
Geraniaceae

Geraniaceae Adans., Fam. Pl. 2:384 (1763), nom. cons.

Hypseocharitaceae Wedd. (1861).

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Herbs, sometimes shrublets or shrubs, occasionally with succulent stems, sometimes geophytic. Leaves alternate or opposite, mostly palmately or pinnately lobed or compound, lobes deeply serrate or lobulate; stipules present or (*Hypseocharis*) absent. Inflorescences pseudoumbellate, or flowers solitary. Flowers perfect, actinomorphic or zygomorphic, pentamerous; sepals free or united at base, imbricate with valvate tips, persistent; petals 5 (4, 2 or 0), free, imbricate; stamens 5 or 10 and 15, then in two whorls, sometimes a few sterile, filaments free or more or less connate at base; gynoecium of 5(4) carpels; style with 5 stigmatic branches (unbranched with capitate stigma in *Hypseocharis*); ovary 5-lobed, with 1–2(–12) pendulous, anatropous ovules in each locule; placentation axile. Fruits schizocarps with five 1-seeded awned mericarps which separate elastically from a central beak (rostrum), or (*Hypseocharis*) with five 1–few-seeded mericarps not connected by a central column or loculicidal capsules; seeds with a more or less curved embryo with green cotyledons or (*Hypseocharis*) with a cochlear embryo with spirally folded cotyledons; endosperm absent or scanty.

A family of five genera and about 835 species, sub-cosmopolitan but mainly in temperate and subtropical regions.

VEGETATIVE MORPHOLOGY. *Erodium* and *Geranium* are generally annual or perennial herbs, often with a basal rosette, occasionally subshrubs. Tall shrubs (to 4 m) are found only in the Hawaiian endemic *Geranium* sect. *Neurophyllodes*. *Monsonia* and *Pelargonium* exhibit a wide range of different growth forms. *Monsonia* comprises small xerophytic shrubs, geophytes, perennials and ephemeral annual herbs. *Pelargonium* exhibits a wide range of growth habits, from short-lived annuals to scrambling herbs and tall shrubs (Van der Walt 1977; Van der Walt and Vorster 1981, 1988), but xerophytes, stem succulents and

geophytes are the dominant type (Albers 2002). Leafless stem succulents are unknown in *Erodium* and *Geranium*.

Species of *Erodium* and *Geranium* usually have fusiform roots or, more rarely, root tubers. In some sections of *Geranium*, the branched rootstock is covered with pale brown stipules and petiole bases. Xerophytic *Monsonia* and *Pelargonium* are characterised by fusiform roots, roots with a series of small tubers or thick rhizomes. *Pelargonium* sect. *Hoarea* has tubers with a cover of paper-like sheaths of exfoliating periderm. *Hypseocharis* forms thick taproots or large tubers.

Most of the species of *Erodium* and *Geranium* are small herbaceous plants with numerous erect or decumbent stems, except for a few higher-growing species in *Geranium* with a single vegetative axis. *Hypseocharis* is an acaulescent or short-stemmed hemicryptophyte. In some *Pelargonium*, the stem is very short (e.g. *P.* sect. *Polyactium*) or totally reduced (*P.* sect. *Hoarea*). The differential development of the hypocotyl, internode elongation and branching system of various life forms in *Pelargonium* have been studied by Jones and Price (1996). The species of *Monsonia* sect. *Sarcocaulon* are short-stemmed, semi-erect to decumbent shrublets whereas the remaining sections of *Monsonia* are herbaceous; only the perennials are woody at the base. A few annuals form carpets by producing stolons.

The shape and size of the leaves vary extremely within genera, subgenera and even sections. The leaves are opposite or alternate, not rarely changing position on the same stem. Especially in *Pelargonium*, a high diversity in leaf shapes and patterns occurs. The margin can be entire, toothed or lobed. The adaxial and abaxial leaf blades can differ in being glabrous or carrying non-glandular and/or glandular hairs of different types. Leaves are stipulate, except in *Hypseocharis*. Especially in *Monsonia* sect. *Sarcocaulon*, long petioles can persist as blunt or sharp spines.

VEGETATIVE ANATOMY. In most genera, the vascular bundles are arranged in one ring, which is often surrounded by a sheath of sclerenchyma. The pith parenchyma contains starch granules. Starch storage sometimes also occurs in the cortical parenchyma. Clustered crystals are frequent. In addition to the primary growth, a continuous vascular cambium produces secondary elements in a normal way. In woody pelargoniums, the secondary xylem contains vessels with simple perforations plates; reticulate plates seem to be rare. Living and septate fibres as well as both paratracheal and apotracheal axial parenchyma are present. The rays are heterogeneous, consisting mainly of square and upright cells (Van der Walt et al. 1987).

Especially in *Pelargonium* sect. *Hoarea*, a phellogen originating in the outermost cortical parenchyma produces numerous periderm layers. In *Monsonia* sect. *Sarcocaulon*, a thick, waxy bark develops from the periderm, which is flammable and therefore called "bushmen candle". Stem succulence in *Pelargonium cotyledonis* is mainly brought about through the production of parenchyma, whereas in *Pelargonium* sect. *Otidia* and sect. *Cortusina* primary and secondary tissues take part in its formation (Jones and Price 1996). Leaves are bifacial, rarely aequifacial. Stomata are anomocytic throughout. Roots are mainly diarch or less often triarch.

INFLORESCENCES. In *Erodium* and *Pelargonium*, normally a cluster of several pedicels arises from a single point, producing a pseudoumbel of two to many flowers, with the younger flowers at the periphery. In *Pelargonium*, the inflorescences are sometimes borne on a peduncle, which is often branched and forms a compound inflorescence with several pseudoumbels. In most species of *Geranium* and *Hypseocharis*, the inflorescence is cymose, composed of axillary, two-flowered cymules. Often, the cymules arise on aerial, leafy or leafless stems. In some geraniums and *Hypseocharis*, flowers arise directly from the short hypocotyl or rootstock. In *Monsonia* sect. *Sarcocaulon*, the flowers are solitary and the peduncles axillary.

FLORAL STRUCTURE. Flowers are usually actinomorphic, apart from some *Erodium* and most *Pelargonium*. Petal aestivation is usually contort in bud. The corolla is usually pentamerous, but the number of petals can be reduced to two in

the zygomorphic flowers of *Pelargonium*. The androecium is obdiplostemonous with 5 + 5 stamens in *Erodium*, *Geranium* and *Pelargonium*, whereas *Monsonia* has 15 (10 staminodial in one species) and *Hypseocharis* has 5 or 15 stamens. In *Erodium*, only 5 and in *Pelargonium* 2–7 stamens are fertile. In *Monsonia* and *Hypseocharis*, the 15 stamens are arranged in two whorls, and in both genera the outer (and later developing) stamens form five antepetalous pairs (Ronse Decraene and Smets 1995) and are shorter than the antesealous stamens. In one *Hypseocharis*, the androecium is reduced to 5 antepetalous stamens (Slanis and Grau 2001), whereas Aldasoro et al. (2001) report a reduction to 5 fertile antesealous stamens for one species of *Monsonia*.

In *Erodium*, *Geranium* and *Monsonia*, generally five hemispherical nectaries are present which alternate with the filaments of the outer staminal whorl. In some *Geranium* there is a ring-like disk, rather than isolated nectaries. Some *Erodium* and *Monsonia* have five nectaries more or less deeply submerged into antesealous hypanthial tubes. In *Pelargonium*, there is usually only one nectary concealed in an adaxial-episealous area in the hypanthium (Link 1990; Vogel 1998). A lobed extrastaminal nectary disk is well developed in *Hypseocharis* (Slanis and Grau 2001).

EMBRYOLOGY. The tapetum in the mature anthers is glandular. Pollen grains are shed at the two-celled stage in *Erodium* and *Monsonia* and at the three-celled stage in *Erodium*, *Pelargonium* and *Geranium*.

The ovules are anatropous, bitegmic and crassinucellate. Embryo sac development is of the Polygonum type; the early endosperm conforms to the Nuclear type, and both endosperm and nucellus are later resorbed by the embryo.

The endospermless seeds of most Geraniaceae contain a large embryo which is bent in the region of the hypocotyl, so that the radicle is folded against one of the cotyledons. The embryo in *Geranium* is chlorophyllous and has a particularly long radicle (Yeo 1990). *Erodium* and *Monsonia* in principle share this morphology whereas in *Pelargonium* the cotyledons are flat (Aedo et al. 1998). The seeds of *Hypseocharis* have cochlear embryos with spirally folded cotyledons and scanty endosperm.

POLLEN MORPHOLOGY. Pollen is tricolpate (*Monsonia*, *Hypseocharis*) or tricolporate (*Erodium*, *Geranium* and *Pelargonium*). The exine sculpture