

Ceratophyllaceae

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Ceratophyllaceae S. F. Gray, Nat. Arr. Brit. Pl. 2: 395, 554 (1821)
("Ceratophyllae").

Submersed, herbaceous, hydrophilous perennials; roots (even embryonic) absent. Herbage glabrous. Stems flexuous or brittle, freely suspended or anchored into the hydrosol by slender rhizoidal branches; branching irregular. Leaves opposite at first plumule node, whorled otherwise; exstipulate; petioles inconspicuous, light-colored; laminae simple-linear or divided dichotomously into linear filiform segments; segments with 2 submarginal rows of persistent thorn-like denticles; segment apices tipped by a medial multicellular mucilaginous appendage. Plants monoecious. Staminate and pistillate inflorescences one-flowered or occasionally with vestigial branches; extra-axillary and alternating with the leaves, 1 to several at a node in distal portions of the shoots, sessile or with peduncles lengthening in fruit, subtended by involucre of basally connate, foliaceous bracts. Staminate flowers actinomorphic; naked; pedicels very short; stamens 3 to numerous, arranged spirally, maturing centripetally; filaments short; anthers 2-celled, dehiscing longitudinally; connective projecting as an apical medial appendage, flanked by 2 to several small denticles. Pistillate flowers actinomorphic; naked; pedicels very short; gynoecium unilocular; ovary superior, unilocular; style single, terminal, terete, persistent, elongate-spinescent or short and awliform, apex acute or occasionally bifid; stigma a minute pocket at the base of a decurrent stylar groove, lacking sticky secretions; ovule solitary, pendulous, orthotropous, unitegmic, crassinucellar; placentation apical/ventral. Achene elliptical, symmetric; surface smooth or variously papillose to tuberculate, facial spines or tubercles present or absent, margins entire or with lateral and/or basal spines or tubercles, winged or wingless, monospermic; seeds elliptical; endosperm mucilaginous or lacking; embryo large, with 2 fleshy cotyledons; plumule massive, highly developed, first leaves simple or forked.

A cosmopolitan family with one genus and six species.

VEGETATIVE MORPHOLOGY. Species of *Ceratophyllum* are extremely similar vegetatively, with some vari-



Fig. 45A-E. Ceratophyllaceae. *Ceratophyllum demersum*. A Habit. B Leaf. C Male flower. D Stamen. E Female flower. (Takhtajan 1980b)

ation in the coarseness of foliage (rough and stiff in sect. *Ceratophyllum*, somewhat finer in sect. *Submersum*, limp and flexuous in sect. *Muricatum*) and in leaf orders. Two groups have been characterised on the basis of different leaf orders (the maximum number of times the leaf axis forks to produce a pair of terminal segments). In sect. *Ceratophyllum*, species have leaves only 1–2 orders forked, whereas, in sects. *Submersum* and *Muricatum*, they attain 3–5th order forking (Les 1986a). The leaves of the latter group are frequently characterised by inflated segments caused by a proliferation of air-space tissue (Les 1986a). Leaf denticles of higher leaf order species are much less exerted. In all species, leaves are slightly “petiolate” (a lighter band of tissue preceding the first dichotomy) and possess well-developed aerenchyma (Jones 1931; Les 1986a). Vegetative and floral primordia are enclosed within “bud-scale”-like leaves which may function to deter parasites (Klercker 1885) and predators (Les 1986a). Branches are extra-axillary and alternate with the leaves (Aboy 1936). Roots are absent even in the embryo which lacks a functional radicle (Jones 1931). Shoots are sometimes attached by “rhizoidal” branches or “holdfasts” (Glück 1906), which can become anchored in fine bottom sediments (Les 1985a).

VEGETATIVE ANATOMY. The epidermis is unspecialised and possesses a thin cuticle, however, there are some interspecific differences in the thickness and texture of the leaf cuticle (Mouraviev 1952). The

cortex is also relatively undifferentiated but may develop schizogenous aerenchyma (Jones 1931). An endodermis is present (Ogden 1974), and the vascular cylinder is essentially a protostele (Jones 1931), although a lacuna may develop in the centre of the xylem (Schenk 1886). The phloem consists of sieve-tubes, companion cells, and parenchyma; sieve-tubes may transform into air-spaces. Cell types are difficult to distinguish in the xylem; the slightly larger cells are reduced vessels, and the smaller ones are parenchyma (Jones 1931). Reduced vessels are parenchymatous and modified to store starch and tannins. The xylem may contain chloroplasts (Jones 1931).

INFLORESCENCE AND FLOWER STRUCTURE. The solitary flowers of *Ceratophyllum* are derived from reduction of a more complex determinate inflorescence (Aboy 1936). The staminate and pistillate flowers are usually borne at different nodes, or less often, at the same node (Aboy 1936; Sehgal and Ram 1981). The flowers are extra-axillary in position and alternate with the leaves (Aboy 1936). Frequently, the pistillate flowers occur near the shoot apex, above the staminate flowers (Jones 1931; Les 1986a). Sex ratios vary widely among individuals, but are commonly male-biased in populations (Les 1988a). Both staminate and pistillate flowers are surrounded by a whorl of foliaceous bracts (Aboy 1936) that are not to be confused as either sepals (e.g. Cronquist 1981) or tepals (e.g. Sehgal and Ram 1981). Vestigial multiple-flowered inflorescences are occasionally observed (Aboy 1936; Sehgal and Ram 1981). Floral morphology in *Ceratophyllum* is highly conserved among species, although some subtle differences have been observed.

FLORAL ANATOMY. Flowers are supplied by vasculature originating at the receptacle. In the female flower, a single, unbranched trace enters the pedicel and divides into two branches at the base of the ovary. A dorsal trace dissipates at the vicinity of the style. Two fused ventral bundles supply the ovule, terminating at its insertion. In the male flower, a single trace enters the pedicel and continues to the receptacle where 3–4 traces diverge to supply the first whorl of stamens. Consecutive whorls of stamens are supplied by traces alternating with the previous ones. The vasculature terminates after supplying the final stamen whorl. Within the stamen, the vasculature passes through the connective, but not beyond its extension above the anthers (Aboy 1936).

EMBRYOLOGY. Amoeboid and secretory tapetum types both occur in *Ceratophyllum*, as well as both simultaneous and successive PMC divisions. Tapetal cells are uninucleate, and dispersed pollen is bicellu-

lar. The ovules are orthotropous, unitegmic, and crassinucellar. There is a single archesporial cell, megaspores occur in linear tetrads, and a hypostase is present. Perisperm is absent. Embryo sac development is of the Polygonum type. The plumule is highly developed and a radicle is absent (Les 1988b; 1986a). The first plumule leaves are either linear or forked (Les 1985b).

POLLEN MORPHOLOGY. Pollen grains of *Ceratophyllum* are globose, inaperturate monads of 17–45 μm diameter. They contain numerous starch grains facilitating their ability to sink. The exine is greatly reduced, unsculptured, and covered by a fine fibrillar (cutin-like) network. The intine is massive. Unusual “saccus-like” exine processes have been observed in some grains. Pollen tubes are extremely long, coiled, and occasionally branch (Les 1988a, b).

KARYOLOGY. The base chromosome number is $x = 12$ with normal diploids of $2n = 24$. Two species reportedly possess hexaploid cytotypes of $2n = 72$. Several anomalous chromosome numbers ($2n = 38, 40, 48$) are reported for the normally $2n = 24$ species, *C. demersum*, a probable result of vegetative perpetuation of aberrant cytotypes (Les 1986a, 1988b).

POLLINATION. All Ceratophyllaceae are hyphydrophilous, i.e. pollination takes place entirely below the surface of the water. Pollination is usually initiated by the formation of gas bubbles which fill the aerenchyma of the maturing stamens and subsequently promote rupturing of the anther wall allowing the pollen to escape into the water (Jones 1931). Stamen dehiscence occurs while they are still attached to the plants (Jones 1931), or after degeneration of the basal cells results in their release (Sehgal and Ram 1981). The buoyant stamens rise and dehisce to fill the water with sinking pollen grains (Ludwig 1881). Reportedly, released pollen must reach the stigmatic opening (a small pocket lacking sticky secretions or hairs) either directly or by rolling into it from a groove along the style (Jones 1931). Germination and pollen tube growth usually follow (Schleiden 1837). Alternately, pollen germinates within the anther to form masses of long, coiled pollen tubes (Sehgal and Ram 1981). Pollen can remain viable for up to 8 days (Schröter 1917). Hydrophily in *Ceratophyllum* is effective only in lentic habitats. Currents orient stigmatic surfaces on flower-bearing shoots away from approaching pollen, making it nearly impossible for the grains to make contact with the stigmas (Les 1986a).

Misconceptions that warm temperatures are necessary for fruit maturation (e.g. Guppy 1895) reflect observations of sterility in cooler river habitats where currents interfere with pollination.

REPRODUCTIVE SYSTEMS. Preliminary crossing studies found several species to be both self- and cross-compatible (Les 1986a). The lack of self-incompatibility permits sexual reproduction in clonal populations. All *Ceratophyllum* species are monoecious; however, outcrossing rates appear to be low (Les 1988b). Genetic diversity in populations is extremely low, and they are structured genetically as those of apomicts (Les 1989a).

FRUIT AND SEED. Fruits of all species are monospermic achenes with two-valved germination (Les 1988b). Parthenocarpic fruits (due to embryo abortion) have been observed in several species (Les 1985b). Fruit size and spinature provide the most useful taxonomic characters. Fruits are basically trispinous with an apical styler spine (which in some species develops only into a short awlform structure), and a pair of basal spines (lacking in some species). Species may also possess additional marginal spines (often joined by a wing) or a pair of elongate facial spines (Les 1986c, 1988c, d, 1989b). The function of fruit spines is uncertain. Fruits are fairly long-lived (viable for at least several years in laboratory storage) but no study of long-term viability has been conducted. The single seed coat is fairly featureless with no apparent differences noted among species studied.

DISPERSAL. The cosmopolitan distribution of *Ceratophyllum* has been attributed mostly to long-distance dispersal by birds (Guppy 1895; Jäger 1964). Floatation and survival experiments with fruits and vegetative fragments of *Ceratophyllum* convinced Guppy (1895) that dispersal across salt water could occur only by endozooic seed transport by migratory waterfowl. *Ceratophyllum* fruits are primary dispersal propagules effective at three levels. Local dispersal of fruits away from the parental plant is probably enhanced by their “fish-like” morphology (Buzek 1982). Dispersal over short distances probably occurs to some extent by adhesion of fruits to waterfowl, and over longer distances by endozooic transport.

PHYTOCHEMISTRY. Colourless anthocyanin pseudobases have been reported by Reznik and Neuhäusel (1959). Phenolics occur widely and an extensive array of at least 19 different flavonoids has been documented including O-glycosyl flavones, glycoflavones, flavonols, and anthocyanins (Les 1986a and unpubl.). Flavonoid chemistry provides some evidence of relationships within certain species groups; however, widespread species are characterized by extensive geographical variability (Les 1986a).

AFFINITIES. Although originally believed to represent a dicotyledonous group closely related to the Nym-

phaeales (e.g. Cronquist 1981), recent evidence argues that the family may have actually arisen from early angiosperms that existed prior to the fundamental evolutionary divergence of monocots and dicots (Les 1988b). By morphological, anatomical, and embryological evidence (Les 1988b), it does not appear that this group shares any close relationship to plants assigned to the order Nymphaeales. Accordingly, it is placed within a separate order, Ceratophyllales (Les 1988b).

DISTRIBUTION AND HABITATS. Distributional patterns of the Ceratophyllaceae correlate with former tectonic provinces. Species of *Ceratophyllum* sect. *Submersum* represent a Laurasian pattern, those of sect. *Muricatum* a Gondwana pattern, and those of sect. *Ceratophyllum* a Pangeic pattern (Les 1989b). Pleistocene glaciations have been implicated in the North American disjunction of *C. echinatum* (Les 1986b). Subspeciation patterns in the genus are supported by geographical discontinuities (Les 1988c, d). Although species of *Ceratophyllum* are regularly sympatric, there is evidence that habitat divergence enforces reproductive isolation in several species (Les 1986b).

PALAEOBOTANY. Fossil evidence documents the existence of the genus *Ceratophyllum* in the early Aptian, 115 Ma B.P. (Dilcher 1989), and extant species as early as 45 Ma B.P. in the Tertiary (Les 1988b; Herendeen et al. 1990). The prolonged stasis of the genus has been attributed to the stability of freshwater habitats, and to interactions of hydrophily and the breeding system of the genus (Les 1988a; Herendeen et al. 1990). A second fossil genus, *Ceratostratiotes*, has been documented for the family from European Miocene deposits (Buzek 1982). Several extinct species of *Ceratophyllum* have also been identified, further indicating greater diversity than exists presently in the family.

ECONOMIC IMPORTANCE. Foliage and fruits of *Ceratophyllum* are important food items for migratory waterfowl (McAtee 1939). Leaves have been used medicinally for treating biliousness, jaundice, scorpion stings, and other minor irritations (Subramanyam 1962; Pareek 1988). Ailments such as elephantiasis, fevers, sunburn and dermatitis have been treated using liniments prepared from leaves of *C. demersum* (Pareek 1988). *Ceratophyllum* species are commonly regarded as nuisance aquatic "weeds" interfering with canal flow, fishing, swimming, navigation, and general water recreation. Populations provide habitat promoting mosquito breeding, and thick infestations have seriously disturbed operations of hydro-electric plants.

Only one genus:

Ceratophyllum L.

Ceratophyllum L., Sp. Pl. 992 (1753).

Fig. 45

Description as for family. *Ceratophyllum* has been thoroughly revised in a series of recent papers by Les (1985b, 1986c, 1988c, 1989b). Publication of a comprehensive treatment of the genus is forthcoming, based upon previous monographic work (Les 1986c). The genus is subdivided into three sections, sect. *Ceratophyllum*, sect. *Muricatum* Les, and sect. *Submersum* Les, each with two spp. (Les 1989b).

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The Families and Genera of Vascular Plants

Edited by K. Kubitzki

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