip and western coast of peninsular Florida, presumably dispersed from the West Indies. The cause of the gap in distribution between Florida and Texas and Oklahoma is not known. On rich soils the foliage develops a deeper or brighter green; on limestone the foliage is pale or glaucous and sometimes coated with lime.

Samolus alyssoides Heller and *S. cuneatus* Small, both described from Texas, are doubtfully distinct. Glandular-pubescent inflorescences, sup-

posedly characteristic of the latter, appear in populations of *S. ebracteatus* in Florida. The former species is based upon quantitative characters of dubious taxonomic significance. The status of these taxa needs critical evaluation.

The perigynous floral condition characteristic of *Samolus* has been investigated anatomically in *S. parviflorus*. The perianth is firmly attached to the ovary wall, producing an inferior ovary and consequent modification of the perianth pattern. The lower half of the hypanthium is a compound structure consisting of ovary wall and perianth combined. Early anatomical stages show a zonal development of five projecting points which form carpellary walls and five bulbous portions at their bases which unite in forming the central placenta. Ontogenetically the separation between carpel wall and placenta occurs in the embryonic stages and the placenta originates from the fusion of the five basal growing points. A similar situation has been described in *Lychnis* (Caryophyllaceae).

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