Alismataceae

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Alismataceae Ventenat, Tabl. Règne Vég. 2: 157 (1799), nom. cons.

Monoecious, polygamous, or dioecious annual or perennial *herbs* with milky juice, glabrous to stellate pubescent, with floating leaves or emergent, in fresh or brackish waters. Roots fibrous, septate or aseptate, at base of stem or lower nodes. Stems short, erect, cormlike, often with rhizomes, the rhizomes occasionally terminated by tubers, the apices without turions. *Leaves* basal, sessile, or petiolate; petioles terete to triangular, with sheathing base, the sheath without auricles; blade linear, lanceolate, ovate to rhomboid, with or without pellucid dots or lines, the margins entire or undulate, the apex obtuse, acute, or acuminate, the base either without basal lobes and attenuate, or otherwise truncate, cordate, sagittate, or hastate, with parallel primary veins and reticulate secondary veins. *Inflorescences* scapose, mostly erect, rarely floating, forming racemes or panicles by verticillate branching, rarely umbellate, without a subtending spathe, bracteate, the bracts whorled, linear, entire, obtuse to acute. *Flowers* hypogynous, perfect or imperfect, subsessile to long-pedicellate; perianth actinomorphic, of 6 separate segments in 2 whorls, the outer 3 sepal-like, green, persistent, erect, and enclosing flower and fruit or spreading to reflexed, the inner 3 petal-like, delicate, caducous; stamens free, 6, 9, or numerous; if 6, then in pairs alternating with the petals; if 9, then in 2 whorls with outer whorl of 6 and inner whorl of 3; if many, densely but irregularly spaced; anthers tetrasporangiate, extrorse, basifixed or versatile, dehiscing by longitudinal slits; carpels 6-many, free, in 1 whorl or irregularly spaced, each with 1(–2) anatropous basal ovules, rarely (*Damasonium*) 2-many on marginal placentae; styluli terminal or lateral; stigma linear. *Fruits* achenes or rarely follicles, mostly numerous. Seeds 1-few, U-shaped; endosperm absent in mature seeds.

A family of 12 genera and ca. 80 species of subcosmopolitan distribution.

VEGETATIVE MORPHOLOGY. The Alismataceae are all marsh plants or aquatic herbs with erect or floating leaves and grow as helophytes or hydrophytes in fresh water. The plants may be terrestrial with the axis buried in water-logged swamp or marsh soils (Figs. 2,3).

The nonchlorophyllous axes are short and erect (corms) or prolonged (rhizomes) and sometimes creeping and elongate (stolons). They are often covered by the remains of vascular bundles from withered petioles. The roots are branched and rarely develop distal tubers. Stem branching is sympodial. The sympodium continues from the axil of the last leaf of the rosette, or the terminal inflorescence or side buds are sometimes modified into pseudostolons.

The leaves are distichous, spirodistichous, or spirally arranged, normally in basal leaf rosettes. The leaves are usually long-petiolate and emergent with a broad lanceolate to cordate or hastate blade, but linear or ribbonlike submerged leaves occur. The blades are mostly erect, but floating blades occur, e.g., in *Luronium* and *Echinodorus*. The petioles are sheathing and triangular or terete. The few primary veins are convergent, and a closed reticulum is formed by the secondary and tertiary veins. The terminal inflorescence arises from a bifurcation of the vegetative meristem. The inflorescences are always emergent, erect panicles, with rather distant whorls of sometimes long-pedicellate flowers; the panicles are often reduced to spikes, pseudospikes, or even umbel-like inflorescences. Squamules are present as a palisadelike series of scales (Tomlinson 1982).

Starch is commonly found in the rhizome and along larger vascular bundles in the petiole.

VEGETATIVE ANATOMY. The anatomy of all 11 genera has been studied by several authors and summarized by Tomlinson (1982). Hairs are generally absent, but simple unicellular hairs, hair bases, or stellate hairs are found in a few species of *Echinodorus*, *Sagittaria*, and *Limnophyton*. The epidermis of submerged leaves is often chlorophyllous, and paracytic stomata are common on the leaf surfaces. Hydropoten are frequent on submerged or floating leaves. The roots, stems, and petioles are extensively aerenchymatous, and the air spaces are traversed by well-developed transverse diaphragms, which are absent in *Echinodorus* and *Alisma*. Secretory ducts (laticifers) containing a milky juice are common in the leaf and stem, but tanniniferous deposits are rare. Crystals are frequent in the leaf mesophyll. The vascular bundles of the peduncle and petioles include a well-developed protoxylem lacuna, with a U-shaped arrangement of metaxylem. Vessels are restricted to the roots, where they occur as single central strands, mostly with simple perforations.

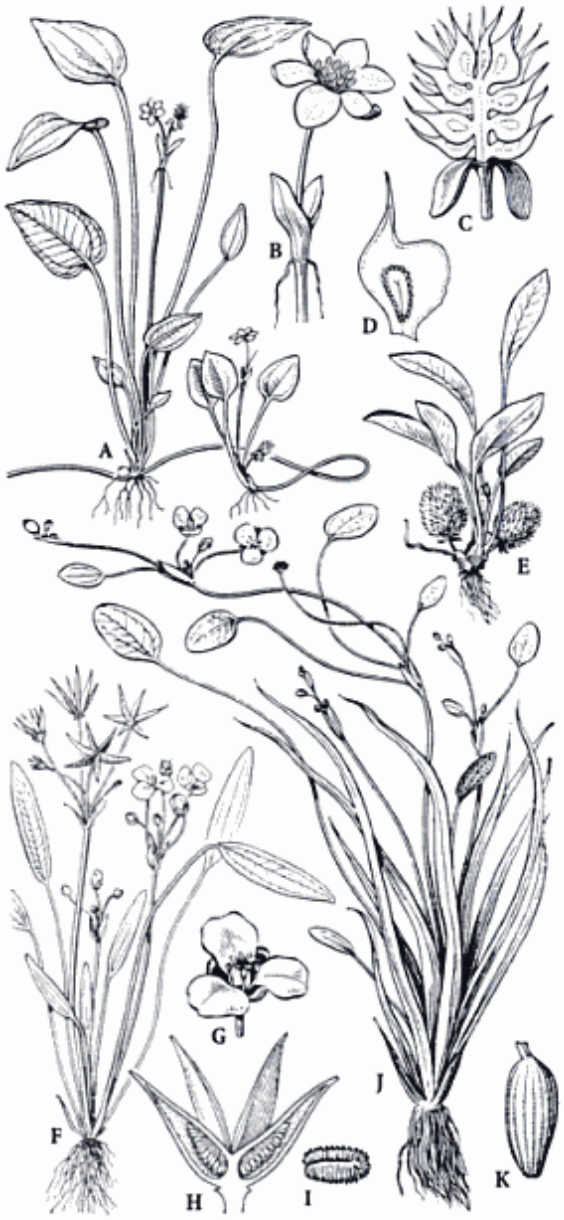

Fig. 2A–K. Alismataceae. **A–D** *Ranalisma rostratum*. **A** Habit. **B** One-flowered pseudo-umbel. **C** Fruit in longitudinal section. **D** Achene, longitudinal section. **E** *R. humile*, habit. **F–I** *Damasonium polyspermum*. **F** Habit. **G** Flower. **H** Follicles, two of which in longitudinal section. **I** Seed. **J, K** *Luronium natans*. **J** Habit. **K** Achene. (Takhtajan 1982)

INFLORESCENCE STRUCTURE. The inflorescences are either paniculate with 1-several branches or

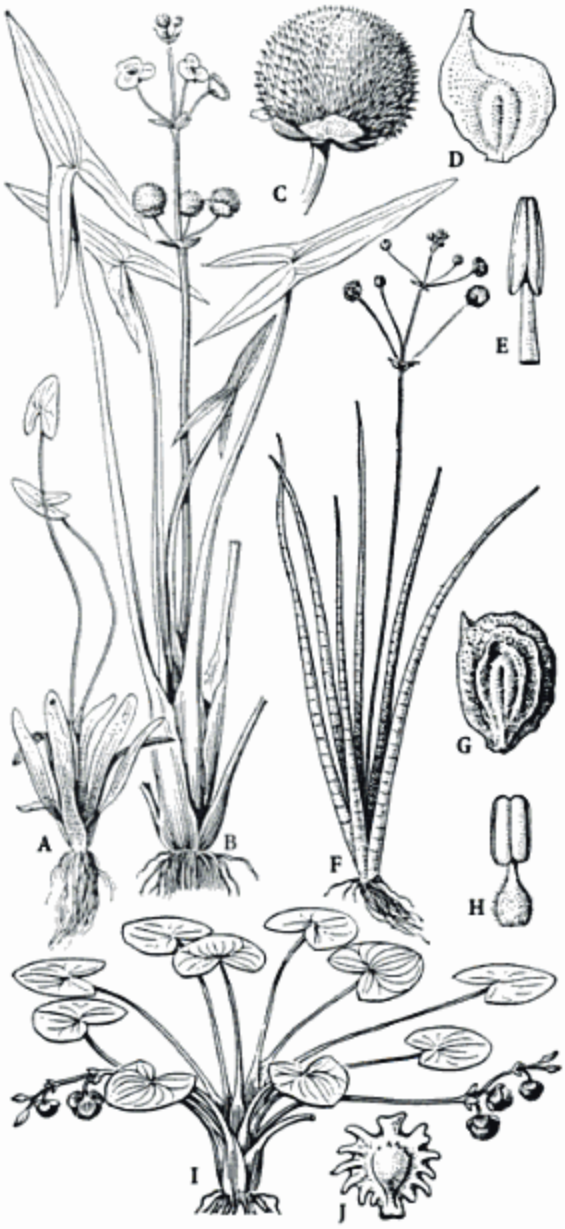

Fig. 3A–K. Alismataceae. **A–E** *Sagittaria sagittifolia*. **A** Plant with submersed and floating leaves. **B** Plant with aerial leaves. **C** Fruiting aggregate. **D** Achene. **E** Stamen. **F–H** *S. teres*. **F** Habit. **G** Achene. **H** Stamen **I, J** *S. guayanensis*. **I** Habit. **J** Achene. (Takhtajan 1982)

spicate and have a low basal internode and 1 or more successive pseudowhorls. The pseudowhorls are separated by further long internodes and normally have 3 bracts subtending on either side branches or flowers. The meristems of the inflorescences are often (under water stress) changed into vegetative meristems, producing richly proliferating, occasionally even stoloniferous, pseudoinflorescences. *Ranalisma* has a sympodial inflorescence type (Charlton and Ahmed 1973).

Floral Structure. The flowers are perfect, or imperfect by abortion of either stamens or carpels in *Sagittaria*, *Limnophyton*, and *Burnatia*. Plants of these latter genera are either monoecious (*Sagittaria*), polygamous (*Limnophyton*, *Sagittaria*), or dioecious (*Burnatia*). The pedicel often expands into a receptacle. The flowers are trimerous with 2 alternate perianth whorls differentiated into sepals and petals. The petals are delicate, white, pink, or purple. In *Burnatia* the petals are reduced or absent.

The androecium has 3, 6, or many stamens. The gynoecium consists of free carpels and is, in general, connate basally. The carpels are often laterally compressed, with short styluli, and the stigmas are apical or slightly decurrent and of the Dry type. Nectar secretion occurs from the base of petals, stamens, and carpels.

The development of multistaminate and multicarpellate flowers is based on a strictly trimerous pattern, with the lateral and centrifugal apposition of additional stamen and carpel primordia; there is no spiral sequence (Singh and Sattler 1972, 1973).

Embryology. Anther wall formation is of the monocotyledonous type. The endothecial thickenings are of the Girdle type, the tapetal cells of the Plasmodial and Amoeboid type and uninucleate. Microsporogenesis is successive and the pollen grains are 3-celled when shed. The archespore cells function directly as megaspore mother cells, and the nucellar epidermis becomes irregularly 2-layered through periclinal divisions of its apical cells (Davis 1966).

The embryo sac is of the Allium type. In *Alisma*, *Damasonium*, and *Luronium* endosperm formation is Nuclear; in *Echinodorus*, *Limnophyton*, and *Sagittaria*, however, Helobial endosperm formation occurs (Johri et al. 1992). The latter may represent the plesiomorphic state. The formation of the strongly curved embryo follows the Caryophyllad type.

The ripe seeds are curved and exalbuminous and have horseshoe-shaped embryos that lack chlorophyll.

Pollen Morphology. The pollen grains are globose to polyhedral and polyforaminate with 9–29 apertures (Fig. 4). Two minor types can be distinguished according to sculpture and shape; their

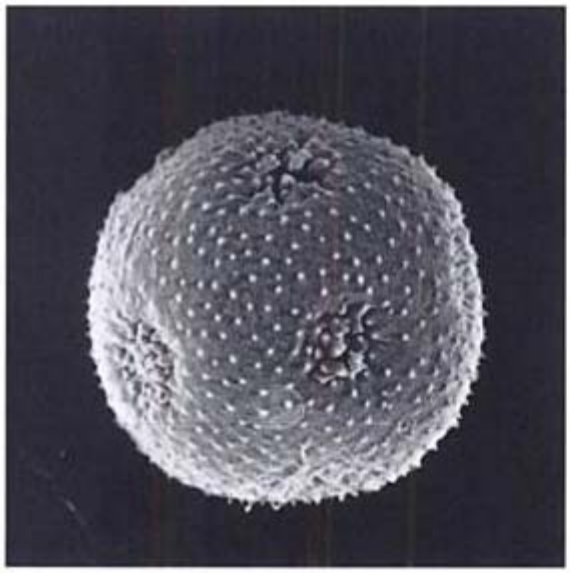

Fig. 4. Alismataceae. *Caldesia parnassifolia*, polyforate spinulose pollen, SEM ×2700. (Palynological Laboratory, Stockholm)

distribution correlates with other traits, as demonstrated by Argue (1976) (see section Subdivisions and Relationships; below). The pollen of 2 out of the 4 species of *Caldesia* is quite aberrant in being lense-shaped and (0–)2(–3) porate.

KARYOLOGY. Base numbers of x = 5–13 have been reported, with 7, 8, and 11 as the most common (Fedorov 1969). See also section Subdivisions and Relationships, below.

POLLINATION. Nectar secretion occurs at the bases of the floral organs, particularly of the staminodes in the pistillate flowers. In *Alisma plantago-aquatica* Daumann (1965) observed nectar secretion from the flanks of the carpels; the nectar later accumulates at the base of the filaments. The flowers open between 09.00 and 11.00 h and close in the afternoon, and they are visited by small Syrphidae and small Diptera. The flowers are homogamous and self-compatible. The pollen is mealy and is also dispersed by the wind.

FRUIT AND DISPERSAL. Each carpel develops into an achene or into a follicle (*Damasonium polyspermum*).

The achenes are often keeled or winged, more or less glandular nutlets, which are dispersed individually. The stylar beak is often peristent and is likely to play a role in dispersal. In some cases, the individual achenes tend to stick together, but in most cases they fall apart at dispersal time. They are water- or animal-dispersed, but the dispersal systems are incompletely known.

PHYTOCHEMISTRY. Condensed tannins are recorded from leaves of *Luronium* and *Wiesneria* and the root of *Echinodorus*. C-glycosylflavones are common in the leaves of *Sagittaria*.

SUBDIVISIONS AND RELATIONSHIPS WITHIN THE FAMILY. The 11 genera of Alismataceae have not recently been investigated in relation to generic delimitation. A systematic study will, in fact, probably reveal that several of the presently accepted genera are congeneric, as *Baldellia*, *Caldesia*, *Luronium*, *Ranalisma*, and *Echinodorus* have a high degree of similarity. A significant correlation among the mode of endosperm formation (Nuclear vs. Helobial), pollen morphology (granular vs. spinose), and chromsomal base number (x = ±7 vs. ± 11) unites *Alisma*, *Luronium*, *Damasonia*, and *Baldellia* against the remaining genera.

AFFINITIES. The generic name *Ranalisma* recalls an earlier taxonomic opinion that the Alismataceae evolved from the dicotyledon family Ranunculaceae. Other than superficial resemblances (e.g., apocarpy, numerous stamens), there has been no support for this hypothesis from any contemporary phylogenetic study. Vegetative organization of *Ranalisma* is typical of other Alismataceae and also similar to the genus *Hydrocleys* of Limnocharitaceae (Charlton and Ahmed 1973). An appraisal of the systematic position of the Alismataceae is presented in several recent papers (Les et al. 1993; Les and Haynes 1995; Les and Schneider 1995). Phylogenetically, the family is placed solidly among the relatively primitive monocots comprising superorder Alismatanae, whose closest sister group may be the family Araceae.

The Alismataceae, along with Aponogetonaceae, Butomaceae, and Limnocharitaceae, have been grouped to comprise the Alismatales (Dahlgren et al. 1985), one of two orders commonly recognized in the superorder Alismatanae. The Limnocharitaceae are believed to represent the family closest phylogenetically to the Alismataceae (Dahlgren et al. 1985; Haynes and Holm-Nielsen 1992) and these families have often been merged. Butomaceae (which have occasionally been merged with Limnocharitaceae) are believed to be the next most closely related family to Alismataceae, with Hydrocharitaceae as the most

ing; petals white, larger than sepals; stamens 9-many; carpels many, achenes terete, often longitudinally costate and glandular. Twenty-seven spp., all but one neotropical, three extending to N America the other N American. Two subgenera, subgenus *Echinodorus*, with versatile anthers and many more than 20 carpels; subgenus *Helanthium*, with basifixed anthers and 20 or fewer carpels.

7. *Caldesia* Parl.

Caldesia Parl., Fl. Ital. 3: 598 (1858).

Monoclinous, emersed. Stems short, rhizomatous. Leaves basal, submersed or floating; petiole aerenchymatous, septate; blade ovate, suborbiculate or subreniform, base truncate to cordate, apex rounded to acute. Plants producing hibernacules. Inflorescence scapose, emergent, paniculate, verticillate. Flowers long-pedicellate, sepals broad-ovate; petals equal to sepals, broad-ovate, rounded, white to bluish white; stamens 6–9(–11); receptacle flattened; carpels 2–9(–20), free. Achenes obovoid, 1-seeded, with obscure dorsal keels or sculptured. $2n = 22$. Four spp., Europe through Africa and Asia to Australia.

8. *Limnophyton* Miq.

Limnophyton Miq., Fl. Ind. Bat. 3: 242 (1856).

Monoecious, emersed. Stems short, rhizomatous. Leaves basal, emersed; petiole aerenchymatous, angled; blade sagittate or linear-lanceolate; apex acute to acuminate; base hastate or attenuate. Inflorescence scapose, emergent, paniculate, verticillate, the upper verticil(s) with staminate, the lower with perfect flowers, bracts green; sepals broad, reflexed after anthesis; petals delicate, larger than sepals, narrow, white; stamens 6, green; receptacle flattened; carpels (10–)15–20(–30), free; style beaklike ventral, caducous, or only the basal part persistent; achenes obovoid, unarmed, with lateral air canals. Two spp., predominantly tropical Africa, *L. obtusifolium* (L.) Miq. extending to Madagascar and S and SE Asia.

9. *Astonia* S.W.L. Jacobs

Astonia S.W.L. Jacobs, Telopea 7: 140 (1997).

Monoecious, emersed. Juvenile leaves linear, submersed, mature leaves sagittate. Inflorescence with up to 8 verticils, the lower perfect or mixed perfect and staminate, the upper staminate; bracts maroon; lower verticils maturing first, peduncle then bending downwards until the nutlets contact the water surface, the tip of the inflorescence then bending upward; sepals green, petals cream or green, constricted at the base; stamens 6, maroon; carpels 5–15; achenes crowded, spinescent when mature, lateral air chambers absent. Only one sp., *A. australiensis* (Aston) S.W.L. Jacobs, NE Queensland.

10. *Sagittaria* L. Fig. 3

Sagittaria L., Sp. Pl. 2: 993 (1753); Bogin, Mem. N.Y. Bot. Gard. 9: 179–233 (1955), rev.; Rataj, Annot. Zool. Bot. Slov. Narod. Muz. Bratislava 76: 1–31, 78: 1–61 (1972), rev.; Haynes & Holm-Nielsen, Fl. Neotrop. 64: 1–112 (1994).

Monoecious or rarely dioecious, perennial or rarely annual, submersed, floating-leaved, or emersed. Roots septate. Stems often with rhizomes. Leaves submersed, floating, or emersed, entire, sessile or petiolate, petioles terete to triangular, blades present or absent, without pellucid markings. Inflorescence erect, floating or submersed, racemose or paniculate, rarely umbelliform, the staminate flowers above, the carpellate below. Flowers mostly imperfect, rarely the lower perfect, pedicellate; sepals reflexed in staminate flowers, reflexed to appressed in carpellate flowers; petals white or rarely with a pink spot or tinge; stamens 7-many; carpels many; achenes compressed, often laterally winged, glandular, dorsally with a conspicuous wing. $2n = 16, 20, 22$. About 25 spp., predominantly western hemisphere genus of two subgenera, subgenus *Sagittaria*, with ascending to reflexed sepals and mostly spreading to ascending pedicels in fruit, and all flowers imperfect; subgenus *Lophotocarpus*, with appressed sepals and pedicels recurved in fruit, and the upper flowers perfect.

11. *Wiesneria* M. Micheli

Wiesneria M. Micheli in A. & C. DC., Monogr. Phan. 3: 82 (1881).

Monoecious, emergent. Stems short, rhizomatous. Leaves basal, submerged or floating; petiole terete; blade linear-lanceolate or not expanded, apex acute, base attenuate. Inflorescence scapose, emergent, racemose, the lower whorls of carpellate flowers, the upper whorls of staminate flowers. Flowers short-pedicellate or sessile; sepals ovate, persistent; petals white to pinkish, reduced or smaller than sepals; staminate flowers with 3

stamens, carpels reduced to nectaries; carpellate flowers with receptacle slightly curved, with 3 staminodes and 3–6 free carpels. Achenes obovoid, rounded, weakly sculptured, with 3 dorsal keels. Three spp., W and Central Africa, Madagascar, and India.

12. *Burnatia* M. Micheli

Burnatia M. Micheli in A. & C. DC., Monogr. Phan. 3: 81 (1881).
Rautanenia Buchenau (1897).

Dioecious, emersed. Rhizome tuberous. Leaves basal; petiole terete; blade linear-lanceolate to ovate, apex acuminate, the base rounded to attenuate. Inflorescence scapose, paniculate, branched, verticillate. Flowers small, sepals persistent; petals white or pinkish, reduced or smaller than sepals; staminate flowers with (6–)9 stamens and ca. 12 aborted carpels; carpellate flowers with flattened receptacle, occasionally with 2 staminodes, and 8–20 free carpels. Achenes obovoid, laterally compressed, forming a small head. Only one sp., *B. enneandra* M. Micheli, Tropical Africa.

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