# THE GENERA OF ALISMATACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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## ALISMATACEAE Ventenat, Tabl. Règne Vég. **2**: 157. 1799, "Alismoideae," nom. cons.

(Water-Plantain Family)

Glabrous or subglabrous, usually perennial, most often emergent herbs of wet places, the petioles and other organs with air spaces traversed by diaphragms. Vegetative axes condensed erect stems, sympodial rhizomes, axillary stolons, and terminal pseudostolons. Vessels confined to the roots, with simple or scalariform perforations. Epithelium-lined laticifers in most organs of most taxa, rare in roots. Single or clustered crystals often present (especially in the leaves), these usually small rod-shaped styloids or rhomboids, sometimes crystal sand, occasionally raphides (these or "Nädelchen" reported in *Alisma, Echinodorus,* and *Sagittaria*), or infrequently druses (reported in *Sagittaria* among our genera). Leaves basal [rarely cauline], spirally arranged or spirodistichous (infrequently distichous), often with hydropoten,[2] highly variable and environmentally plastic, submersed, floating, or (usually) erect and emergent, usually petiolate, the blade linear (especially in submersed forms) to cordate or sagittate, the principal nerves parallel with the margins and tending to converge at the apex; stomata usually paracytic, sometimes tetracytic, [rarely otherwise]; petioles with broadened, open, sheathing bases. Intravaginal scales

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Thanks are due Carroll Wood for his careful review of the manuscript. Translation of literature from Chinese by Shiu-Ying Hu was a valuable contribution. Donna Rogers, my wife, translated literature from French and participated adeptly in troubleshooting the manuscript. Figure 1 is the work of Laszlo Meszoly, who used materials of *Alisma subcordatum* collected and dissected by the author. Karen S. Velmure drew Figure 2, for which dissections were prepared by K. R. Robertson and C. E. Wood.

[2]This seldom-encountered term refers to groups of specialized, flattened cells on submersed leaves and petioles; these are involved in the uptake of salts and facilitate the passage of water.


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usually present. Inflorescences terminal (vegetative growth proceeding by a precociously developed meristem in the axil of the leaf immediately beneath the inflorescence), usually [spikes,] racemes, or panicles, sometimes umbelliform, sometimes lax, even horizontal, the bracts in (pseudo-)whorls of 3 at the nodes, sometimes with vegetative buds mixed with or completely replacing flowers. Flowers and branches borne either in condensed, sympodial, bostrycoid complexes (usually in *Alisma* and *Echinodorus*) or singly in axils of bracts (with exceptions, *Sagittaria*). Flowers regular, hypogynous, perfect or imperfect, with 3 imbricate, green sepals, and 3 imbricate, usually white [sometimes reddish or yellow], delicate, ephemeral petals [these infrequently reduced or absent]. Stamens [3–]6 to many, with 2-locular, mostly extrorsely dehiscing anthers; pollen grains more or less spherical or polyhedric, pantoporate (ours), with granules or spinules on the sexine, 3-nucleate when released. Gynoecium of [3 to] many free carpels (sometimes slightly connate at the base), these usually laterally compressed, on a flat or rounded receptacle, each carpel with a terminal or adaxial style and 1 [or more in *Damasonium*] adaxial-basal, anatropous or variably bent, apotropous [or epitropous] ovule. Fruits achenes [or follicles in *Damasonium*], usually with variously developed longitudinal ridges; seed with a thin integument, without endosperm; embryo U-shaped with the 2 tips toward the base, the radicular end thickened, germination epigeal. TYPE GENUS: *Alisma* L.

Excluding the three genera of Limnocharitaceae Takhtajan, about 12 genera of temperate and tropical regions, with most species in the Northern Hemisphere. The genera are typically small, mostly with one to 10 species, except *Echinodorus* and *Sagittaria,* which together may account for over 80 species and which clearly will expand with further exploration of the tropics. This estimate, based largely on the attention focused on those two genera in recent years by Rataj, indicates that the total number of species in the family is considerably larger than the 70–100 estimated by most authors. Ranges of four genera extend into the continental United States, three are found in the Southeast, and *Damasonium californicum* Torrey (*Machaerocarpus californicus* (Torrey) Small) occurs in northern California, Oregon, western Nevada, and southwestern Idaho.

In the monocotyledonous families to which Engler's name Helobiae is still often applied (*cf.* Alismatidae of some recent authors), the Alismataceae are usually placed near the Hydrocharitaceae, Butomaceae (here regarded as monogeneric), and Limnocharitaceae, these four making up the Alismatales of Takhtajan (1980) and of Thorne (who, however, did not recognize the Limnocharitaceae at the familial level). Cronquist excluded the Hydrocharitaceae from this order, which is even more restricted in the scheme of Dahlgren & Clifford, in which the Alismataceae (including the Limnocharitaceae) alone comprises the Alismatales.

The Butomaceae differ from the Alismataceae most saliently in their subpetaloid calyces, persistent petals, exclusively linear leaves, lack of secretory canals, straight embryos, uniaperturate pollen, monosporic embryo sacs, numerous ovules scattered on laminar placentae, and uniformly follicular fruits.

Often included in the Butomaceae, the Limnocharitaceae agree with that family in having follicular fruits and many ovules on laminar placentae, but resemble the Alismataceae anatomically, in all of the other characters listed above, and in other ways. (The Limnocharitaceae may differ from both the Alismataceae and the Butomaceae in having stamens develop in a centrifugal pattern; see Sattler & Singh.) The Limnocharitaceae have been included in the Alismataceae by a number of botanists, including Dahlgren & Clifford, Pichon, and Thorne. This position is supported by the intermediacy of two alismataceous genera, *Damasonium* Miller (vasculature of carpels, follicular fruits, number and arrangement of ovules) and *Ranalisma* Stapf (sympodial inflorescences, these atypical of Alismataceae but occurring in Limnocharitaceae).

The flowers of the Alismataceae and related families have often been interpreted as primitive, especially because of their distinct, sometimes numerous, and seemingly spirally arranged stamens and carpels, the latter sometimes remaining open (*Alisma*) and with more or less decurrent stigmas. These features have been taken as indicators of an ancestral position among the helobian monocots and as ties to presumably primitive ranalian dicots, especially the Ranunculaceae and Nymphaeales, some of which (principally the latter) show vegetative resemblances in addition to having flowers of similar appearance. Hutchinson, for example, thought *Ranalisma* (otherwise universally accepted as alismataceous) to be an intermediate link between the Alismataceae and the Ranunculaceae. Affinity with the similarly aquatic Nymphaeales was advocated by Takhtajan (1969). However, the accumulated anatomical, embryological, developmental, and morphological evidence has shown the Alismataceae to be specialized in several ways and contradicts close affinity with the Ranales. (For a concise discussion of the relationship with the Ranunculaceae, see Tomlinson; see also Dahlgren & Clifford; Eames; Eckardt; Maheshwari, 1964; Meyer, 1932; Sculthorpe, pp. 279, 280; Stant; and Thorne, pp. 97, 98.)

In this connection, in a recent series of papers particular attention has been paid to the nature of the androecium and gynoecium. Unlike the spirally arranged but superficially similar flowers of Ranales, the alismataceous flower appears to be fundamentally trimerous. According to Sattler & Singh, this trimery is unlike that found in some Ranales ("Magnoliidae"). Unlike those of the putatively related dicots, the three petals and first six stamens in most genera of Alismataceae arise in a (pseudo?)whorl of three complexes, each of these a petal primordium and an antipetalous stamen-pair. Each complex usually originates as a single protrusion termed a "CA primordium." Primordia for carpels, too, arise in variable, basically trimerous patterns. That additional stamens and carpels in certain genera are secondarily superimposed in nonspiral arrangements on the originally trimerous plan during development has led to the view that their elaboration is phylogenetically secondary, not primitive. (See Leins & Stadler; Sattler & Singh; Singh & Sattler, 1972, 1973, 1977.)

Pichon's division of the Alismataceae *sensu lato* into two tribes and 10 subtribes on the basis of floral characters was not supported by Argue (1976), who found that pollen morphology, in correlation with base chromosome numbers and other characters, points to very different (informal) generic groups.

Punt & Reumer in turn objected to Argue's categories, leaving the matter of infrafamilial subdivisions unsettled.

Leaves are highly variable in the Alismataceae, with their form often plastic in response to water depth and such factors as light intensity and stored food reserves. Submersed (and juvenile) leaves tend to be linear, those borne out of water to have variably expanded blades, and floating leaves to be intermediate. The parts of this range expressed in different taxa are not constant: leaf shape appears to be more or less genetically fixed in connection with habitat in some taxa while varying with environment in others. Heterophylly is discussed further under the individual genera.

Although often described as being of the Scilla-type, development of the megagametophyte in the Alismataceae differs from that of *Scilla* and might better be described as a variant of the Allium-type (see Maheshwari, 1950, p. 98; 1964, p. 89). The megagametophyte is bisporic and is derived from the lower dyad cell, which divides into two chalazal and two micropylar nuclei, the micropylar nuclei each dividing again to yield typically a six-nucleate sac. One or both chalazal nuclei occasionally divide, resulting in megagametophytes with seven or eight nuclei, although suppression of an early division in some cases limits the number of nuclei to five.

Early development of the embryo is of the Caryophyllad-type (as defined by Johansen), the basal cell of the two-celled proembryo enlarging and usually remaining undivided (but see Swamy for a deviating report). Endosperm development of the helobial type is usual; nuclear endosperm has been reported in extraregional genera and repeatedly in species of *Alisma* (Dahlgren, 1928; Frey; Johri, 1936; Pogan, 1965); however, Hasitschka-Jenschke's description of a basal cell in the endosperm of *A. lanceolatum* indicates presence of the helobial type in this genus also. Endosperm is absent from mature seeds. (For embryological details see also Cook, Davis, Dahlgren & Clifford, and Johri.)

Fruits of most Alismataceae, including those in the Southeastern United States, are achenes adapted for aquatic dispersal. Buoyancy is provided by spongy tissue (well developed in *Alisma*) in the pericarp, space between the seed and pericarp (FIGURE 1, i), and resin ducts or "glands" on the lateral faces in *Sagittaria* and *Echinodorus* (and probably by inconspicuous deposits of resin in pericarps of *Alisma*). The surface of the pericarp is (at least when young) resistant to wetting (Arber, 1920; Buchenau, 1903). Flotation for several months has been observed in *Alisma, Echinodorus,* and *Sagittaria,* and maintenance of viability in wet seeds for over a year has been reported for species of *Alisma* and *Sagittaria.* Persistent styles, lateral ribs (*Sagittaria, Echinodorus*), and elaborate protuberances from margins and ribs (some sagittarias) may enhance flotation and/or help the achenes cling to aquatic birds and mammals. That alismataceous achenes are ingested by ducks has often been observed; enhancement of germination by passage through an avian digestive tract has been shown in *Alisma.* The pronounced marginal wing on achenes of species of *Sagittaria* suggests dispersal by wind and probably promotes flotation.

As shown for *Alisma Plantago-aquatica* L. (see particularly Crocker & Davis) but observed in our other genera as well, germination is delayed by mechanical restraint from the seed coat. When this is broken, the radicle penetrates the pericarp through a basal aperture or weak area, then becomes anchored to the substrate by an encircling tuft of hairs (FIGURE 1, l). Food reserves are in the hypocotyl and the cotyledon, which begins photosynthesis early, sometimes while still capped apically by the pericarp. (For further discussion of germination and establishment, see Kaul, 1978. Other references concerned with dispersal and germination of the achenes are Björkqvist, 1967 (see *Alisma*); Ewart; Glück & Kirchner; Holm; Lubbock; Schaumann; and Sculthorpe.)

The fossil history of the Alismataceae was recently reviewed by Daghlian, and the palynological record by Muller.

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### KEY TO THE GENERA OF ALISMATACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Aquatic or palustrine herbs with short, fleshy, erect or horizontal stems sheathed in the bases of usually petiolate leaves, bearing laticifers in most organs; scapes with bracts in apparent verticils of 3, these subtending pedicels or branches; flowers actinomorphic, usually pedicellate, hypogynous, generally with separate parts; perianth of 3 green sepals and 3 usually white, delicate petals; pollen grains polyporate; gynoecium of usually numerous, free carpels, each with an adaxial or terminal style and 1 adaxial-basal ovule; achenes each with a seed bearing a horseshoe-shaped embryo but no endosperm.*

A. Carpels in flat ring; stamens 6; lateral faces of achenes smooth (notched abaxially), without ribs or glands; inflorescences highly branched, paniculate. ...... 1. *Alisma.*

A. Carpels usually on rounded receptacle, not in ring; stamens usually more than 6; lateral faces of achenes usually with 1 or more ribs and/or glands; inflorescences usually either unbranched or branched only at lowest node(s) (*Echinodorus Berteroi* sometimes with panicles as in *Alisma*).

  B. Flowers perfect; inflorescences (usually) with more than 3 flowers per node or umbelliform. .............................................. 2. *Echinodorus.*

  B. Flowers mostly imperfect; inflorescences (usually) with only 3 flowers per node. ........................................................ 3. *Sagittaria.*

1. **Alisma** Linnaeus, Sp. Pl. **1:** 342. 1753; Gen. Pl. ed. 5. 160. 1754.

Perennial (or sometimes annual?), glabrous (or nearly so), usually emergent, sometimes submersed [or terrestrial] herbs with rosettes and scapes arising apically from upright, fleshy, bulb-shaped stems, these sometimes forming a series by growth of axillary buds. Leaves highly variable in shape and size, earliest leaves linear, later leaves [sometimes remaining submersed and linear], sometimes floating, then narrow-lanceolate [to linear], blade of emergent or terrestrial leaves elliptic, lanceolate, or ovate, obtuse to acuminate, often cuspidate at the apex, cuneate to cordate at the base, with a conspicuous midvein, the longitudinal nerves diverging from the base of the blade or from the midvein, these interconnected by fairly regularly spaced, parallel, ascending veinlets; petiole usually longer than the blade. Inflorescences 1 to several, erect [sometimes bent in *A. gramineum*], usually taller than the leaves [except on submersed plants], pyramidal, compound panicles with long peduncles and (including the long pedicels) [1 or] 2 or 3(–5) orders of branching, sometimes bearing several hundred flowers, branches and pedicels often mixed, in (pseudo-)whorls of up to 7(–10) [or more] members, with [1–]3–8(–10) nodes, each branch terminating in a flower, this often appearing as a member of an umbelliform cluster; bracts sometimes basally connate, usually subulate to lanceolate (sometimes oblong or ovate). Flowers perfect, with all parts separate (except for varied connate and adnate relationships at their bases). Sepals with hyaline margins, concave, persistent. Petals white (in *A. subcordatum* with a faint yellowish spot near the base when fresh) [to pink or purplish], persisting only 1 day, with entire or slightly wavy margins [to coarsely notched or lobed toward the apex], usually rounded, about as long as or longer than the sepals. Stamens 6, originating as 3 antepetalous pairs (but this relationship not remaining obvious), approximately as long as or longer than the carpels, anthers oblong, elliptic, [or nearly orbicular], filaments broadened toward the base, variably inserted on a ring of tissue above the receptacle, longer than the anthers; pollen grains with granulate, circular (or nearly so) pores, exine tectate, granular to spinulose. Gynoecium a ring of many nearly free carpels on a flat receptacle, these elliptic to obovate (tending to have the adaxial edges straighter than the abaxial edges), or D-shaped, not completely closed at anthesis, with nectaries at the basal adaxial edges, each with an outwardly curled style shorter than the length of the ovary [or the style straight and up to twice the length of the ovary], style inserted at or slightly below the adaxial edge of the broad summit of the ovary [sometimes inserted nearly centrally at the apex to below the middle of the adaxial side]; ovule anatropous or amphianatropous. Achenes ca. [10–]13–20[–35], flattened, obovate to elliptic, sometimes ovate, with rounded apices, the adaxial edges often straight below the remnants of the styles (when present), with 1 or 2 abaxial grooves. Seed flattened, elliptic or obovate-oblong in outline (*A. subcordatum*). LECTOTYPE SPECIES: *Alisma Plantago-aquatica* L., the only one of Linnaeus's original species not removed to other genera; see also J. K. Small, N. Am. Fl. **17:** 43. 1909. (Name ancient, adopted by Linnaeus from Dioscorides.) — WATER-PLANTAIN.

A genus of nine species (as recognized by Björkqvist, 1968) distributed nearly throughout the temperate Northern Hemisphere, extending northward slightly beyond the Arctic Circle (in the Old World), and to the south mostly above the Tropic of Cancer (with some notable transgressions in eastern Asia). *Alisma* only rarely occurs south of the equator: along eastern Africa south to Zimbabwe, in South Africa, Chile, Australia, and New Zealand. *Alisma Plantago-aquatica* accounts for most of these southern outposts, although *A. lanceolatum* With. grows in Australia and Chile. Other than in eastern Africa, these occurrences probably stem from introduction by humans, although this matter is not settled in every case, with some authors especially prone to accept *A. Plantago-aquatica* as possible native to Australia (*cf.* Aston; Björkqvist, 1967; Hultén, 1962; Samuelsson, 1932).

*Alisma triviale* Pursh and *A. gramineum* Lej. are widespread in the United States, but north and west of the range of the Generic Flora.[3] *Alisma subcordatum* Raf. (*A. Plantago-aquatica* L. var. *parviflora* (Pursh) Torrey, *A. parviflora* Pursh, *A. Plantago-aquatica* L. subsp. *subcordatum* (Raf.) Hultén) grows in every state (except Louisiana?) east of a line connecting Texas, Nebraska, and South Dakota, in southern Canada (perhaps as far west as Saskatoon), and possibly in Arizona and/or in northern Mexico. Rubtzoff reported it (as probably an introduction) in the Yosemite Valley of California.

*Alisma subcordatum* shares the northern part of its range with the similar *A. triviale.* Although Samuelsson (1933) found intermediates not to be formed between these two species despite the wide geographic overlap (his *A. Plantago-aquatica* subsp. *brevipes* (Greene) Samuels. corresponding to *A. triviale* as used here), other authors (e.g., Hellquist & Crow; Voss, 1972) have noted difficulties in distinguishing them. All of these authors (and Hendricks) included one or both in *A. Plantago-aquatica,* which (as circumscribed by Björkqvist, 1968) is native only to the Old World. That the three are distinct has been advocated by Björkqvist (1968), Fernald (1946), and Pogan (1963, 1964). *Alisma subcordatum* differs from *A. triviale* in being diploid (vs. tetraploid), and in a subtle set of characters probably largely related to the levels of ploidy: *A. subcordatum* has smaller floral parts, pollen grains, stomata, and achenes, and its styles are much shorter than the ovary (vs. about as long). (For detailed comparison see Björkqvist, 1967, 1968; Fernald, 1946; Pogan, 1964.) Not surprisingly, the two species are intersterile.

*Alisma* is distinguished by its six stamens, its usually complex, highly branched panicles, its many carpels in a flat ring, and its achenes with one or two pronounced abaxial furrows. Although in his recent revision and related studies Björkqvist (1967, 1968) thought *Alisma* to be closest to *Echinodorus, Baldellia* Parl., *Luronium* Raf., *Caldesia* Parl., and *Damasonium,* he (1968, p. 98) found these genera "clearly distinguished from each other by many different morphological characteristics" and, on the basis of crossing experiments, asserted

[3]Contrary to Hendricks's (p. 484) mention of *Alisma Plantago-aquatica* L. var. *americanum* (= *A. triviale*) in Arkansas, I have identified *Demaree 17866* (GH), a duplicate of the collection he cited, as *A. subcordatum* sensu Björkqvist.

that *Alisma* is "isolated from all other genera by absolute sterility barriers." (However, see *Echinodorus* for discussion of a possible intergeneric hybrid involving *Alisma.*) *Alisma, Caldesia,* and *Limnophyton* Miq. comprised Pichon's subtribe Alismatinae.

Except for the well-known *Alisma Plantago-aquatica,* the several species included in *Alisma* by Linnaeus and Micheli have since been removed to other genera. (Indeed, most species assigned to this genus by the authors who described them have since been placed elsewhere.) Buchenau (1903), in the first revision since that of Micheli, narrowed the generic circumscription by treating *A. Plantago-aquatica* as the sole species. His several varieties and forms of this species reflected the modern circumscription of the genus but not the trend by later botanists toward recognition of multiple species within this assemblage.

Misleading environmental plasticity within species in contrast with relatively low variation in the genus as a whole, coupled with a worldwide distribution and a paucity of type material, has contributed to a confusing lack of accord in the delimitation and nomenclature of species in the three latest revisions. In the first of these, Samuelsson (1932) examined more specimens than his predecessors, recognized six species (one new), and provided particularly useful details of distribution and floral morphology. The revision by Hendricks, who accepted only four species, contributed a unique North American emphasis. His opinions differ radically from Samuelsson's and from Björkqvist's, partly in that his specific delimitations are least correlated with geographic areas. Nomenclatural and other problems with this treatment were outlined by Voss (1958).

A detailed historical survey is available in Björkqvist's revision (1967, 1968), which is buttressed by broadly based and clearly presented anatomical-morphological studies, new experiments to evaluate environmental modification, breeding experiments, and new cytological studies. Nine species emerged as reproductively and morphologically distinct, although as Björkqvist stated, nomenclatural research on these remains incomplete.

Spontaneous hybridization between *Alisma Plantago-aquatica* and *A. lanceolatum* appears to be rare (Björkqvist, 1968; Kloos; Pogan, 1965). Some additional species can be crossed in the laboratory, but the resulting hybrids are sterile or reduced in fertility. Björkqvist detected no sterility barriers between populations of the same species.

*Alisma* has been the subject of numerous cytological studies, culminating in that by Björkqvist (1968), who reviewed and criticized the considerable previous work. His determinations of chromosome number and morphology are backed by a broad sampling of specimens from each of the species in his revision. The base number in the genus is 7, with *A. Plantago-aquatica, A. gramineum, A. Wahlenbergii* (Holmb.) Juz., *A. subcordatum,* and *A. orientale* (Samuels.) Juz. all being diploids, with $2n = 14$. *Alisma lanceolatum* ($2n = 26$, 28), *A. triviale* ($2n = 28$), and *A. rariflorum* Samuels. ($2n = 26$) are tetraploids. *Alisma canaliculatum* Braun & Bouché is hexaploid ($2n = 42$). However, these figures (as well as the observations on the chromosomal morphology below) are not consistent throughout the cytological literature, with nomenclatural, taxonomic, and technical difficulties contributing to the inconsistencies. As was already mentioned, *A. subcordatum* is not free from such problems. Björkqvist (1968) found $2n = 14$ for this species in 60 specimens. This number was also reported by Baldwin & Speese and Pogan (1963, 1964). Reports of $2n = 28$ by Björkqvist (1961, retracted in 1968), Brown, and Heiser & Whitaker appear to be based upon misidentified material.

The haploid chromosomal sets in each of the nonaneuploid species are fairly uniform: five chromosomes with median or submedian centromeres and two shorter chromosomes with subterminal centromeres. Consolidation between the two short types via reciprocal translocation in tetraploid plants is thought to account for the deficiency in number of chromosomes and the peculiar appearance of one pair in the aneuploids. (For elaboration see Björkqvist, 1968; Castro & Noronha Wagner; Erlandsson; Frey; Hendricks; Mikkola; Oleson; Pogan, 1962, 1967; Sharma; Sharma & Mukherji; Tschermak-Woess; and Wulff.)

*Alisma subcordatum* grows on wet or periodically flooded soil or in shallow water in bogs, marshes, ditches, ponds, and streams. This species usually does not grow submersed and tends to have the broader forms of leaves, with linear leaves formed only by the seedling. When grown underwater, it produces lax floating leaves with narrow blades (Rhoades). *Alisma gramineum* and *A. Wahlenbergii,* on the other hand, are adapted for growth completely submersed (the former tolerating depths to 4 m, according to Glück & Kirchner) and consequently have predominantly linear leaves. They do not form floating leaves. When these species are grown out of water, the blade is narrow and tapered at both ends. (For additional information on heterophylly in *Alisma,* consult Arber, 1920; Björkqvist, 1967; Glück, 1905; Glück & Kirchner; and Sculthorpe.)

*Alisma gramineum* (sometimes) and *A. Wahlenbergii* (characteristically) flower and set fruit underwater; the flowers of both have been described as cleistogamous or not opening underwater (Björkqvist, 1968; Wendt).

The most common floral visitors to species of *Alisma* at some European and North American localities have been a variety of dipterans and short-tongued bees. Daumann (1964, 1965; see also Glück & Kirchner, p. 607) found the pollen to be less cohesive than usual for entomophilous plants and demonstrated transfer of pollen by wind. Absence of agamospermy was shown by Björkqvist (1968), who also found every species to be self compatible, a condition of interest in connection with the several disjunct stations for some species.

Since *Alisma gramineum* is particularly well suited to submerged growth, it is useful as an aquarium plant (see Stodola, Wendt). Other species are nuisances as weeds in rice and wild rice (*Zizania*) fields and in drainage ditches (Meeklah & Darwin; Ransom & Oelke; Samuelsson, 1932; Sculthorpe, p. 457). Members of the genus are used only rarely as food (Rickett, Wood *et al.*), probably because of noxious and bioactive compounds in the plants. Several reports indicate toxicity to humans and other mammals, including irritation to human skin (Mitchell & Rook, Wood *et al.*). By far the greatest economic significance of *Alisma* is in medicine, with a history extending from modern pharmacology back to A.D. 200 in China. *Alisma* species (probably mainly *A. orientale*) are cultivated in eastern Asia chiefly for the rhizome, which is sometimes sold sliced or powdered to be used alone or mixed with other drugs. The sundry properties attributed to "*Alismatis Rhizoma*," too many to list here, are enumerated in Perry, Stuart, and other references.

Most of the pharmacological study concerning *Alisma* involves the ability of the crude drug or compounds isolated from it to diminish concentrations of cholesterol (while altering the balance of other lipids) in the liver and blood of laboratory animals fed certain diets (Imai *et al.*; Kobayashi; Murata *et al.*, 1970a). The lipotropic agent choline was detected by Kobayashi (1960a), but most work has been centered on a group of triterpenes (alisols) that reportedly have diuretic and antiinflammatory activity in rats (Murata *et al.*, 1970a) beyond their effects on metabolism of lipids. Isolation and determination of structures of the alisols have been pursued by Murata and collaborators (see also Kamiya *et al.*). Imai *et al.* refined observations on the hypocholesterolemic activity of alisols (particularly one), compared their efficacies (see also Murata *et al.*, 1970a), discussed the relationship between structures and activities, and mentioned that the alisol they studied most seemed to interfere with the absorption of cholesterol by the intestine.

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2. **Echinodorus** Engelmann in Gray, Man. Bot. 460. 1848.

Annual or perennial, submersed or emergent aquatic herbs, glabrous [or with sparse, single, stellate, or tufted hairs on stems, leaves, petioles, axes of the inflorescence, calyces, and bracts]. Leaves sometimes polymorphic (in our area true of *E. tenellus* and especially *E. Berteroi*), submersed leaves tending to be ribbonlike and emersed leaves petiolate, the blade highly variable, linear to elliptic, lanceolate, deltoid, or cordiform, [retuse or] rounded to long-acuminate at the apex, cuneate to cordate at the base, often with translucent markings,

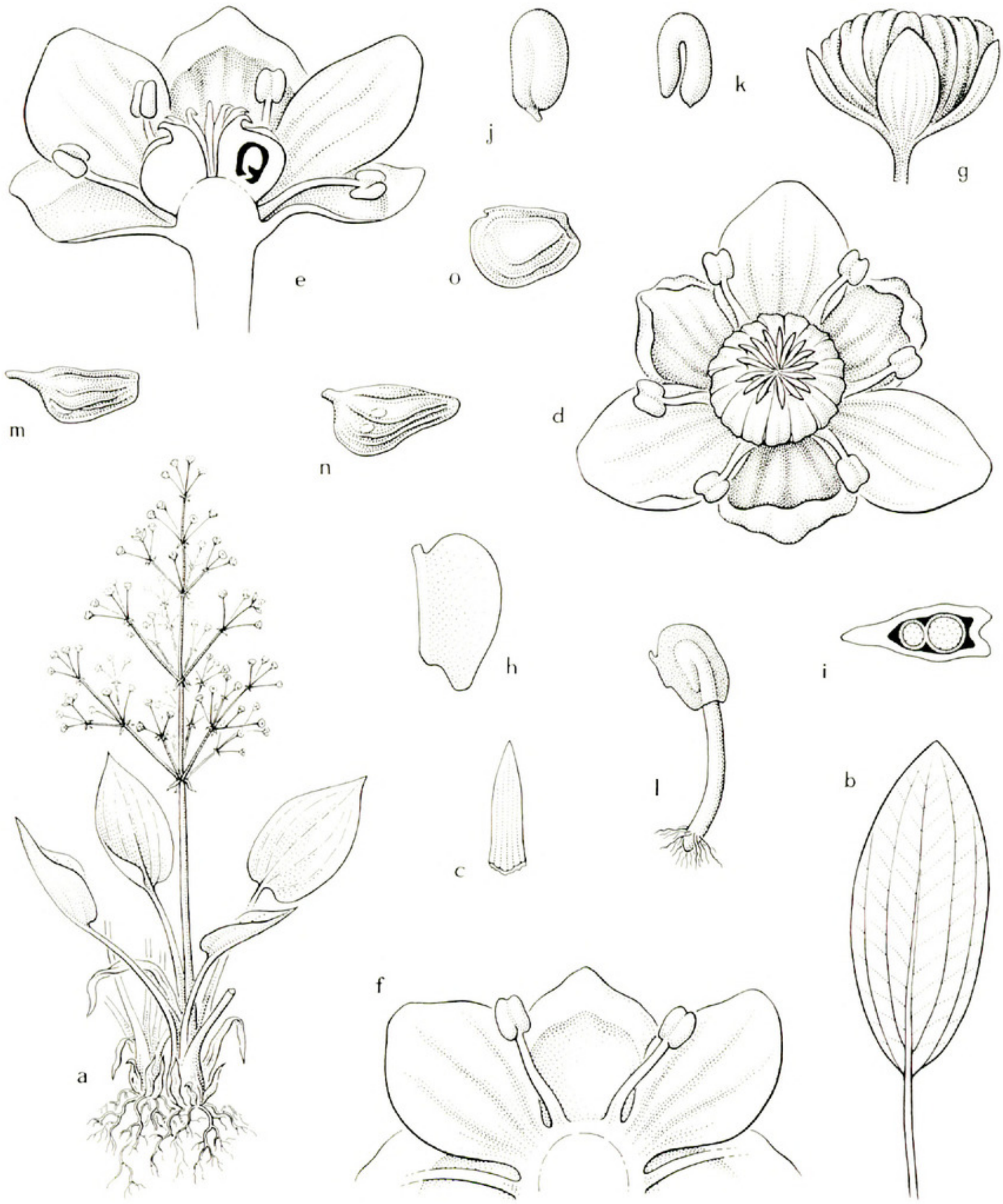


FIGURE 1. **Alisma** and **Echinodorus.** a–l, *A. subcordatum:* a, small plant with fruits, note base of second plant of axillary origin, × ¼; b, leaf blade, × ¾; c, bract from lower whorl of main axis of scape, × 1; d, flower, showing separate carpels in a ring, × 10; e, flower in vertical section slightly off center, carpel opened to show the single ovule, × 15; f, stamens, petals, and sepals from above, × 12; g, cluster of achenes enclosed by persistent sepals, × 10; h, achene, remnant of style at upper left, × 10; i, diagrammatic transverse section of achene cut near the middle, adaxial edge at left, pericarp unshaded, the 2 arms of the bent embryo at center (stippled) surrounded by thin seed coat, endosperm absent, × 15; j, seed, showing embryo beneath thin seed coat, endosperm absent, × 10; k, embryo, × 10; l, seedling emerging from achene, ring of anchoring root hairs at base of hypocotyl, × 6. m–o, achenes of *Echinodorus:* m, *E. Berteroi,* with pointed resin gland near apex, × 6; n, *E. cordifolius,* resin glands on side, × 6; o, *E. tenellus* var. *parvulus,* without resin glands, × 12.

lateral nerves usually originating from the base of the blade (sometimes from the midvein), extending to the apex or margin, interconnected by usually parallel and conspicuous veinlets (in some narrow leaves the veinlets arising pinnately from the midvein and extending to or nearly to the margin, or veinlets sometimes inconspicuous or absent). Scapes single or clustered, erect to prostrate, generally longer than the leaves, racemose, paniculate, or umbelliform, bearing at the nodes (pseudo-)whorls of sometimes basally connate, subulate to ovate [or oval] bracts, these subtending a variable number of pedicels and/or branches, often enclosing a cluster of smaller inner scales. Flowers perfect. Sepals with conspicuous longitudinal nerves, usually concave. Petals white or sometimes pink [rarely yellow], longer than the sepals, in our species rounded or emarginate at the apex; nectaries adaxial on the bases of petals and on carpels. Stamens (6–)9–30 [or more], with basifixed or versatile, latrorsely dehiscing anthers; pollen grains usually more or less spheroidal, with circular or irregularly shaped, granular pores, exine granular to spinulose (grains ovate to reniform with the exine reticulate in *E. Berteroi* fide Argue, 1976). Carpels numerous and free on a usually convex receptacle, variably elongate, each with an apical or lateral style. Fruit a usually spinose, aggregate head of beaked (beak small or absent in *E. tenellus* var. *parvulus*), ribbed [ribs rarely absent], compressed, elongate achenes, elliptic or widest above the middle, often slightly curved or roughly D-shaped, usually with 1 or more yellowish (dry) glands (absent in *E. tenellus*). Seed with a smooth or spotted integument. (Including *Helianthium* (Engelm. ex. J. D. Hooker) J. G. Smith in Britton, Manual, ed. 2. 54. 1905. Type species: *H. tenellum* (Martius) Britton = *E. tenellus* (Martius) Buch.) LECTOTYPE SPECIES: *Alisma rostratum* Nutt. = *Echinodorus Berteroi* (Sprengel) Fassett; see J. K. Small, N. Am. Fl. **17:** 46. 1909. (Name probably from Greek, *echinos,* hedgehog, and *doros,* a leather bag, in reference to the spinose achenes.) — BURHEADS.

Nearly 50 species in two subgenera and 13 sections distributed from the northern United States to Patagonia. Inasmuch as most of the species are from Central and South America and are known from meager collections (many by only one, and some only from cultivated plants), the genus as a whole remains poorly known. Over half of the species have been described within the last three decades, and more will surely be discovered with continued exploration in the neotropics. Hence generalizations about *Echinodorus*—especially those made before the efforts of Fassett and Rataj—still rest upon a superficial sampling. Three species of three sections from the two subgenera are indigenous to the United States, all of them occurring in the Southeast.

Subgenus HELIANTHIUM (Engelm. ex J. D. Hooker) Fassett (carpels 20 or fewer in a loose head, anthers basifixed) is represented by *Echinodorus tenellus* (Martius) Buch. (*Alisma tenellum* Martius, *E. parvulus* Engelm., *Helianthium parvulum* (Engelm.) Small). This member of sect. TENELLI Fassett (leaf blades linear-lanceolate to elliptic, ribs of achenes not crested, inflorescences with one or few whorls) ranges from the northern United States to southern Brazil. Fassett recognized four varieties; Rataj (1975), only two (he reduced one to synonymy with var. *tenellus* and elevated the other to the rank of species, thereby eliminating most of the West Indies from the range of *E. tenellus*). The variety in our area, *E. tenellus* var. *parvulus* (Engelm.) Fassett, treated by some recent authors as a distinct species, grows in Cuba and Mexico, and sporadically in the area defined by Texas, Kansas, Michigan (see Voss), Massachusetts (possibly extirpated in this state), and Florida (not in the Appalachians). Reports from the northern shore of Lake Superior remain questionable (see Agassiz, Parry, Scoggan, Rosendahl & Butters). These small plants are distinguished from the other two species in the Southeast by having (6–)9 (vs. 12 or more) stamens, no pellucid lines in the leaves, umbelliform inflorescences (vs. racemes or panicles), and achenes lacking glands and conspicuous beaks, and by their pseudostoloniferous habit (because of which this species sometimes forms mats).

Subgenus ECHINODORUS (carpels many in a dense head, anthers versatile) is represented in our area by two species from two sections. The sole species of sect. ECHINODORUS (sect. *Berteroii* Rataj) (strongly heterophyllous, stamens (9–)12, achenes rostrate, these with one gland or none), *Echinodorus Berteroi* (Sprengel) Fassett (*Alisma Berteroi* Sprengel, *A. rostratum* Nutt., *E. rostratus* (Nutt.) Engelm.), has often been confused with or included in our other species, *E. cordifolius* (L.) Griseb. (Hence "*E. cordifolius*" in literature before clarification by Fernald and Fassett should be interpreted with care.) *Echinodorus Berteroi* var. *Berteroi* (as circumscribed by Rataj) ($2n = 22$?; see Heiser & Whitaker) is distributed along the southern edge of the United States from mid-California to Georgia, and southward to southern Mexico; in much of the drainage of the Mississippi River in the area defined by Ohio, South Dakota, Oklahoma, and Arkansas; and throughout the West Indies. (See Fassett for discussion of doubtful reports that would broaden the range.) A disjunct variety (var. *patagonicus* Rataj) grows only in Argentina. *Echinodorus Berteroi* var. *lanceolatus* (Engelm.) Fassett (*E. cordifolius* var. *lanceolatus* Mack. & Bush) was found in Rataj's (1975) experiments to differ from var. *Berteroi* merely as a result of environment and was accordingly reduced to synonymy. This highly variable species produces at least three distinct forms of leaves and sometimes occurs as dwarf individuals only a fraction of the usual size.

*Echinodorus Berteroi* differs from *E. cordifolius* by having upright, often compound inflorescences; sepals with smooth (vs. papillose) abaxial nerves; glands (when present) extending farther toward the apex of the achene; and usually 12 (vs. over 20) stamens.

One of eight species of sect. CORDIFOLII Rataj (stamens 24–30, leaves with nonreticulate pellucid lines or spots), *Echinodorus cordifolius* (*A. cordifolia* L., *S. radicans* Nutt., *E. radicans* (Nutt.) Engelm.), $2n = 22$, is distributed along the Coastal Plain from southern Texas (and according to some reports in Mexico) to the vicinity of Washington, D. C., and in the drainage of the Mississippi River to mid-Tennessee in the east, extending westward to Kansas and Oklahoma and ranging north to central Illinois. Rataj (1975) reported this species in Venezuela. *Echinodorus cordifolius* differs conspicuously from the other two species in having young plantlets mixed with flowers at the nodes on arching or procumbent inflorescences. (Note, however, that De Wit reported that *E. Berteroi* under cultivation in deep water also forms plantlets on the inflorescence.)

Plantlets arise from vegetative buds on upright and horizontal inflorescences in several species of subg. ECHINODORUS, where such buds terminate lateral, bostrycoid, flower-bearing complexes and sometimes also occur singly in axils of bracts. In *Echinodorus tenellus, E. quadricostatus* Fassett emend. Rataj, and probably other species of subg. HELIANTHIUM, modified prostrate inflorescences on submersed individuals form only plantlets, never flower buds. These indeterminate, runnerlike pseudostolons resemble typical alismataceous inflorescences in bearing pseudowhorls of scale leaves at the nodes; on the pseudostolons the only other structure at each node is a single vegetative bud (Charlton, 1968, 1973).

Richard published the name *Echinodorus* in 1815 accompanied only by the scarcely informative "alismae polyandrae" long before Engelmann's generic description in the first edition of Gray's *Manual.* Buchenau (1868) listed 15 specific names and discussed the application of some of them. Micheli monographed *Echinodorus* in 1881 and included 17 species, about half of which have since been removed to other genera or have otherwise undergone changes in name. Buchenau contributed comments the following year, and a revision including 20 species in 1903. Fassett's treatment of the species in North America and the American tropics contains useful explanations of decisions concerning taxonomy and nomenclature. In a revision of the entire genus that followed preliminary papers, Rataj (1975; see also 1970, 1973, 1974, 1978), agreeing with Pichon and apparently with Fassett, diverged from Buchenau and Micheli by excluding all species in the Old World. Rataj's infrageneric classification corresponds closely to Fassett's, except that several species were added to both subgenera and subg. ECHINODORUS was subdivided into 11 sections.

*Echinodorus* and *Sagittaria,* both in Pichon's subtribe Sagittariinae, are more similar to each other than either is to *Alisma.* They both usually have achenes with glands or resin ducts on the faces, carpels crowded onto a dome-shaped receptacle, spherical pollen (vs. polyhedric in *Alisma*), and the diploid chromosome number of 22 (vs. multiples of $x = 7$ in *Alisma*; note, however, that the chromosome number is established for only one species of *Echinodorus*). *Echinodorus* differs from *Sagittaria* in having perfect (vs. usually imperfect or a combination of perfect and imperfect) flowers; usually plumper carpels and achenes; a stronger tendency toward bostrycoid complexes in the inflorescence (and thus more than three flowers per node); pollen grains with smaller spinules (Argue, 1976); one pair (vs. two or three pairs) of chromosomes with nearly median centromeres; and two (vs. no) pairs of chromosomes with satellites (see Baldwin & Speese; Beal, 1960). Although similar in appearance to the terminal pseudostolons produced by species of *Echinodorus,* stolons of *Sagittaria* are axillary branches.

Differences in the circumscription of *Echinodorus* complicate comparison of generalizations made about it by different authors. After the first appearance of the generic name but before the monographic works enumerated above, *Echinodorus* was usually included in *Alisma.* Baillon placed it under *Sagittaria.* Several species previously regarded as components of *Echinodorus* by one or more botanists have been the bases of other genera of Alismataceae. Among these are *Baldellia* (containing the often-mentioned *Echinodorus ranunculoides* (L.) Engelm.), *Ranalisma, Burnatia* M. Mich., *Rautanenia* Buch., *Albidella* Pichon, and *Helianthium.* Except for the last two, all are limited to the Old World. *Echinodorus* is compared with some of these genera in Argue (1976), Charlton (1973), Pichon, and Rataj (1975). Even as *Echinodorus* is circumscribed by modern authors, a troublesome heterogeneity has repeatedly been mentioned.

In 1974 Argue believed that palynological evidence substantiated the separation of *Baldellia* from *Echinodorus.* Similarly, Wodehouse thought that *Baldellia* (*Echinodorus*) *ranunculoides,* together with "*E. cordifolius*" (probably *E. Berteroi*), comprised a palynological type apart from five other species of *Echinodorus.* In a later survey involving 20 species of *Echinodorus,* Argue (1976) found that evidence from palynology "might ultimately provide some clues for its dismemberment" and assigned the pollen of *Baldellia* and *Echinodorus* to different morphological categories (acknowledging intermediacy), but he did not repeat his assertion of 1974. On the other hand, Charlton (1973) found *Baldellia ranunculoides* to show "strong similarities" to Fassett's sect. TENELLI (but not, he emphasized, subg. ECHINODORUS sensu Fassett) in having pseudostolons and a determinate, morphologically similar inflorescence. *Baldellia* differs from *Echinodorus* in its 6 (vs. usually more) stamens and tends to have more terminal styles.

Although *Ranalisma* likewise resembles species of *Echinodorus* in producing pseudostolons, those of *Ranalisma* (*humile*) differ in being sympodial (vs. monopodial) and in having bracts in pairs as opposed to pseudowhorls of three (Charlton, 1968, 1973; Charlton & Ahmed, 1973b). That the aerial inflorescences of *Ranalisma* are sympodial further separates *Ranalisma* from *Echinodorus* and from the Alismataceae in general (Charlton, 1968, 1973; Charlton & Ahmed, 1973b). Charlton & Ahmed (1973a, b) concluded that the sum of evidence from floral and vegetative structures indicates an isolated position for *Ranalisma* within the Alismataceae (*cf.* Gagnepain).

Development of secretory canals, a familial characteristic, reaches an extreme in leaves of species of *Echinodorus.* Sometimes branched, the canals may accompany veins or be free in the mesophyll. Appearing as translucent lines or spots or as a reticulum, these pellucid markings are helpful in recognizing the genus, and they vary sufficiently in shape, size, and distribution to serve as taxonomic characters for species. Elaboration on their structure and distribution can be found in Meyer's (1932) anatomical survey of leaves from several species.

All three species of *Echinodorus* in the Southeastern United States grow in permanently or periodically wet mud or sandy soil, usually in (or on the shores of) streams, ponds, temporary pools, ditches, marshes, and swamps. *Echinodorus Berteroi* tolerates "almost dry places" as well as brackish water according to Rataj (1975). Rand noted that *E. tenellus* seemed sometimes to bloom in Massachusetts while completely underwater.

Rataj (1975) indicated that hybridization occurs among several of the extraregional species and also noted alleged hybrids between *Echinodorus tenellus* var. *tenellus* and var. *parvulus.* Such hybrids were collected even in Texas and

Florida, states far from the geographic range he provided for var. *tenellus*. Certain collections suggested "introgression" between *E. Berteroi* and *E. cordifolius* to Fassett.

The intergeneric hybrid between *Echinodorus* (*Baldellia*) *ranunculoides* and *Alisma Plantago-aquatica* has been reported not entirely independently by Durand & Pittier, Glück (1913), Knobloch, and Wehrhahn. In a comprehensive comparison of supposed hybrids and parental species, Glück encountered numerous points of intermediacy, the most impressive in the anatomy of the fruit. Wehrhahn assigned the name *Alismodorus Muretii* to the plant he identified as resulting from the cross under consideration. However, after artificially pollinating over 100 flowers, Björkqvist (1968, see *Alisma*) failed to produce this hybrid and suggested alternative identifications for specimens and drawings considered by others to represent it.

Because of their attractive foliage (which is varied in color, texture, and shape), hardiness, ease of cultivation, and in some cases vegetative propagation from the inflorescence, species of *Echinodorus* are popular for cultivation in aquaria; at least 20 have been used this way, among them the three species native to the United States. Confusing disharmony between specific names applied by aquarists and those applied by taxonomists is partly alleviated in Rataj's revision. The plants are usually marketed as "Amazon swordplants" or under other names with "swordplant" a component, sometimes also as "cellophane plants" (e.g., *E. Berteroi,* with its membranaceous submersed leaves). (For information on *Echinodorus* in the aquarium see De Wit, Klee, Stodola, and Wendt.)

A phycomycete tentatively identified as *Aphanomyces euteiches* Drechsler caused severe loss of "*E. brevipedicellatus* Buch." (*E. amazonicus* Rataj?) at a nursery in Florida during 1970 and 1971. Four other species of *Echinodorus* appeared to be resistant to the disease (Ridings & Zettler).

In South America and the West Indies, species of *Echinodorus* are attributed with impressive medicinal benefits. Tea from the leaves, extract from underground parts, and other preparations have been used as an invigorating beverage, a diuretic, a laxative, and an astringent gargle. They have been used to clean and heal the skin, to "purify the blood," and to counter edema, various ailments of the kidneys and liver, and other afflictions (Corrêa, Peckolt, Penna, Roig y Mesa). As reported by Grosourdy, chopped roots (and, to a lesser extent, leaves) from *E. cordifolius* (*E. Berteroi*?) rubbed onto the skin cause blistering. "Tubers" of *E. grandiflorus* (Cham. & Schlecht.) M. Mich. are boiled and consumed by the Mataco Indians in Argentina (Steward). According to Torrey, Mohave Indians used "seeds" of *E. rostratus* (*E. Berteroi*?) as food. Brazilian species are used as a source of dye for textiles (Peckolt).

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3. **Sagittaria** Linnaeus, Sp. Pl. 993. 1753; Gen. Pl. ed. 5. 429. 1754.

Annual or (usually) perennial, often amphibious herbs. Usually glabrous (*S. latifolia* var. *pubescens* (Muhl.) J. G. Sm. and sometimes *S. guayanensis* HBK. pubescent on most organs, other species sometimes with pubescent filaments). Roots usually conspicuously septate. Most species producing one to many thin axillary stolons, these sometimes branching, sometimes forming a chain of

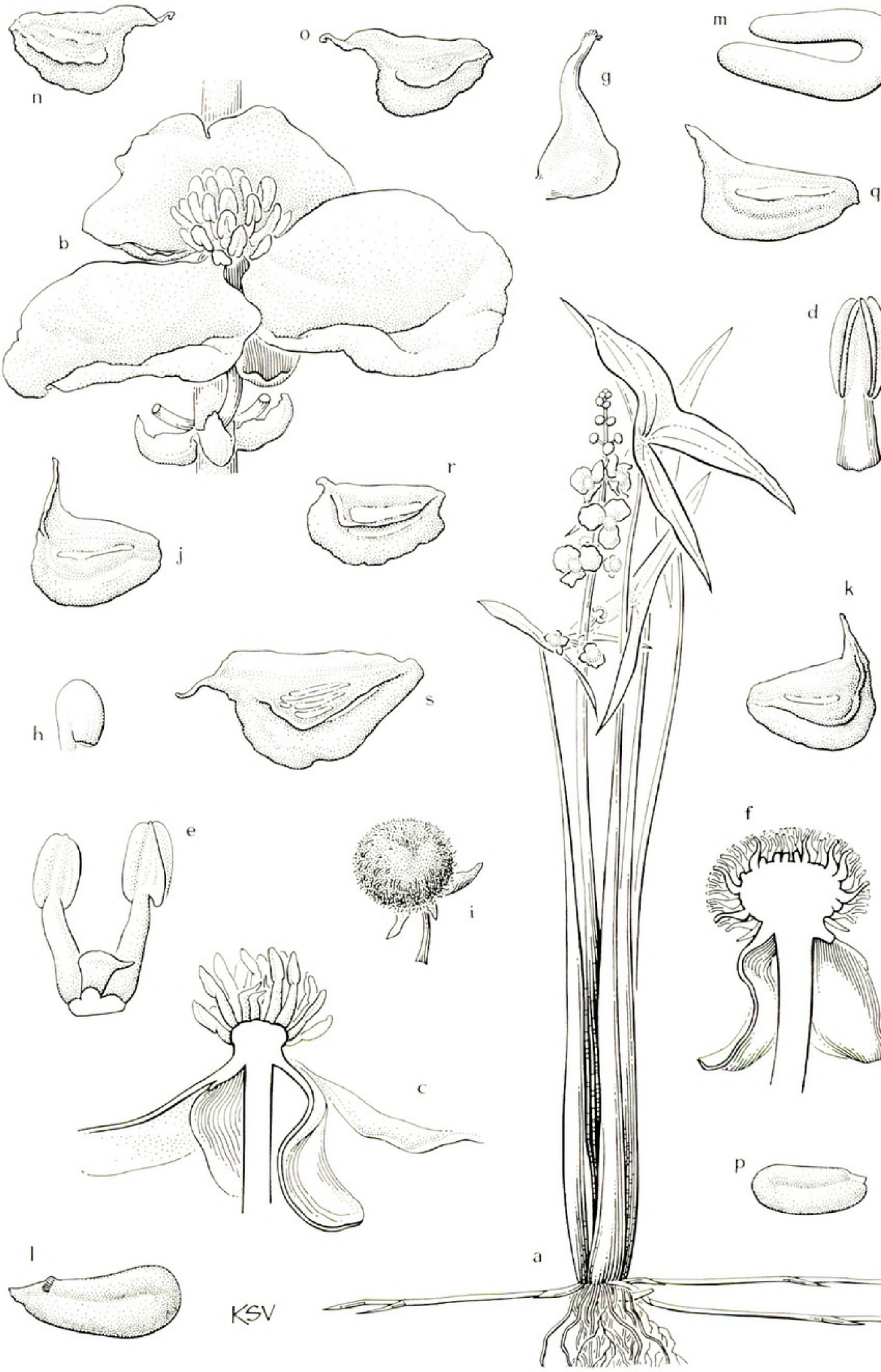


FIGURE 2. **Sagittaria.** a–m, *S. latifolia:* a, flowering plant with stolons, plant monoecious, the inflorescence with carpellate flowers below and staminate flowers above, × ¼; b, staminate flower, bracts and pedicels of 2 other flowers below, × 2; c, central

plantlets, the terminal bud often distal to an egg-shaped or subcylindrical storage organ comprised of 2 or more thickened internodes, this "tuber" sheathed in scale leaves, sometimes forming a plantlet or (in the year it was formed or after overwintering) the bud distal to the tuber growing into a new stolon, this sometimes very short and becoming vertical before terminating in a young plant. Plants usually with short upright stems sheathed (at least at the top) in leaf bases, some species with a horizontal rhizome bearing leaves along its length. Plants sometimes yielding milky sap when broken. Leaves highly variable in shape and size, submersed (then linear, flattened or terete to rarely sagittate-hastate, sometimes spongy), floating (then assuming almost the entire range of shapes, commonly elliptic or lanceolate), or growing out of water, then the blade linear to sagittate, usually acute to long-acuminate, sometimes rounded or obtuse at the apex, with a midrib and lateral nerves, these usually interconnected by more or less regular, parallel veinlets; petioles often spongy, especially at the broadened bases. Plants usually monoecious, with carpellate flowers toward the base of the scape, sometimes polygamous (then usually with staminate flowers distal to perfect flowers), sometimes dioecious. Scape(s) 1 to several per plant, erect or lax and floating, characteristically racemes, sometimes once branched at the basal node, on some small plants umbelliform or with only 1 flower, the main axis with up to 10(–18) nodes, each bearing a (pseudo-)whorl usually of 3 flowers subtended by usually basally connate, persistent or scarious, (often broadly) ovate to linear bracts. Flowers pedicellate (infrequently sessile). Petals white [rarely reddish or yellowish], sometimes with a dark spot at the base, larger than the sepals, usually with irregular margins. Nectaries on filaments, staminodes, and carpels, these sometimes modified. Staminate flowers with the sepals usually reflexed, sometimes with abortive carpels, stamens many in a dense cluster on the receptacle, the filaments tending to be dilated at or above the base, the anthers [linear or] narrowly to broadly elliptic-oblong, basifixed or dorsifixed near the base, dehiscence extrorse or latrorse. Pollen grains circular in outline, the pores often irregularly shaped, sexine usually markedly spinulose. Carpellate flowers sometimes with staminodes, the sepals appressed to reflexed, with numerous flattened carpels crowded on an expanded, rounded receptacle, the tapered styles shorter or longer than the ovaries, apical or adaxial; ovules anatropous. Perfect flowers appearing

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part of staminate flower in vertical section (note sterile carpels in center), × 3; d, abaxial side of stamen, anther dehiscing, × 6; e, adaxial side of 2 stamens and sterile carpel, × 6; f, vertical section of carpellate flower immediately after fall of petals, × 3; g, carpel from carpellate flower, × 12; h, anatropous ovule, × 25; i, fruiting "head," an aggregate of achenes, × 1; j, k, opposite sides of mature achene (note crest on side in "k," and resin duct on both sides), × 6; l, seed removed from achene, oriented as in achene in "k," × 12; m, embryo from soaked seed, oriented as in seed in "l," × 12. n–p, *S. australis:* n, o, opposite sides of achene, showing crest on both sides and lack of resin ducts, × 6; p, seed removed from achene, oriented as in achene in "o," × 12. q, *S. lancifolia:* achene with 1 resin duct, × 12. r, *S. graminea:* achene with 1 resin duct above crest and another below it, × 12. s, *S. Engelmanniana* subsp. *Engelmanniana:* achene with crest and several resin ducts, × 6.

like carpellate flowers but with stamens. Achenes usually strongly compressed, mostly obovate or dolabriform, the margins drawn more or less out into wings, the abaxial margin often broadest and often with an irregular edge (or both edges sometimes irregular), often with facial glands (resin ducts) and ribs, these frequently with irregular, even ornamented edges, the remnant of the style projecting laterally or apically from the apex or from the upper half of the adaxial edge. $x = 11$. (Including *Lophotocarpus* T. Durand.) LECTOTYPE SPECIES: *Sagittaria sagittifolia* L.; see J. K. Small, N. Am. Fl. **17:** 51. 1909. (Name from Latin *sagitta*, arrow, from the shape of some leaves, adopted by Linnaeus from earlier use.) — ARROWHEAD, WAPATO(O), DUCK-POTATO, SAGITTARIA.

Approximately 35 species, with subgenus SAGITTARIA distributed throughout the Northern Hemisphere, primarily in North America, from subarctic to subtropical and some tropical regions. The most widespread species in the New World, *S. latifolia* Willd., ranges from Canada to northern South America. *Sagittaria lancifolia* L. extends as far south as Brazil, perhaps beyond. Most species of subgenus LOPHOTOCARPUS are native to the New World between southeastern Canada and southern South America; *S. guayanensis* is pantropical. Disjunct populations of a number of species occur at great distances from their apparent natural ranges; for example, according to Aston, none of the four species in Australia is native. There are roughly 20 or more species in the United States, approximately three quarters of them in the Southeast.

Taxonomic confusion and disagreement make a definitive listing of species impossible. The enumerations below include the species within the range of the Generic Flora that were recognized by Bogin, plus others added in accordance with subsequent work. Bibliographic references and comments are provided to facilitate further efforts toward clarification and enumeration of the extensive synonymy. Only the most noteworthy synonyms are given.

Subgenus LOPHOTOCARPUS (T. Durand) Bogin (carpellate flowers with sepals appressed or spreading, pedicels recurved and thickened in fruit, flowers often perfect) is represented by *Sagittaria calycina* Engelm. (Beal, 1960), *S. guayanensis* (a weed in rice fields; Thieret, 1969), *S. montevidensis* Cham. & Schlecht. (adventive), and *S. subulata* (L.) Buch. (including or not *S. Kurziana* Glück and *S. stagnorum* Small).

Subgenus SAGITTARIA (carpellate flowers with sepals reflexed, pedicels typically ascending, or recurved but not thickened, flowers rarely perfect) is represented by *S. australis* (J. G. Sm.) Small (*S. longirostra* auct. non M. Mich.; see Beal, Hooper, & Rataj), *S. brevirostra* Mack. & Bush (Beal, Wooten, & Kaul), *S. Engelmanniana* J. G. Sm., *S. falcata* Pursh (Beal, 1960), *S. fasciculata* Beal (1960), *S. graminea* Michx., *S. lancifolia*, *S. latifolia* (*S. sagittifolia* L. var. *longirostra* M. Mich.), *S. papillosa* Buch., *S. platyphylla* (Engelm.) J. G. Sm. (Wooten, 1973b), *S. rigida* Pursh (probably in Tennessee), and *S. secundifolia* Kral. Whether or not *S. teres* S. Watson and especially *S. isoetiformis* J. G. Sm. are distinct from *S. graminea*, and whether *S. teres* ranges as far south as the Carolinas, are points of disagreement (see Beal, 1960, 1977, especially p. 60; Bogin; Godfrey & Adams; Godfrey & Wooten).

Probably only one of the three species originally assigned to *Sagittaria* by

Linnaeus, *S. sagittifolia,* belongs to the genus in its modern sense. Even though *S. trifolia* L. frequently appears in modern publications, the illustration of it that Linnaeus cited either is very inaccurate or represents a plant referable to some other genus (Bogin thought *Ranunculus*). The 13 species tentatively recognized by Micheli in 1881 reflect both a generally modern circumscription of *Sagittaria* and trouble with the long-standing question of its relationship with *Lophotocarpus.* Smith (1895, 1900), due in large part to discovery of new entities, recognized 23 species in North America alone. He differed from Micheli in not including any of the New World taxa within *S. sagittifolia,* a view upheld in all subsequent revisions. Buchenau (1903) included most of Smith's species among the 31 in *Das Pflanzenreich.* Stressing that examination of extensive materials revealed new intermediacy between previously recognized taxa, Bogin (1955) reduced the number of species to 20 (including those added by treating *Lophotocarpus* as a subgenus of *Sagittaria*). Rataj (1972a, b) counterbalanced the North American emphasis of the preceding studies by revising the species of the Old World, the West Indies, and Central and South America. With a small number of exceptions, his species and subgenera are congruent with those of Bogin.

The predominant problem concerning the delimitation of *Sagittaria* is its relationship with *Lophotocarpus* (*Lophiocarpus* Miq.), which appears as a subgenus of *Sagittaria* in recent revisions. *Lophotocarpus* has been thought to differ in being annual and polygamous (vs. without perfect flowers), in having hypogynous stamens (vs. stamens erroneously perceived as inserted above the receptacle in *Sagittaria*), and in having three (vs. two) pairs of chromosomes with nearly median centromeres (see Smith, 1895, 1900; Baldwin & Speese; and the other papers cited in this paragraph). Mason, who provided a taxonomic history of *Lophotocarpus,* argued that some distinctions have been inaccurately and unclearly described, that they are of insufficient character to allow unambiguous identifications, that conditions ascribed to one genus appear in the other, and that at least one species assigned to *Sagittaria* based on some of these characters is obviously closer to *Lophotocarpus* in other regards. Beal (1960) doubted the significance of the cytological difference (which was indeed based on only one species of *Lophotocarpus*). Evidence from floral vasculature and development and from palynology reinforce merging the genera (Argue, 1976; Kaul, 1967). After Pichon advocated synonymy, Bogin broadened the circumscription of *Lophotocarpus* and reduced it to a subgenus of *Sagittaria,* emphasizing the nature of the sepals and pedicels rather than the presence of perfect flowers. (Other distinguishing features of *Sagittaria* are presented in its comparison with the similar *Echinodorus* in the treatment of that genus.)

Bogin treated problematical complexes as species composed of infraspecific taxa. The largest, centered around *Sagittaria graminea,* has been studied by Wooten (1970; 1971a, b; 1973a, b). Drawing data from transplant experiments, experiments to assess environmental plasticity, chromatography, and analysis of edaphic factors, she established three varieties within this species, and with emphasis on edaphic considerations, observations in the field, and crossing studies, she recognized several additional species. (Note that *S. secundifolia* subsequently described by Kral also appears to be closely related to this assemblage.) Adams and Godfrey, employing observations on living populations and transplant experiments, did not think taxonomic recognition of any of the components of the *S. subulata* complex to be justified but advocated further studies of which Houk undertook one. (Later, Godfrey & Wooten recognized *S. stagnorum* and *S. Kurziana* as species distinct from *S. subulata.*) Crossing experiments, analysis of ecological parameters, and morphological observations contributed to the decision by Beal, Wooten, & Kaul to elevate Bogin's subspecies of the "*S. Engelmanniana* complex" to species.

Hybridization occurs, but to an as yet inadequately investigated degree. The plasticity of the plants and related taxonomic confusion make recognition of hybrids difficult. Crossing experiments have shown *Sagittaria graminea* to be interfertile with four other species (Wooten, 1973b), with other possibilities suspected (see Bogin). On the other hand, Beal *et al.* (1982) tried and failed to demonstrate interfertility among *S. australis, S. brevirostra, S. cuneata* Sheldon, *S. Engelmanniana,* and *S. latifolia.*

If a small number of possibly incorrect deviating reports are disregarded, *Sagittaria* appears to have the uniform chromosome number $2n = 22$ (Baldwin & Speese; Beal, 1960; Bloom; Bogin; Brown, 1946; Larsen; Löve & Löve; Oleson; Sharma). The only indication of polyploidy is the ca. 44 count by Bogin for *S. subulata* var. *gracillima* (S. Watson) J. G. Sm. Species of subg. SAGITTARIA have one long pair of chromosomes with nearly median centromeres, nine pairs of intermediate length with subterminal centromeres, and one short pair with submedian centromeres (Brown, 1946; Baldwin & Speese; but see Oleson for a somewhat different report).

Sagittarias grow in diverse aquatic habitats, commonly in shallow water or on wet banks in or bordering on streams, ponds, swamps, marshes, and ditches, sometimes in tidal areas, sometimes constantly submersed, and sometimes on sites that dry periodically. The degrees of submersion or drying tolerated by different species vary widely and are closely related to the diversity of their foliage.

The alismataceous propensities for submersed and juvenile leaves to be straplike phyllodia and for aerial leaves to have expanded blades reach extremes in *Sagittaria. Sagittaria* (*subulata* var.) *Kurziana* grows underwater and has linear leaves, these reportedly sometimes exceeding 3 m in length (said by one collector to be as long as 50 ft). At the other extreme (according to Bogin), *S. longiloba* Engelm. ex Torrey invariably forms emergent, sagittate leaves. Foliar variation in several species, among them *S. latifolia* and *S. sagittifolia,* spans most of the range in the genus. The relative roles of ecological and genetic control vary among the taxa, a matter in need of continued investigation. Within the *Sagittaria graminea* complex, Wooten (1970) demonstrated that differences in the forms of emergent leaves and phyllodia between seven populations (of three varieties and four ecotypes) are attributable more to genetic differences than to adjustment to depth of water. Generalization of Houk's similar conclusion from transplant experiments on "genecodemes" in the *S. subulata* complex must be tempered by observations made by Adams & Godfrey on populations of this complex. They showed great diversity in the forms of phyllodes at certain localities (in some populations ranging between linear and sagittate), with the shapes obviously related to the water regime and even changing from year to year. (Supplementary references dealing with foliar variation in *Sagittaria* are Arber, 1920; Glück, 1905; Glück & Kirchner; Hroudová; Schanderl; and Sculthorpe.)

Although usually described as monoecious, plants of subg. SAGITTARIA are at times entirely staminate or carpellate and often bear perfect flowers. In *Sagittaria latifolia,* staminate and carpellate flowers are of variable proportions in individual inflorescences, but of nearly equal overall frequency (Schaffner, 1924, 1929). After observing cultivated plants and wild populations, Wooten (1971b) concluded that whether the flowers are staminate or carpellate in this species was not affected by environmental fluctuations to which plants were subjected, and is therefore under genetic control; that monoecious plants are self fertile; that germination of achenes from dioecious plants is especially inhibited; that reproduction in dioecious populations (which sometimes form "unisexual" stands) may be mostly asexual; and that dioecious populations generally seem to be distributed along major rivers, which could convey their propagules. In *S. brevirostra,* Kaul (1979) found a ratio of more than three staminate flowers per carpellate flower to remain fairly constant over a decade in one lake, despite changes in environmental conditions.

In Europe and North America, floral visitation by an array of insects—mostly various flies and short-tongued bees—has been observed (Glück & Kirchner, Lovell, Robertson, Turner). In *Sagittaria subulata* completely submersed carpellate flowers possibly produce achenes (Adams & Godfrey).

Winged, sometimes ornamented achenes (as discussed under the family) are not the only disseminules: dispersal is also linked to asexual reproduction. In extensive, probably highly clonal stands large numbers of plants are sometimes connected by stolons (e.g., in the *S. subulata* complex). Flotation of tubers, rhizomes, and entire plants with buds at the base (described by Lohammar) surely brings about effective relocation. Moreover, as in species of *Echinodorus,* plantlets form at nodes within inflorescences of *S. subulata* (Adams & Godfrey; Buchenau, 1903).

Multiple proembryos in an embryo sac of *Sagittaria graminea* were interpreted by Johri (1936) probably to have resulted from fertilization of synergids by a second pollen tube.

A number of species of *Sagittaria* are cultivated as ornamentals. Doubled forms have been designated *S. japonica* Hort. (Porterfield, W. Smith). Several species (including *S. subulata*) producing attractive band-shaped leaves when submersed are grown in aquaria, sometimes under the name *S. natans* (see especially Wendt). Some serve as green manure (and as bothersome weeds) in rice fields, and as oxygenators in ponds where fish are raised.

Preparations involving sagittarias have been attributed with diverse medicinal benefits, primarily in eastern Asia, but also by North and South American Indians and others. Most commonly mentioned are applications to soothe and cleanse afflictions of the skin. In this connection it is noteworthy that Sharma and colleagues (1975b), during screening of Indian plants over a wide range of biological activities, observed antiinflammatory activity in an extract from *S. sagittifolia* from which they isolated a new diterpene, sagittariol. Conversely, contact with tubers or extracts from some species has caused dermatitis in humans (Mitchell & Rook, Morton).

Throughout most of its range *Sagittaria* is a source of food. Tubers of several species, produced abundantly toward the end of the growing season, are commonly compared to and prepared like potatoes. Baked, boiled, fried, ground into flour, or cooked in more elaborate fashion, the tubers are highly esteemed, but when raw they are acrid and likely to be toxic (Pammel, Stuart). *Sagittaria* is cultivated and the tubers marketed in eastern Asia, and it is sold among Chinese foods in the United States. American Indians, who acquired caches from the homes of muskrats and beavers, candied *Sagittaria* tubers with maple sugar or dried them for long-term storage. Not surprisingly, it has been suggested that human activity has historically played a role in the distribution of *Sagittaria*. (The tubers presumably were transported by ancient peoples, and the achenes from sagittarias growing as weeds probably contaminated rice.) The tubers remain popular among modern enthusiasts for edible wild plants. (Selected extra references concerned with *Sagittaria* as a source of remedies and nourishment are Fernald & Kinsey; Gibbons; Harrington; Peckolt; Perry; Porterfield; Smith, 1932, 1933; and Winton & Winton.)

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