

Scheuchzeriaceae

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Scheuchzeriaceae F. Rudolphi, Syst. Orb. Veg.: 28 (1830), nom. cons.

A glabrous rhizomatous *perennial*. Rhizome horizontal, sympodial, covered with persistent fibrous remains of older leaves. Adventitious roots inserted just below the node. Aerial stem erect, to ca. 35 cm. *Leaves* basal and cauline, alternate, distichous, linear, compressed-terete, several-veined, with sheathing base, the apex obtuse with a distinct pore; sheath open, marginally hyaline, fibrous remains often persisting, with 2 delicate, obtuse auricles; infravaginal hairs numerous. *Inflorescence* a simple bracteate raceme with a terminal flower. *Flowers* perfect, hypogynous, trimerous and pentacyclic. Tepals distinct, all similar, lanceolate-elliptic. Stamens distinct; anthers bithecate, 4-sporangiate, extrorse, dehiscing by longitudinal slits, with short connective tip. Carpels 3(-6), only basally connate, with decurrent, ventral, sessile, dry stigmas. Ovules (1-2) per locule, basal-axile, erect, anatropous. *Fruits* adaxially dehiscing follicles. Seeds 1(-2), oblong, exalbuminous.

Only one species, *Scheuchzeria palustris* L., from the arctic and temperate regions of the Northern Hemisphere.

VEGETATIVE MORPHOLOGY. *Scheuchzeria* is a rushlike, glabrous herb of *Sphagnum* bogs. The branched roots are developed from the rhizome just below the nodes. The blades are more or less terete below, becoming flattened above, and taper to a rounded apex, which is terminate adaxially by a conspicuous pore. The sheath is wider than the blade and has a hyaline margin that extends upwards as 2 small rounded auricles (Fig. 107). In the axis of the sheaths are numerous hairs that surround the nodes. These are obviously homologous to the infravaginal squamules found in related families.

VEGETATIVE ANATOMY. The sieve-tube plastids contain cuneate protein bodies and lack starch or filamental protein. The anatomy is reduced in relation to the wet habitat, with well-developed air

lacunae in the mesophyll, root cortex, and throughout the ground tissue of the axis. Hypodermal files of crystals line the vascular bundles of the leaf. Long vessels with scalariform perforation plates occur in the roots. Tannin cells are present (Tomlinson 1982).

FLORAL MORPHOLOGY. Developmental studies provide no indication of spiral inception of floral organs; instead, floral organs of each whorl arise



Fig. 107A-E. Scheuchzeriaceae. *Scheuchzeria palustris*. A Flowering plant. B Fruiting plant. C Flower. D Fruit. E Seeds. (Takhtajan 1982)

almost simultaneously in acropetal sequence (Posluszny in Tomlinson 1982: 233).

EMBRYOLOGY. The walls of the uninucleate tapetal cells disintegrate and a periplasmodium is formed that intrudes between the pollen tetrads. Microsporogenesis has not been studied (Davis 1966). The pollen is shed as dyads in the 3-celled stage. The ovules are anatropous and bitegmic, the micropyle is formed by the inner integument, and a parietal cell is formed and gives rise to 4 layers of parietal tissue. The megaspore tetrad is linear. Embryo sac formation follows the Polygonum type, and endosperm formation is Helobial. The micropylar chamber becomes coenocytic, but later cellular, while the nucleus of the chalazal chamber does not divide or exhibit any haustorial activity (Stenar 1935). Embryo development follows the Caryophyllad type, in which the basal cell does not divide but enlarges and forms the terminal cell of the short suspensor. The ripe seeds are exalbuminous. The embryo is chlorophyllous and has a small plumule and a single rounded cotyledon.

POLLEN MORPHOLOGY. The pollen grains are dispersed in dyads (Erdtman 1952). They are globose, inaperturate, and the exine is reticulate and tenuimurate. The reticulum is continuous between the 2 cells.

KARYOLOGY. The basic chromosome number is $n = 11$ (Löve and Löve 1961).

POLLINATION. This is probably by wind.

SEED. There is an obvious raphe arising at the micropyle and running nearly the entire length of the seed. The testa is glossy, smooth, and unornamented.

PHYTOCHEMISTRY. Silica bodies, saponins, and alkaloids are absent in the family. The plants are especially rich in the cyanogenic glucoside triglochinin. Flavonoids are unknown in the family (McClure 1970). The nonlignified cell walls contain no ferulate.

DISTRIBUTION AND HABITATS. *Scheuchzeria* grows in temperate to subarctic regions in the northern hemisphere. In North America it ranges in the south to N California and New Jersey, in Europe to Italy and Jugoslavia, and in Asia to Japan.

It grows in transitional and ombrogenous *Sphagnum* bogs, especially in bogs extending over postglacial kettle lakes.

AFFINITIES. The phylogenetic position of *Scheuchzeria* is usually believed to be close to the Juncaginaceae (including *Lilaea*). An expanded concept of Scheuchzeriaceae that include *Lilaea* and other genera of Juncaginaceae was suggested by Buchenau (1903). The relationship between Scheuchzeriaceae and Juncaginaceae is supported by the restricted occurrence of the cynogenic glucoside triglochinin in these families.

Characteristics of Scheuchzeriaceae that differ from Juncaginaceae include pollen dyads, infravaginal hairs, tetracytic stomata, follicular fruits, 2 ovules per carpel, and subterete leaves with a conspicuous apical pore. Because of these (and other) distinctive features (Tomlinson 1982), the majority of authors have recognized Scheuchzeriaceae as a monotypic family.

Early classifications (e.g., Lindley 1853; Bessey 1915; Skottsberg 1940) placed Scheuchzeriaceae in the Alismatales. Hutchinson (1959) also followed this convention and considered the family to be derived from the Alismataceae. Most contemporary authors (e.g., Cronquist 1981; Dahlgren et al. 1985) have placed the Scheuchzeriaceae in the Zosteriales ("Najadales").

Molecular data (Les and Haynes 1995; D.H. Les, unpubl.) do not support the merger of Scheuchzeriaceae and Juncaginaceae. Despite their shared occurrence of triglochinin, these families are not phylogenetic sister groups, but are more distantly related. The significant morphological and anatomical divergence of these families (Tomlinson 1982) is paralleled by a considerable level of molecular divergence. Morphological and molecular data support the retention of Scheuchzeriaceae and depict a more distant relationship between these families than many authors have assumed. Cladograms of the Alismatidae constructed from molecular data clearly place the Scheuchzeriaceae among families of the Zosteriales, with no indication of a close relationship to families of the Alismatales. In these analyses, Scheuchzeriaceae follow Aponogetonaceae as the most basal members of the Zosteriales.

Only one genus:

Scheuchzeria L.

Fig. 107

Scheuchzeria L. Sp. Pl.: 338 (1753).

Description as for family.

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Edited by K. Kubitzki

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