

Alismatales (Water Plantains)

Robert R Haynes, *University of Alabama, Tuscaloosa, Alabama, USA*

Donald H Les, *University of Connecticut, Storrs, Connecticut, USA*

The Alismatales comprise an angiosperm order commonly known as 'water plantain'. All members are aquatic or wetland plants with vegetation totally submersed and flowers floating or emergent, or with floating leaves and floating or emergent flowers, or with emergent vegetation and flowers. Most species have a totally submerged juvenile phase, and some species, for example *Baldellia ranunculoides*, *Luronium natans*, *Ottelia ovalifolia*, *Ottelia alismoides*, and *Blyxa alternifolia*, develop submerged cleistogamous flowers.

Introduction

Many members of aquatic and wetland species, as well as three genera of marine vascular plants ('sea-grasses') are members of the Alismatales Dumortier (**Figure 1**). A few genera have showy flowers and are used in water gardens. Most, however, are not cultivated or are cultivated in aquaria for their foliage.

Families Included

A recent classification of the angiosperms (the Angiosperm Phylogeny Group (APG) classification) suggested that the order Alismatales should be expanded to include the families Cymodoceaceae, Potamogetonaceae, Zosteraceae, Juncaginaceae and Zannichelliaceae. We believe, however, that a more limited circumscription of the order is necessary. Les (1997), for example, showed phylogenetic evidence for two distinct, well-supported clades in the subclass Alismatidae, which correspond to traditional concepts of the orders Alismatales (*sensu stricto*) and Zosterales (*sensu stricto*). Even textbooks that adopt the APG classification (e.g. Judd *et al.*, 2002) state (p. 242) 'two major clades are recognized' [within the group], where each is supported by numerous apomorphies. We both believe that in such instances of obviously distinct lineages there

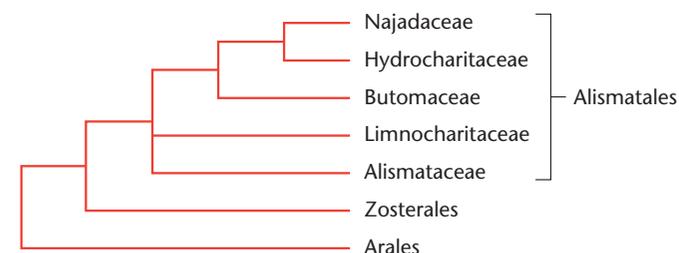


Figure 1 Photograph of *Sagittaria latifolia* in flower and fruit.

Introductory article

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should be a level of taxonomic recognition to reflect the phylogenetic history. Because it would be confusing to combine all taxa into just two families, we elect to recognize these well-marked clades at the next highest major taxon – the order. Thus we adopt two orders for classification within this larger group, which we still hold at the subclass level (i.e. Alismatidae).

In our circumscription, the Alismatales are divided taxonomically into three to five families (**Figure 2**): Alismataceae (water plantain family), Butomaceae (flowering rush family), Hydrocharitaceae (frogbit family), Limnocharitaceae (water poppy family) and Najadaceae (water sprite family) (**Table 1**). Alismataceae contain 12 genera and approximately 95 species. Butomaceae are monotypic *Butomus umbellatus*. Hydrocharitaceae contain 17 genera comprising approximately 74 species. Some authors merge Limnocharitaceae (8 species in 3 genera) with



Figure 2 Diagram (adapted from results of phylogenetic DNA sequence analysis in Les *et al.*, 1997) showing hypothetical relationships among the five families of Alismatales and other closely related monocotyledon orders. At present, there is insufficient evidence to determine whether to merge Najadaceae with Hydrocharitaceae, or Limnocharitaceae with Alismataceae.

Table 1 Genera within the families of the Alismatales

| Alismataceae | Butomaceae | Hydrocharitaceae | Limnocharitaceae | Najadaceae |
|--|----------------|---------------------|--------------------|--------------|
| <i>Alisma</i> | <i>Butomus</i> | <i>Apalanthe</i> | <i>Butomopsis</i> | <i>Najas</i> |
| <i>Baldellia</i> | | <i>Appertiella</i> | <i>Hydrocleys</i> | |
| <i>Astonia</i> | | <i>Blyxa</i> | <i>Limnocharis</i> | |
| <i>Burnatia</i> | | <i>Egeria</i> | | |
| <i>Caldesia</i> | | <i>Elodea</i> | | |
| <i>Damasonium</i> | | <i>Enhalus</i> | | |
| <i>Echinodorus</i> | | <i>Halophila</i> | | |
| <i>Limnophyton</i> | | <i>Hydrilla</i> | | |
| <i>Luronium</i> | | <i>Hydrocharis</i> | | |
| <i>Ranalisma</i> | | <i>Lagarosiphon</i> | | |
| <i>Sagittaria</i> (in- cl. <i>Lophotocarpus</i>) | | <i>Limnobium</i> | | |
| <i>Wiesneria</i> | | <i>Maidenia</i> | | |
| | | <i>Nechamandra</i> | | |
| | | <i>Ottelia</i> | | |
| | | <i>Stratiotes</i> | | |
| | | <i>Thalassia</i> | | |
| | | <i>Vallisneria</i> | | |

Alismataceae. Indications based on molecular evidence, whether to include Limnocharitaceae within Alismataceae or to maintain it as a distinct family, are equivocal; however, there is no justification for merging Limnocharitaceae with Butomaceae as some have done in past treatments. Older literature completely excluded the water sprite family (Najadaceae) from Alismatales; however, recent studies clearly show the family to be related. A close relationship between Najadaceae and Hydrocharitaceae is evidenced by a variety of molecular and nonmolecular data. However, some molecular data place Najadaceae within Hydrocharitaceae, whereas other analyses position the two families phylogenetically as separate sister groups. Thus, despite the apparent close relationship of these two groups, their recognition as either one or two families currently remains unsettled.

Economic Significance and Local Uses

Various species of *Sagittaria* (notably *Sagittaria cuneata*, *S. latifolia*, *S. sagittifolia*, *S. trifolia*) produce starchy, edible tubers with up to 7% protein content and a taste similar to potato. Native Americans roast or boil the tubers to remove the bitter milky juice that is present when raw. It is a staple food of the Chinooks of the lower Columbia River and was among the food plants eaten by members of the Lewis and Clark expedition in the early nineteenth century. *Sagittarias* are also eaten in Sweden and are cultivated for food in China, Japan and by the Kalmuck, who also eat the bulb-like base of *Alisma*. *Limnocharis flava* is cultivated for

food in India, Java and much of southeast Asia where its leaves (with 1–1.6% protein content) are eaten as an alternative to spinach. Its stems and flower clusters are also cooked and eaten. It is often planted along with rice as a secondary crop. All parts but the roots of *Ottelia alismoides* are cooked as a vegetable in Asia. *Ottelia* leaves are used to season rice in Thailand. Seeds of *Enhalus acoroides* are eaten in the Old World tropics. Baked roots of *Butomus umbellatus* are eaten in northern Asia and are dried and powdered to make bread flour in Norway.

Many Alismataceae contain acrid juices and have been used medicinally. Properties can be so potent as to cause serious illness in cattle feeding on plants and can completely paralyse a human when administered as a drug. Tubers of *Alisma plantago-aquatica* were once used in Russia and *A. subcordatum* in Carolina as a remedy (but doubtfully successful) for hydrophobia (rabies), snakebite and tetanus poisoning. *Alisma* has astringent properties and was used as a diuretic, diaphoretic and to treat urinary disorders. *Sagittaria* has been listed as a diuretic and antiscorbutic. In Sri Lanka, cooked salads (Mallum) of *Limnocharis flava* are eaten as a cure for rheumatism.

Limnocharis flava, *Sagittaria trifolia* and *Sagittaria guayanensis* are sources of pig fodder in Bangladesh, Indonesia and other parts of Asia. On a dry-weight basis, *Egeria* and *Najas* far exceed the crude protein content of young alfalfa hay. *Hydrilla verticillata* is used as manure in India as is *Limnocharis flava* in Malaysia. *Sagittaria latifolia* has been used for nutrient removal from wastewater.

Many Alismatales are noxious aquatic weeds that can contaminate rice fields, obstruct irrigation canals, and interfere with the operation of hydroelectric dams. Several,

such as *Limnocharis flava*, *Hydrilla verticillata*, *Vallisneria*, *Egeria densa*, *Elodea canadensis* and *Elodea nuttallii* have become serious weeds in many parts of the world.

Horticulturally Important Species

Exclusively aquatic and wetland species, Alismatales are a major source of plants for freshwater aquaria and water gardens. Genera used as aquarium plants include *Blyxa*, *Egeria*, *Elodea*, *Hydrilla*, *Lagarosiphon*, *Limnobium*, *Ottelia* and *Vallisneria* (Hydrocharitaceae); *Echinodorus*, *Limnophyton* and *Sagittaria* (Alismataceae); *Hydrocleys* (Limnocharitaceae); and *Najas* (Najadaceae). Genera used in ornamental water gardens include *Butomus* (Butomaceae); *Hydrocleys*, *Limnocharis* (Limnocharitaceae); *Hydrocharis*, *Limnobium*, *Stratiotes* (Hydrocharitaceae); and *Alisma*, *Echinodorus*, *Sagittaria* (Alismataceae). Showy double-flowered ('*flore pleno*') cultivars exist for *Sagittaria sagittifolia* (also as *S. sagittifolia* var. *japonica* '*flore pleno*') and *S. gracilis* (also as *S. variabilis* '*flore pleno*').

Morphology

The Alismatales include annuals (*Appertiella*, *Blyxa*, *Maidenia*, *Najas*, *Nechamandra*, *Wiesneria*) or perennials (most other species). Some genera (e.g., *Echinodorus*, *Ottelia*, *Sagittaria*) contain both annual and perennial species. The perennial species have corms (*Sagittaria*, *Butomus*, *Limnocharis*), rhizomes (*Echinodorus*, *Sagittaria*), stolons (*Vallisneria*, *Limnobium*, *Hydrilla*, *Sagittaria*, *Hydrocleys*), which usually give rise to an erect leafy stem or a basal rosette of leaves. *Elodea* and *Hydrilla* produce turions (shortened stem tips that break off and grow into a new plant) terminally on the erect stem. *Sagittaria* and *Hydrilla* produce starchy tubers from which new erect stems can grow.

Leaves have sheathing bases and are submersed, floating or emersed. They are phyllodia (petiole-like leaves that are not divided into blade and petiole) *Butomus*, *Sagittaria*; sessile, linear blades (*Vallisneria*, *Najas*, *Egeria*, *Hydrilla*, *Elodea*) or divided into a blade and a petiole (*Ottelia*, *Sagittaria*, *Echinodorus*, *Limnocharis*, *Hydrocleys*, *Butomopsis*, *Limnobium*). The blades are oval to ovate to sagittate.

The flowers are bisexual, as in Alismataceae (except *Astonia*, *Burnatia*, *Limnophyton*, *Sagittaria*, *Wiesneria*), Butomaceae, Limnocharitaceae, and *Apalanthe* (Hydrocharitaceae) or unisexual as in Hydrocharitaceae (except *Apalanthe*) and Najadaceae. Plants with unisexual flowers are either monoecious (carpellate and staminate flowers on same plant) as in most *Najas* spp., polygamous (perfect, carpellate, and staminate flowers on same plant) as in *Astonia*, *Limnophyton*, and *Sagittaria*, or dioecious

(carpellate and staminate flowers on separate plants), as in *Burnatia*, *Najas marina*, and most Hydrocharitaceae. Stamens and carpels are separate and number from one (*Najas*) to fewer than 10 (*Butomus*, *Hydrocleys*, *Elodea*, *Limnobium*) to 20 or 30 (*Echinodorus*, *Sagittaria*). Some species of *Sagittaria* may have several hundred separate carpels. The ovary is inferior in the Hydrocharitaceae and superior in all other families (partly inferior in Butomaceae and *Damasonium*). The fruits are achenes (Alismataceae, Najadaceae), capsules (Hydrocharitaceae) or follicles (Alismataceae, Butomaceae, Limnocharitaceae).

Ecology

Plants of the order occur in nearly all aquatic and wetland situations, from seasonally flooded forests and marshes to lakes, streams and small rivers. Substrate types range from sticky clay to organic deposits over sand to nearly sterile sands. Species of *Echinodorus* occur in dense shade on the forest floor of Amazon swamp forests that are annually flooded. The species survive the deep floods as underground rhizomes and flower when the water recedes to approximately substrate level. Other species occur in full sun of open marshes.

Species of Alismatales occupy most areas of lakes and small rivers that are shallow enough for light to penetrate to the substrate and that are protected from wave action. Plants are especially abundant on downwind sides of small peninsulas. Three genera of Hydrocharitaceae (*Halophila*, *Thalassia* and *Enhalus*) are restricted to warm waters of the open oceans. They occur at all depths to which light can penetrate. *Halophila*, for example, has been collected in the Caribbean Sea at depths up to 90 m.

All members of the Alismatales are important components of the aquatic ecosystem. Many species serve as food for aquatic animals and as substrate stabilizers. Wave and currents are slowed slightly in vegetation beds, and as the water slows, suspended particles often settle either to the substrate or on to the vegetation. After the plants die, their bodies settle to the substrate along with any adhering silt, aiding in build-up of the substrate.

Biogeography

Hydrocharitaceae, Alismataceae and Najadaceae are nearly cosmopolitan. Butomaceae are native to Eurasia and have become naturalized in northern North America. Limnocharitaceae are more or less pantropical, with *Limnocharis* and *Hydrocleys* native to Latin America, and *Butomopsis* native to the paleotropics. *Limnocharis flava* has also become naturalized in south and southeast Asia.

Fossil History

The Alismataceae are known in the Tertiary from Oligocene and Miocene. Fossils from Lower and Upper Cretaceous and the Palaeocene that have tentatively been referred to the Alismataceae are inadequate for proper identification (Daghlian, 1981; Friis, 1985; see Further Reading). The Hydrocharitaceae are known in the fossil record from the Middle Eocene, mainly by the genus *Stratiotes*, which, according to Cook and Urmi-König (1983), contains 15 extinct species. Additional Hydrocharitaceae genera include *Hydrochartites* from the Miocene and *Hydromystria* from the Tertiary. The Butomaceae are known from Cenozoic, Neogene (Pliocene and Miocene), Cenozoic, Palaeogene (Oligocene) and Quaternary (Pleistocene), and the Najadaceae are known from the Pleistocene. The Limnocharitaceae are not known in the fossil record.

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