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## Saxifragaceae

Saxifragaceae Juss., Gen. Pl.: 308 (1789), 'Saxifragae', nom. cons.

D.E. SOLTIS

Perennial herbs, rarely annual or biennial, often rhizomatous. Leaves rosulate, alternate, on the inflorescence axis rarely opposite, simple or less often pinnately or palmately compound or decompound, margin various, from entire to lobed, crenate, or toothed; leaf base often sheathing, leaves on inflorescence often stipulate. Inflorescences cymose to racemose. Flowers perfect or sometimes some or all unisexual, regular to less often irregular, perigynous to often partly or wholly epigynous, homostylous (heterostylous in *Jepsonia*); hypanthium free from or variously adnate to base of ovary; calyx lobes (3–)5(–10); petals generally (4)5(6), sometimes 0, clawed or rarely cleft or dissected, well-developed or less often relatively small and inconspicuous; stamens usually 5 or 10, anthers basifixed in basal pit, tetrasporangiate and dithecal, opening by longitudinal slits, bisporangiate and opening terminally in *Leptarrhena* and *Tanakaea*; gynoecium of 2(3) carpels, these connate at least at very base and distally free to form hollow or solid stylodia terminated by capitate, rarely decurrent stigmas; ovules numerous and anatropous, usually bitegmic (unitegmic in *Micranthes* and *Darmera*), crassinucellate, on axile or parietal placentae. Fruit capsular or follicular; seeds typically numerous, small; endosperm present.

A family of 33 genera and approximately 500 species, nearly worldwide in distribution but preferably in temperate, often mountainous parts of the Northern Hemisphere, with the greatest number of genera occurring in western North America. Plants generally flower in spring to early summer; *Jepsonia* is distinctive in flowering in fall.

**VEGETATIVE MORPHOLOGY.** Plants are typically herbaceous perennials from a rhizome that varies from short and slender to large, thick and scaly. The leaves are generally basal, usually simple and pinnately or often palmately veined, rarely pinnately or palmately compound or decompound. Leaves on the inflorescence axis (when present) are alternate

or less often opposite. Sheathing leaf bases are well-developed in the basal and lower cauline leaves of genera such as *Boykinia*, *Heuchera*, *Peltoboykinia*, *Bolandra*, *Tolmiea*, *Mitella*, *Tellima*, *Suksdorfia*, *Hieronymusia*, and *Lithophragma*. In many species of these genera, the upper leaves have distinct, usually foliaceous stipules adnate to the cauline leaves (Weberling 1975; Benschel and Palser 1975; Wells 1984; Gornall and Bohm 1985).

**VEGETATIVE ANATOMY.** Multicellular glandular hairs are common; in *Bergenia* they are immersed. Tanniniferous secretory cells containing proanthocyanidins and/or ellagitannins are widespread; idioblasts with cyanogenic compounds or containing crystal druses are uncommon; crystals of calcium oxalate are known from species of *Micranthes*, *Saxifraga*, and *Bergenia* (Engler 1930; Gornall 1987a). Stem bundles occur in a more or less continuous cylinder, sometimes accompanied by cortical and/or medullary bundles; cork arises usually in the outermost layer of the pericycle or subepidermally. Vessel-segments have simple or, in some primary (?) tissue, scalariform perforations with 6–11 bars; imperforate tracheary elements, when present, are small, with bordered pits (Benschel and Palser 1975). Nodes are most commonly trilacunar, but sometimes multilacunar (as in *Astilbe*), and unilacunar, 1-trace in *Chrysosplenium*, and unilacunar, 2-trace in *Micranthes*. Rays in secondary tissue are difficult to distinguish. The leaves often have hydathodes, which sometimes function as chalk-glands (Webb and Gornall 1989); stomates are most commonly anomocytic (Moreau 1984), but sometimes are anisocytic or diacytic.

**INFLORESCENCE STRUCTURE.** Flowers appear in various cymose or racemose inflorescences; rarely, they are solitary. Members of the *Heuchera* group have indeterminate (polytelic) inflorescences, whereas other members of the family have de-

terminate (monotelic) inflorescences (Rosendahl et al. 1936; Wells 1984; Troll and Weberling 1989; Soltis et al. 1993). The thyrsoids of *Rodgersia* and *Bergenia* have scorpioid cymes void of prophylls; *Bergenia* is bractless.

**FLOWER STRUCTURE AND ANATOMY.** The pollen-conducting tissue of the stylodia does not seem to merge (Rabe and Soltis 1999); in other words, a compitum is lacking. The complete range of ovary positions, from superior to inferior, has been reported for the family, as well as for individual genera (e.g., *Lithophragma*, *Saxifraga*). Recent developmental studies demonstrate, however, that those ovaries referred to as 'superior' in the family may be technically inferior. Most species reported to have superior ovaries actually have developmentally epigynous flowers in which the ovary has a small portion below the insertion of the perianth and androecium. Such ovaries of epigynous flowers that mimic superior ovaries are termed pseudosuperior (Kuzoff et al. 2001; Soltis and Hufford 2002). Apparent differences in ovary position in the family may be the result of allometric shifts in the growth proportions of the superior vs. inferior regions of the ovary (Kuzoff et al. 2001).

**EMBRYOLOGY.** Placentation is variously axile or parietal; ovules are several to usually numerous on each placenta, anatropous, bitegmic or sometimes unitegmic (as in *Micranthes* and *Darmera*; Webb and Gornall 1989), and crassinucellate; embryo sac development follows the Polygonum or Allium type; endosperm development is cellular, helobial, or nuclear (Davis 1966; Johri et al. 1992).

**HYBRIDIZATION.** Hybridization has occurred both within and between genera of Saxifragaceae, with certain groups more prone to hybridization than others. Members of the *Heuchera* group of genera seem particularly prone to hybridization, with naturally occurring intergeneric hybrids reported between *Conimitella* and *Mitella*, *Tellima* and *Tolmiea*, *Mitella* and *Tiarella*, and *Heuchera* and *Tiarella* (reviewed in Soltis et al. 1991a). Most of these proposed examples have been documented with molecular markers. Within genera, hybridization appears to be fairly common in *Heuchera* (Rosendahl et al. 1936; Wells 1984; Soltis and Kuzoff 1995) and in *Saxifraga* (Webb and Gornall 1989). Molecular studies have also revealed a number of unexpected examples of hybridization, both within genera (e.g., distantly

related species of *Heuchera*) and between genera (e.g., *Tellima* × *Mitella*; Soltis et al. 1991a, b). For example, molecular data reveal that some populations of the monotypic *Tellima* have in the past hybridized with, and captured the chloroplast genome of a species of *Mitella* (Soltis et al. 1991b). Also of interest are stepping-stone chloroplast capture events in *Heuchera* in which one species has hybridized with a second species and the second species with a third species, ultimately transferring the cpDNA genome of the first species to the third species (Soltis et al. 1991a).

**KARYOLOGY.** Most members of the family have  $x = 7$ . Karyotypic studies have been conducted on many of those taxa having  $x = 7$ . These data further support some of the well-marked clades, such as the *Boykinia* and *Heuchera* groups; these two groups differ in their basic karyotypes. In some species having  $2n = 14$ , tetraploids with  $2n = 28$  also occur, and genetic studies have revealed that several of these tetraploids are autopolyploids (reviewed in Soltis and Soltis 1993). A base number of  $x = 11$  is found in *Peltoboykinia*, and  $x = 11$  and 12 are found in *Chrysosplenium*. These cytological data support a close relationship between these two genera, in agreement with recent phylogenetic hypotheses (Soltis, Kuzoff et al. 2001). Members of the *Darmera* group are also united by base chromosome number as well as the karyotype; most genera have  $x = 17$ , others having  $x = 15$  and  $x = 18$  (Fedorov 1969; Soltis 1986); this well-marked clade is presumed to be of polyploid origin. In contrast to other genera, *Saxifraga* and *Micranthes* are cytologically complex. A large range of numbers is found in both genera; in *Micranthes*,  $2n = 10$ –120; in *Saxifraga*,  $2n = 12$ –approx. 220. Because these two clades are well-separated phylogenetically, multiple events of aneuploid and polyploid increase have evidently occurred in the family.

**POLLEN MORPHOLOGY.** Most taxa are 2–3-colporoidate or -colpate with predominantly diffuse or simple endoapertures; they exhibit a wide range of tectum structures, with a reticulate pattern common (Hideux and Ferguson 1976). The details of exine sculpturing are of considerable help in defining the sections of the genus *Saxifraga* (in the broad sense); four main types can be recognized (Ferguson and Webb 1970). These palynological differences also support the segregation of *Micranthes* from *Saxifraga* s. str. (Soltis et al. 1996b).