Penthoraceae

Penthoraceae Rydb. ex Britton, Man. Fl. N. States: 475 (1901), nom. cons.

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Erect perennial rhizomatous herbs; nodes unilacunar, 1-trace; roots fibrous. Leaves alternate, serrulate, simple, shortly petiolate, estipulate; lamina elliptic to lanceolate, venation pinnate with prominent midvein, attenuate at base. Inflorescences terminal or axillary, secund, scorpioid (or corymb-like) cymes; floral bracts lateral and perpendicular to the pedicels; flowers perfect, small, regular; 5(–8)-merous; tetra- or pentacyclic, slightly perigynous; perianth with distinct calyx and corolla, or only sepaline; calyx valvate, of 5(–8) unequal sepals, united below, regular, erect during anthesis, becoming reflexed in fruit, persistent; corolla absent or, when present, inconspicuous with 1–8 greenish or whitish, lanceolate, slightly clawed petals inserted on rim of hypanthium, usually shorter than calyx lobes; stamens free, 10(–16), inserted in 2 whorls on edge of hypanthium; filaments terete-filiform, tapering only slightly towards anthers; anthers oblong, 2-loculate, basifixed, latrorse, longitudinally dehiscent, and caducous; gynoecium 5(–8)-carpellate; ovary 5(–8)-locular, syncarpous in lower half and sunken in hypanthium below placental area, thus partly inferior at anthesis but wholly superior at maturity; stylodia short, submarginal, erect during anthesis; stigmas capitate; each carpel with a single, marginal, pendulous placenta in its distal, free part with 30–100 ovules; ovules anatropous, bitegmic, crassinucellate; fruiting carpels becoming obliquely oriented in fruit, dehiscing circumscissile above the syncarpous region of the gynoecium. Fruit many-seeded; seeds ellipsoid to obovoid, surface papillate (tuberculate to echinate); embryo large, straight, endosperm of the ab initio cellular type, scanty.

A monogeneric family with 2 helophytic species, disjunct between eastern North America and East Asia.

Vegetative Structure. The anatomy was studied in detail by Haskins and Hayden (1987). Both species are erect perennial herbs up to 1 m tall, and multiply, spread and perennate by horizontal stolons or rhizomes produced from the rootstock towards the end of the growing season.

The roots are fibrous. The cortex consists of an outer exodermis and a broad, inner aerenchymatous region. The endodermis frequently contains dark deposits and remains un- or only slightly sclerified with age. The primary xylem is pentarch to polyarch, the secondary xylem resembles that of the stem. Pith is absent.

The primary stem exhibits an epidermis with dark deposits and a collenchyma beneath. The cortex is aerenchymatous. Cortical bundles are absent, druses are common. The primary vasculature is an eustele without primary medullary rays. The pith is circular and often contains darkly staining deposits and druses.

Nodes are one-trace unilacunar, the leaf trace forming a continuous collateral arc of xylem and phloem. The petiole has a simple, arc-shaped collateral vascular bundle. The simple leaves are lanceolate and willow-like in *P. chinense* and (narrowly) elliptic in *P. sedoides*. The apex is acute and the base cuneate and shortly petiolate. The margin is serrate with glandular, irregularly spaced teeth which often have an apical hydathode. Trichomes, which are present in *P. sedoides* only, are multicellular, 3–4-seriate, glandular, and distributed abaxially and commonly attached to the veins. The venation is pinnate-brochidodromous. Both epidermises are uniseriate with a thin cuticle, dark-stained deposits being common except near the primary vein. The leaves are amphistomatic with anomocytic stomates. The mesophyll is bifacial.

Secondary thickening of the annual stems is absent or develops from a conventional cambial ring. The wood is without growth rings. Vessels are very numerous and evenly distributed, and exhibit exclusively scalariform perforation plates with many bars. Vessel elements are of medium length (480–760 µm) and without spiral thickenings. Imperforate elements are intergrading fibre-tracheids and

vascular tracheids. Fibre-tracheids are non-septate and short to medium in length (310–1,300 µm). The numerous rays are homocellular and mostly uni-to biseriate. Axial xylem parenchyma is absent.

Reproductive Morphology and Anatomy. The anthers are oblong, 2-loculate with a thick connective without ventral and dorsal furrows, basifixed without basal pit, latrorse, longitudinally dehiscent, and caducous (Endress and Stumpf 1991). For gynoecium structure, see Hayden and Lewandowski (1997). The gynoecium consists of a central/basal ovule-bearing syncarpous region and a separate lateral/distal plicate region which comprises lateral portions of the ovary walls and the separate stylodia and stigmas. The ventral sutures of early plicate distal primordia are continuous with the first evidence of locular spaces within the floral apex. The placentae are apical, pendulous and (in contrast to other reports) restricted to the central region. The carpels are vascularized by a dorsal bundle which ramifies through the distal region and one ventral bundle mostly supplying the placenta. The fruiting carpels are intensively reddish and dehisce by circumscissile abscission of each distal/plicate carpel region, thus exposing the relatively proximal seed masses. Variation in the number of sepals, petals and carpels is considerable, and may occur within flowers even of a single inflorescence. Flowers with more than 5 carpels occur at the base of the inflorescences.

The seed coat consists of an exotesta only, consisting of protruding tannin-bearing cells with ± thickened outer walls. The tegmen is crushed and persists only in the micropylar region where it forms an endostomal micropylar operculum (Nemirovich-Danchenko 1994). The testa cells bear distinct papillae flattened along the longitudinal axis (Fig. 100), very similar to those of some Saxifragaceae (*Boykinia*) and Crassulaceae (*Crassula*) (Krach 1976; Knapp 1997).

Embryology. The ovules are borne on long funiculi on a well-developed, pendulous, marginal placenta on the adaxial suture above the syncarpous region. The nucellus is weakly developed and multi-layered only in its chalazal part. The embryo sac mother cell develops into a normal tetrad. The embryo sac develops from the chalazal tetrad cell and is normal 8-celled. The basal suspensor cell gives rise to a well-developed micropylar haustorium. Pollen formation is simultaneous (Rocén 1928).

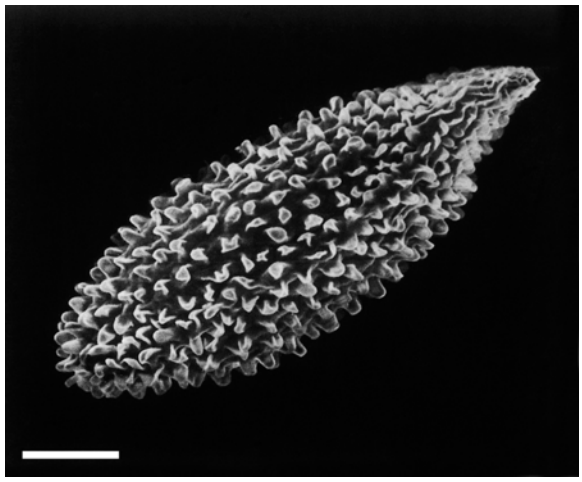

Fig. 100. Penthoraceae. *Penthorum sedoides*. Seed surface structure. Scale: 100 µm. (Knapp 1997)

Pollen Morphology. The pollen grains are subprolate, 14–16 µm long and 3-colporate (colporoidate). The sexine is as thick as the nexine and exhibits a psilate or finely reticulate pattern (Erdtman 1952; Wakabayashi 1970).

Pollination and Dispersal. Flowering occurs more or less continuously throughout summer until frost. Pollinators of the hermaphroditic plants are unknown. Seeds are dispersed floating on the water surface, although many sink; the small seeds can certainly also be dispersed by wind (Ikeda and Itoh 2001). The buoyancy of the seeds can be attributed to an oil coating on the seed surface. After a moist-chilled pretreatment, seeds were found to germinate well in light at 10–25 °C, but not in darkness. Seed germination does not differ between floating and sunken seeds (Ikeda and Itoh 2001), and only takes place at moderate depths of water up to 11 cm (Kimura et al. 1999, cited in Ikeda and Itoh 2001).

Karyology. Chromosome numbers are based on $n = 8$ (*Penthorum chinense*), and $n = 8$ and 9 (*P. sedoides*) (Baldwin and Speese 1951; Fedorov 1969); this points to $x = 8$ as the base number of Penthoraceae, which has also been determined as basal in Crassulaceae (Mort et al. 2001) and occurs in some Haloragaceae, too.

Phytochemistry. In their serological reactions of seed proteins, *Penthorum* is close neither to Saxifragaceae nor to Penthoraceae (Grund and Jensen 1981). In its flavonoid chemistry, *Pentho-*