

Limnocharitaceae

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Limnocharitaceae Takhtajan ex Cronquist, *Integr. Syst. Class.*
Fl. Pl.: 1048 (1981).

Perennial latescent *herbs*, emergent, submersed, or floating in freshwaters. Roots fibrous, few to many, from a stout rhizome or stolon. Stems fleshy, erect, unbranched. *Leaves* basal or alternate, spirally inserted, petiolate; petioles terete to triangular, mostly considerably longer than blade, with sheathing base, the sheath without auricles, intravaginal scales lacking; leaf blades orbicular to lanceolate, the margins entire, the apex obtuse to round-acute, the base cordate to attenuate, venation reticulate, with parallel primary veins from base of blade to apex and transverse secondary veins. *Inflorescence* a scapose, erect to floating, terminal, involucre umbel, subtending spathe lacking, with an involucre of few to several membranous, acuminate bracts. *Flowers* hypogynous, perfect, pedicellate; perianth actinomorphic, of 6 separate tepals in 2 whorls, the outer 3 sepal-like, persistent, mostly erect and enclosing flower and fruit; the inner 3 petal-like, usually delicate, caducous. Stamens free, 6-many; anthers 2-locular, basifixed, 4-sporangiate, dehiscing by longitudinal slits. Carpels 3-many, separate or basally coherent, 1-locular, each with numerous anatropous or campylotropous ovules; placentation laminar; styluli short or absent, stigma linear. *Fruits* follicular. Seeds numerous, glandular pubescent or costate, U-shaped, without endosperm.

Three genera and eight species in the tropics of the Old and New World.

VEGETATIVE MORPHOLOGY. The roots arise from the rhizome or the nodes of the stem. The nonchlorophyllous axes are short and erect or elongated and creeping. The stems, including stolons and scapes supporting floating inflorescences, and petioles have extensive aerenchyma. Branching is sympodial and continued from buds developed in the axil of the last leaf of the rosette. The ultimate bud of the inflorescence of *Limnocharis flava* always develops into a vegetative bud (Wilder 1974), which forms a new vegetative shoot after the fruits have fallen, and

ultimately forms a new erect plant. The leaves are spirodistichously arranged in basal rosettes. The bracts of floating inflorescences are often foliose, but smaller and generally less developed. The long petiolate leaves have an open sheathing base and a linear-lanceolate, ovate, or cordate blade (Fig. 70). The petioles are triangular or terete, with conspicuous diaphragms. No ligule or squamules are present. There are few primary veins, these usually converging, and a closed reticulum is formed by the secondary and tertiary veins.

VEGETATIVE ANATOMY (based on Tomlinson 1982). Roots are branched and have a thin-walled epidermis with trichoblasts that may develop into root hairs. The outer cortex is compacted into an exodermis of 2 or 3 cell layers, and the remainder of the cortex is composed of lacunose parenchyma. An endodermis with Casparian strips surrounds a single-layered pericycle. The stele is composed of a single metaxylem vessel and few protoxylem tracheids, which alternate with single sieve tubes. Secretory canals are absent.

The rhizome in *Limnocharis* has a persistent epidermis underlayered by a suberized exodermis. The well-developed cortex parenchyma is lacunose and reticulate without diaphragms and often stellate. An endodermis similar to that in the roots is present. The central xylem strands are irregular. In the stems of *Limnocharis* and *Hydrocleys*, the vascular system is supported by about 6 principal vascular bundles in the central parenchymatous core, these bundles without a fibrous sheath. Secretory canals are abundant.

The petiole is angular in *Limnocharis* and terete in *Hydrocleys* and *Butomopsis*. A hypodermis of 1-4 layers of chlorenchyma is present in *Hydrocleys*. The aerenchyma consists of a network of uniseriate parenchyma plates enclosing large lacunae traversed by diaphragms of sometimes stellate cells. The core of the vascular system is a V-shaped arc of large central vascular bundles. Secretory canals are abundant.

The floating leaves have hydropoten on the abaxial epidermis. The epidermis is thin-walled, but the outer surface is weakly thickened and cutinized. Stomata are paracytic. The mesophyll is dorsiventral with 1(-2) layers of peglike palisade cells and a very lacunose, spongy parenchyma. The abaxial hypodermis is continuous and compact. Secretory canals are abundant in the leaves and form a continuous network. An apical pore is formed abaxially by dissolution of mesophyll cells at the endings of vascular elements of the major veins.

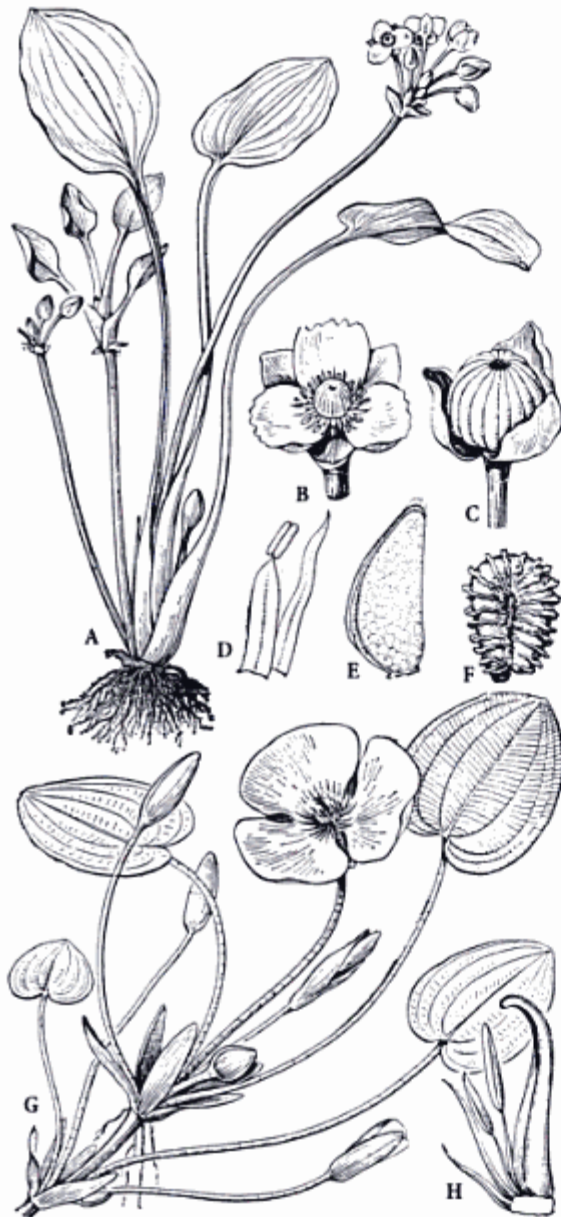


Fig. 70A-H. Limnocharitaceae. A-F *Limnocharis flava*. A Habit. B Flower. C Fruiting flower with numerous follicles. D Stamen and staminode. E Follicle. F Seed. G, H *Hydrocleys nymphoides*. G Flowering plant. H A carpel with two stamens and two staminodes. (Takhtajan 1982)

INFLORESCENCE STRUCTURE. The inflorescence is umbel-like and composed of cymose units, with bracts subtending individual flowers. The inflorescences often proliferate, especially in *Hydrocleys*, where 1 of the flowering axes elongates and develops into another inflorescence (Fig. 70G).

FLORAL STRUCTURE. The flowers are perfect and are borne on pedicels longer than the bracts. The perianth consists of 3 green sepals and 3 white to bright yellow petals. The petals are twice as large as the sepals to inconspicuous and smaller than the sepals. The androecium consists of three to numerous stamens. An outer circle of up to many staminodia is found in some species of *Hydrocleys* and *Limnocharis* (Fig. 70D,H). The anthers are subbasifixed, extrorse or, more generally, latrorse, as in *Limnocharis*. Anther dehiscence is by longitudinal slits.

The gynoecium consists of 3 to about 20 carpels. The carpels of *Limnocharis* are closely laterally appressed and scarcely coherent at the base, while those of *Butomopsis* and *Hydrocleys* are fused below for up to 1/3 of their length. Stigmas are sessile and capitate in *Limnocharis*; in *Butomopsis* and *Hydrocleys*, they are horseshoe-shaped surfaces at the apex of the beaklike hollow apex of the carpels.

Floral ontogeny in *Hydrocleys* reveals a centrifugal stamen inception and a basically trimerous developmental pattern, in spite of the considerable deviation from the monocotyledonous ground plan of the mature flower (Sattler and Singh 1973).

EMBRYOLOGY (Davis 1966). Anther wall formation follows the monocotyledonous type. The endothecium develops fibrous thickenings, and the middle layer is ephemeral. The tapetum is amoeboid and in the early stages consists of uninucleate cells. Microsporogenesis is of the successive type and the tetrads are tetrahedral or isobilateral, rarely linear or T-shaped. The pollen grains are 3-celled at dispersal.

The placentation is laminar. A parietal cell is not cut off from the primary archesporial cell, but the nucellar epidermis divides periclinally to form a nucellar cap.

The embryo sac is of the Allium type. The endosperm formation is Helobial. Free nuclear divisions follow for some time at least in the micropylar chamber, and usually more abundantly than in the chalazal chamber. The formation of the horseshoe-shaped embryo follows the Caryophyllad type. The ripe seeds are without endosperm or perisperm, and the embryo is cylindrical, curved, linear, and lacks chlorophyll.

POLLEN MORPHOLOGY. The pollen grains are dispersed singly. They are globose, tri- to pantoporate (Fig. 71) or inaperturate. In *Hydrocleys* and *Butomopsis* the exine is sculptured by broad-

Alismataceae (D.H. Les, unpubl.). However, the paraphyly of Alismataceae remains uncertain because trees only 3 steps longer resolve both Alismataceae and Limnocharitaceae as monophyletic families (see discussion for Alismataceae). Given the questionable paraphyly of Alismataceae, and the several defining characteristics of the Limnocharitaceae, we have retained these families as distinct taxonomically.

DISTRIBUTION AND HABITATS. The Limnocharitaceae are pantropical, *Limnocharis* and *Hydrocleys* occur naturally from Argentina to Mexico and the Caribbean. *Butomopsis* occurs in Africa, Asia, and northern Australia. *Hydrocleys* and *Limnocharis* are naturalized in the USA and in the Paleotropis.

All species of the Limnocharitaceae occur in aquatic habitats, especially those with stagnant or nearly stagnant freshwater. *Limnocharis* and *Butomopsis* grow in muddy substrates as amphiphytes or rosette-helophytes. *Hydrocleys* is a typical hydrophyte with floating leaves and more or less floating inflorescences. Although *Hydrocleys* has been reported as free-floating it is mostly rooted in muddy substrates or, if floating, then a member of floating island associations.

ECONOMIC IMPORTANCE. Members of the family are often troublesome weeds in the tropics, particularly in paddy fields, although not as serious as *Eichhornia*. *Limnocharis flava* is cultivated in ponds in India and SE Asia, where the leaves are used as a vegetable and as pig fodder. *Limnocharis* and *Hydrocleys* are now receiving much attention in the aquarium and ornamental plant trade.

KEY TO THE GENERA

1. Carpels 15 or more in number, semicircular; stigmas sessile
1. *Limnocharis*
- Carpels 3-9, linear-lanceolate; styles present 2
2. Leaf blades about as broad as long; petioles terete; inflorescences decumbent or floating; Neotropical 3. *Hydrocleys*
- Leaf blades much longer than broad; petioles triangular; inflorescences erect; Paleotropical 2. *Butomopsis*

Genera of Limnocharitaceae

1. *Limnocharis* Humb. & Bonpl. Fig. 70A-F

Limnocharis Humb. & Bonpl., Pl. Equinoct. 1: 116 (1808).

Plants emersed. Stems short, rhizomatous, occasionally with stolons; leaves basal, emersed, petiole triangular, aseptate, blade lanceolate to

oval. Inflorescences up to 10, on aseptate scapes, occasionally proliferating; the pedicels somewhat dilated, often winged, inflated trigonous; petals yellow, ovate to suborbicular, longer than the sepals; stamens many, the outer often sterile, filaments flattened; carpels 15-20, laterally compressed, scarcely coherent at base. Follicles semicircular, membranous, dorsally furrowed; seeds transversely multicostate. Two spp., neotropics.

2. *Butomopsis* Kunth

Butomopsis Kunth, Enum. Pl. 3: 164 (1841).

Tenagocharis Hochst. (1841).

Plants partly submersed, stems terete; leaves basal, erect, petiole triangular, oblong-lanceolate, the base cuneate. Inflorescences 1-3, on a long septate scape, 1- to 2-whorled with cymes of usually 3-11 flowers; pedicels angular; petals white, delicate, oblong-ovate, orbicular, slightly smaller than sepals; stamens 8-12, in 3 whorls; filaments filiform; carpels 4-9, basally coherent, tapering into a style, this curved outward. Follicles dehiscent along the inner margins. Seeds with testa ornamented with small papillae. Only one sp., *B. latifolia* (D. Don) Kunth, tropical Africa, S and SE Asia and N Australia.

3. *Hydrocleys* Rich.

Fig. 70G,H, 71

Hydrocleys Rich., Mém. Mus. Nat. Hist. 1: 368 (1815); Haynes & Holm-Nielsen, Fl. Neotr. 56: 1-34 (1992), rev.

Plants submersed; stems short, stolons often present; leaves basal, either floating and petiolate, or submersed phyllodia; petioles terete, with a sheathing base. Inflorescences few to many on long septate scape, comprising few to numerous flowers, occasionally proliferating; pedicels terete; petals yellow to white, delicate, longer than or shorter than the sepals; stamens 6-many, in 1-several series, the outer often sterile, the filaments linear or lanceolate; carpels 3-8, basally cohering, attenuate into the style, this curved inward. Follicles dehiscent along the inner margins. Seeds sparsely to densely glandular pubescent. Five spp., tropical America.

Selected Bibliography

- Argue, C.L. 1973. The pollen of *Limnocharis flava* Buch., *Hydrocleis nymphoides* (Willd.) Buch., and *Tenagocharis latifolia* (Don) Buch. (Limnocharitaceae). Grana 13: 108-112.

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