# Potamogetonaceae

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Potamogetonaceae Dumort., Anal. Fam. Pl. 59, 61 (1829), nom. cons.

Perennial or rarely annual floating-leaved or submersed glabrous *herbs* growing in fresh or brackish waters, sometimes stranded by receding water levels. Roots fibrous, few, nonseptate, from lower nodes of stems. Stems slender, branched or unbranched, often dimorphic, the lower stems rhizomatous or stoloniferous, occasionally with tubers, the upper erect, leafy, the tips often modified into turions. *Leaves* alternate and the upper 2–12 subopposite, or opposite throughout, entire to serrulate, sessile, or petiolate, 1-many-veined, mostly ligulate; ligules forming a tubular sheath around the stem, free from or adnate to the base of the blade; veins when several or numerous parallel or arching, often connected by cross-veins; axillary infravaginal scales present, membranous; submersed leaves thin, linear to orbicular; floating blades often leathery, lanceolate to elliptic or ovate. *Inflorescences* pedunculate, axillary, or terminal, with 2 opposite flowers or more than 2 flowers in a capitate to interrupted spike, with a subtending spathe. *Flowers* perfect, hypognous, actinomorphic; tepals 4(–2), in one series, distinct, rounded, flat to convex, short-clawed, greenish, reddish, or brownish. Stamens 4, rarely 2–3; anthers extrorse, 2-locular, dehiscing by longitudinal slits; filaments adnate to the perianth claw; pollen grains shed singly, spherical. Gynoecium of (1–) 4 (–7) distinct carpels, the carpels unilocular, sometimes with an indistinct stipe; ovules solitary, attached to the ventral margin of the carpel; styles short; stigmas capitate. *Fruits* usually drupelets with a membranous exocarp, fleshy mesocarp, and stony endocarp, or rarely berries, opening by decay of the pericarp. Seeds solitary, exalbuminous, with coiled embryo.

A subcosmopolitan family with 2 (or 3) genera and 85–90 species. Additionally, 40–50 putative hybrids have been described, which are concentrated predominantly in Great Britain, Scandinavia, and Japan (Preston 1995).

VEGETATIVE MORPHOLOGY. The Potamogetonaceae are aquatic or rarely semiaquatic herbs growing either entirely submersed or with emergent inflorescences and submersed leaves or with both submersed and floating leaves and emergent inflorescences (Figs. 96, 97). Those that are semiaquatic are stranded by receding water levels, often appearing terrestrial. The roots are adventitious and unbranched, arising singly or, more commonly, in whorls of up to 10 from the nodes of rhizomes, stolons, or lower nodes of erect stems.

The stems often are divided into a short to elongate, non-chlorophyllous rhizome and an erect chlorophyllous stem. The rhizome varies in length up to 2 m or more. It may be clearly different from the erect stem.


**Fig. 96A–I.** Potamogetonaceae. **A, B** *Potamogeton lucens*. **A** Fruiting shoot. **B** Drupelet. **C–E** *P. perfoliatus*. **C** Fruiting shoot. **D** Flower. **E** Drupelet. **F–I** *Groenlandia densa*. **F** Flowering shoot. **G** Two-flowered spike. **H** Flower, from above. **I** Drupelet. (Takhtajan 1982)


**Fig. 97A–J.** Potamogetonaceae. **A–F** *Potamogeton natans*. **A** Fruiting shoot. **B** Flowering spike. **C** Fruiting spike. **D** Flower. **E** Tepal with stamen. **F** Drupelet. **G–H** *P. gramineus*. **G** Shoot with submersed and floating leaves. **H** Wholly submersed shoot. **I, J** *P. alpinus*. **I** Flowering shoot. **J** Drupelet. (Takhtajan 1982)

Rhizomes lack chlorophyll and have scalelike, non-chlorophyllous leaves. These consist essentially of a sheathing base that nearly or completely encircles the stem. The 1st scale is solitary and lacks an axillary bud, the next 2 scales are paired and subopposite, each with an axillary bud. The bud of the 1st scale of the subopposite pair in some species gives rise to a regenerative rhizome. This supersedes the rhizome apex and makes branching sympodial. The bud of the 2nd scale of the subopposite pair gives rise to the erect stem. Some *Potamogeton* species produce elongate overwintering rhizomes. These develop in the axil of the 1st of the paired scales. In *Groenlandia* and other species of *Potamogeton* which do not produce overwintering rhizomes, the bud of the 1st scale of the subopposite pair remains dormant.

The erect stems vary in length to 6 m, depending partly on water depth. Each node produces one or rarely more axillary buds. These generally remain dormant, but sometimes grow into branches. The apex of *Potamogeton* shoots produces an inflorescence subtended by 2 subopposite leaves. Each leaf has an axillary bud, one or both of which may break dormancy, in which case a sympodium is formed.

The leaves are predominantly alternate, opposite or in whorls of 3 in *Groenlandia*, and consist of a sessile or petiolate blade and, usually, a basal stipular sheath. The leaves in *Groenlandia* are sessile and usually exstipulate, or stipulate on young shoots (Fig. 96F). The leaf axils have 2-several intravaginal squamules. The squamules lack veins and are mostly linear to subulate, rarely ovate, entire, and acute.

The blades vary in shape from linear to lanceolate or oval. They are glabrous and predominantly entire, although serrations are rarely present. Serrations are evenly spaced along the margins (*P. crispus*). Some species of *Potamogeton* such as *P. pulcher* have minute denticles along the margin that become dislodged shortly after leaf maturation. Venation is basically parallel, with an obvious midvein and from 0–30, rarely more, lateral veins. Cross-veins are normally present between the longitudinal veins. The leaves of many species are entirely submersed. Floating leaves are present in several species of *Potamogeton*. They are usually coriaceous, whereas the submersed leaves are delicate. The two types are often widely different in shape.

The ligules (often called stipular sheaths) are normally free from the leaf base but in some species adnate to it from the leaf base up to 3/4 of its length. The ligules, when separate from the blade, encircle the stem. The margins of the ligules may be fused, forming a tube, but are more commonly free and overlap basally. The sheath is mostly delicate and hyaline.

Vegetative reproductive structures and perennating organs are produced at the tips of erect stems and branches by several species of *Potamogeton*. These are variously called winter buds, turions or hibernacula, and primarily produced in species without elongate rhizomes. Turions are short, hard stem apices with short internodes. The effective propagation of turions was demonstrated by Yeo (1966) who planted 1 turion of *P. crispus* on 1 April 1963 and, at the end of the growing season, found 23 520 turions produced.

The inflorescences are pedunculate, solitary, and terminal or axillary. The penduncles vary in length from few to 50 mm or more. They are cylindric and filiform to clavate and inflated and may be erect to recurved.

VEGETATIVE ANATOMY (from Tomlinson 1982). The sieve tube plastids have cuneate protein bodies but no starch or filamental protein. Silica bodies and calcium oxalate crystals are lacking. Vessels with scalariform perforations are often present in the roots of *Potamogeton* but absent in *Groenlandia*; they are absent in stems and leaves. The root epidermis is differentiated into long and short cells, from the latter of which root hairs are produced in *Groenlandia*, but this exodermis is absent in *Potamogeton*.

The erect stem lacks stomata and has a thin to slightly thickened cuticle. The epidermal cells contain chlorophyll and surround a fairly wide cortex that contains chlorenchyma and is copiously lacunose. The outer 1 to 3 cell layers of the cortex often comprise a hypodermis (pseudohypodermis in some literature), which is absent in *Groenlandia* and some species of *Potamogeton*. Immediately inside the cortex is an endodermis. The endodermal cells in *Groenlandia* are thin-walled but are variously thickened in *Potamogeton*. Vascular and supporting tissues are restricted to the stele in most species but in some species of *Potamogeton* are present both in stele and interlacunar and/or subepidermal bundles. The cortex in the nodal area is compact and lacks lacunae. The nodes are probably the only break in the longitudinal gas canals.

The leaf anatomy varies considerably between genera and within *Potamogeton*.

*Groenlandia* leaves have 3 veins at the base and apex but 5 to 7 in the widest parts. The epidermal layer is continuous except at the apex where a well-developed apical pore is present, exposing the tracheids. The cuticle is thin or absent. The mesophyll consists of only 1 layer, except along the veins. Lacunae are restricted to the midvein area. All mesophyll and epidermal cells contain chlorophyll. A fibrous strand extends along the margin from the base nearly to the apex.

Floating and submersed leaves of *Potamogeton* differ in anatomy, although a pore is always present. In floating leaves, the cuticle is thick on the upper surface and thin on the lower, stomata are common on the upper surface and rarely present on the lower. Epidermis on both sides is uniseriate, and the mesophyll consists of normal palisade and spongy parenchyma. Large lacunae traverse the spongy mesophyll on each side of the midvein. In submersed leaves, stomata are rare and nonfunctional, the cuticle is thin or nearly absent, and the mesophyll varies from 1 to 4 or 5 cell layers, but a palisade is not developed. Lacunae are common along the midvein and sometimes occur in the mesophyll. All cells of *Potamogeton* leaves, except those associated with the veins, contain chlorophyll.

INFLORESCENCE STRUCTURE. The plants are monoclinous. The inflorescences are usually pedunculate with capitate to elongate spikes, or reduced to 2 flowers.

FLORAL STRUCTURE. The flowers (Figs. 96D,H, 97D,E) are sessile and without subtending bracts. There is a perianth of 2–4 tepals that are adnate to the filaments or connectives of the opposing stamens. The perianth segments initially completely enclose the other floral parts. The structures here regarded as tepals in Potamogetonaceae are frequently interpreted as staminal processes, an interpretation supported by the stamen structure in the distantly related Posidoniaceae. Sattler (1965) and Posluszny and Sattler (1973) demonstrated that for the Potamogetonaceae, however, the structures are best considered to be tepals. There are mostly 4 stamens, rarely 2–3. Each theca dehisces by a longitudinal slit.

The carpels are separate, mostly 4, rarely 1–3, but there may be up to 7. The carpels are shortly stipitate in *P. robbinsii*, these never exceeding 1–2 mm. After fertilization, the peduncle often bends laterally or becomes recurved. The peduncle curvature serves to bring the developing fruits under water.

EMBRYOLOGY. Anther-wall formation type is apparently unknown. The epidermis persists during anther wall development, and the endothecium has Girdle-type thickenings. The tapetum cells are predominantly 1-nucleate, rarely, e.g., in *Potamogeton natans*, 2-nucleate. The walls eventually disintegrate and a periplasmodium is formed. Microsporogenesis is of the successive type. The tetrads are usually isobilateral. The mature grains are then 3-celled.

The ovules are bitegmic and atropous in *Potamogeton* (Davis 1969). A parietal cell is formed and gives rise up to 7 parietal layers below the nucellar epidermis. The micropyle is formed by the inner integument.

Embryo sac formation is of the Polygonum type. Endosperm formation is Helobial. Embryo formation follows the Caryophyllad type in which the basal cell does not divide but enlarges. It comprises the terminal cell of the suspensor.

The ripe seeds lack endosperm and perisperm. The embryo is coiled, macropodous, and linear. It fills the entire seed cavity and lacks chlorophyll.

POLLEN MORPHOLOGY. Pollen grains are in monads, inapertuarate, ellipsoid to spheroidal, and semitectate. The exine is less than 1.5 μm thick, homobrochate, consisting of muri with a tectal solid part and an infratectal columellar part. Lumina number varies from 10–31 per 50 $\mu m^2$ (Sorsa 1988).

KARYOLOGY. Chromosome reports are available for about half of the species of the family. The basic chromosome number for *Potamogeton* was proposed as $x = 7$ by Les (1983). *Potamogeton* exhibits extensive polyploidy, ranging from $2n = 14$ to $2n = 52$, and even $2n = 104$, and several aneuploid series. *Groenlandia* is reported to be $2n = 30$.

POLLINATION. Most species are considered to be wind-pollinated. Dragon flies have been observed to land on *P. nodosus* spikes and to carry the pollen, but there is no evidence of actual pollen transfer. Daumann (1963) detected minor amounts of pollenkitt on the exines of *P. fluitans* and *P. natans*, which led to slight stickiness of the pollen. *Potamogeton lucens*, however, was found never to have any pollenkitt. Daumann suggested that the presence of pollenkitt may indicate that

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