Haloragaceae

Haloragaceae R. Br. in Flinders, Voy. Terra Austral. 2: 549 (1814), nom. cons.

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Small trees, shrubs, subshrubs, or perennial or annual terrestrial or aquatic herbs, glabrous or scabrous with simple uniseriate hairs; stems erect, ascending, procumbent or creeping, often rooting at lower nodes; nodes unilacunar. Leaves opposite, alternate or verticillate, sessile or petiolate, simple or deeply dissected, entire or toothed, estipulate, heterophyllous in *Proserpinaca* and *Myriophyllum*. Inflorescence thyrso-paniculate, thyrsoid or racemose, or flowers solitary; partial inflorescences usually dichasial; prophylls persistent or caducous. Flowers regular, hermaphroditic or unisexual-monoecious, epigynous, 4(–2)-merous; sepals valvate, persistent (0 in female flowers of *Myriophyllum*); petals imbricate, keeled, hooded, ± unguiculate, falling with the stamens (0 or rudimentary in *Proserpinaca* and female flowers of *Myriophyllum* and *Laurembergia*); stamens equal to or twice the number of sepals; filaments short, slender; anthers 4-sporangiate, dehiscing by slits; gynoecium 4(–2)-carpellate; stylodia free, clavate, from bulbous base; ovary 4(–1)-locular but septa sometimes weakly developed and present only at base and apex of ovary or reduced; ovules 2 or 1 per loculus (if 2, then one aborts at an early stage), anatropous or hemitropous, bitegmic, crassinucellar, with weakly developed funicular obturator. Fruit an indehiscent, 4–1-seeded nutlet, or indehiscent and comprising 4 pyrenes (*Meziella*), or splitting septicidally into (2–)4 mericarps (*Myriophyllum*), the exocarp often ornamented with tubercles, wings or ribs; seeds with straight, cylindrical embryo and usually with ± copious, fleshy endosperm. $x = 7$ (9, 21, 29). A subcosmopolitan family of 8 genera and c. 150 species, most south hemispheric, particularly Australian

Morphology. In terrestrial forms, the primary root persists and builds a root system whereas, in the aquatic/amphibious genera *Proserpinaca* and *Myriophyllum*, it is replaced by adventitious roots which fasten the plant in the substrate, rather than taking up water; they lack root hairs (Schindler 1905). In the northern hemisphere species of *Myriophyllum*, condensed vegetative shoots act as overwintering and dispersal units (turions). From most species of *Myriophyllum*, near the leaf axils and also in other positions, small filiform appendages are known which have been called hydathodes or pseudostipules, although nothing is known as to their function.

The leaf blades are simple in terrestrial species but more or less deeply dissected in the aquatic genera; on aerial shoots of the latter, the degree of dissection is gradually diminished. The phenotypic plasticity of *Proserpinaca* and *Myriophyllum*, as expressed in changes of their shoot organisation, permits them to cope with, or anticipate, environmental changes such as desiccation of their aquatic habitats; in *P. palustris*, short photoperiods induce the submersed, and long photoperiods the aerial leaf form (Bowes 1987). Heterophylly may also be advantageous in giving direct access to gaseous CO_2 from the air, and dissolved CO_2 from the water.

Anatomy (from Schindler 1905 and Orchard 1975). Hairs are simple and unicellular or multicellular. The leaves of the aquatic and helophytic species are amphistomatic and their mesophyll is little differentiated. Stomata are usually anomocytic. The primary cortex of the stems contains numerous air-cavities, which are particularly well developed in aquatic species. The vessels have simple perforations with narrow lumina and simple pits. Rays are heterogeneous to homogeneous. The wood is ring-porous with scanty or no wood parenchyma, bordered pits and both uniseriate and multiseriate homogeneous and heterogeneous wood rays. In *Haloragis*, the inner parts of the rays are uniseriate and homogeneous, and composed of vertically elongated cells. In *Haloragodendron*, the multiseriate rays are reduced in width and have lengthened uniseriate tails. In *Glischrocaryon* and *Gonocarpus*, multiseriate rays are entirely

lacking in the stems but retained in the roots. Sieve element plastids are of the S-type.

Inflorescences. Their structure has been analysed by Schindler (1905) and more fully by Orchard (1975). Most genera have thyrsoids, i.e. determinate systems with usually multiflorous dichasia as lateral inflorescences. In the thyrses of *Haloragis*, the main axis lacks the terminal flower. *Proserpinaca* has thyrses similar in structure to those of *Haloragis*, and with hermaphroditic flowers. *Laurembergia* inflorescences are structured likewise but the flowers are unisexual and, in the dichasia, the distal positions are occupied mostly by male or hermaphrodite flowers, which stand out on a long pedicel from the almost sessile female flowers (Fig. 64B; Orchard 1975). In *Gonocarpus*, the individual dichasia are reduced to single flowers which, however, retain a pair of prophylls. Similarly, *Myriophyllum* has the bracteolate flowers in racemes, with females in the lower part of the inflorescence, and males in the upper.

Flower Structure. The epigynous, 4-merous flowers with valvate sepals and imbricate petals, a diplostemonous androecium with 4-locular anthers, and a gynoecium provided with four stylodia represent the basic condition in the family. With or within several genera, various reductions have occurred, such as the complete or near loss of petals, the loss of the antepetalous or antesepalous stamen whorl and of part of the carpels, or the transition to unisexual flowers.

Embryology (Corner 1976, and the literature cited in Orchard 1975 and Takhtajan 1997). In *Laurembergia* and probably in *Haloragis*, anther wall formation follows the Monocotyledonous type, in *Myriophyllum* the Dicotyledonous type. The tapetum is glandular, and pollen is shed in the 3-celled stage. The ovules are anatropous, bitegmic and crassinucellate; the raphe is dorsal. In *Myriophyllum*, the integuments are very short. Embryo sac development is of the Polygonum type; both cellular and nuclear endosperm development have been reported (Johri et al. 1992).

Pollen Morphology. This section is based on the detailed, well-documented study by Praglowski (1970), which has been related to the modern classification of the family by Orchard (1975). Pollen of Haloragaceae is isopolar to slightly anisopolar, spheroidal to oblate, 4–6(–20)-colpate or -porate, and usually radially symmetric; columellae are distinct, and the tectum is microperforate and provided with minute processes. Three main pollen types can be distinguished.

1. *Glischrocaryon* and *Haloragodendron* have isopolar, subspheroidal, 4–6-colpate pollen grains; the colpi are relatively long and usually tenuimarginate; the sexine is thicker than the nexine.
2. Among the remaining genera (*Meziella* excepted, of which the pollen is unknown), *Haloragis*, *Gonocarpus*, *Lauremburgia*, *Proserpinaca* and most *Myriophyllum* have usually shortly 4–6-colpate or -porate pollen grains which are isopolar to slightly anisopolar; the apertures are short colpi or, more rarely, pores and are crassimarginate and frequently protruding.
3. Two species of *Myriophyllum*, *M. alterniflorum* and *M. muelleri*, are peculiar in having comparatively large apertures, which are restricted to part of the circumference of the grain and thus make the pollen radially asymmetric.

Karyology. Counts from several *Myriophyllum* species document a polyploid series based on $x = 7$, extending from the diploid to the hexaploid state. This agrees with the single count available for *Haloragis* ($2n = 14$) and a possibly octoploid *Gonocarpus* ($2n = 56$), although another *Gonocarpus* has been counted as having $2n = 12$.

Pollination. Haloragaceae are usually anemophilous, which to some degree correlates with the mostly small, inconspicuous, greenish petals and extensive papillosity of the stigmatic surfaces. *Glischrocaryon* species are exceptional in having showy, bright yellow or reddish flowers with plane petals and unilaterally papillose stigmas, which Schindler (1905) considered indicative of entomophily.

Fruit and Seed. The inferior ovary of Haloragaceae is enclosed in a receptacle, which in the fruiting stage forms the often conspicuously ornamented or sometimes winged pericarp. Air-cavities, which are found in the pericarp of wind- (*Glischrocaryon* spp.) or water- (*Laurembergia*) dispersed fruits, develop early at flowering. In *Haloragis*, *Haloragodendron* and *Gonocarpus*, the ovaries initially have four locules each with one ovule; sometimes reduction to 3 or 2 locules occurs. In *Haloragis*, all four ovules can develop