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; Bensel 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 (Bensel 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 crassinucellulate; 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 endoaperatures; 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).

Pollination. A surprisingly diverse array of pollinators has been suggested for Saxifragaceae, including Diptera (e.g., Chironomideae, Calliphoridae, Muscidae, Syriphidae), Hymenoptera (e.g., Cephidae, Ichneumonidae, Formicidae, Eumenidae, Halictidae, Apidae), Coleoptera (e.g., Dermestidae, Nitidulidae, Curculionidae), Lepidoptera, and Trichoptera (Ornduff 1971; Spongberg 1972; Savile 1975). Okuyama et al. (2004) studied the pollination of four streamside species of *Mitella* in Japan, the principal pollinators of which are fungus gnats (Mycetophilidae). In spite of very few visits by the pollinators, fruit set is high, which suggests that these animals can be highly efficient pollinators. In most instances, however, pollination has not been well-studied (but see Segraves and Thompson 1999); additional research is encouraged. In many species, nectar is secreted from a disc of tissue that surrounds the base of the ovary, or (in the case of inferior or partially inferior ovaries) the base of the stylodia. Diverse floral visitors have been observed, including Syrphidae and unspecialized Hymenoptera for species of *Saxifraga* (Holdregger 1996), ovary parasitic *Greya* moths for species of *Lithophragma* (Thompson 1994), and *Lasioglossum*, bombyliid flies, and *Greya* moths for species of *Heuchera* (Segraves and Thompson 1999). *Tolmiea* is bumblebee-pollinated, and *Tellima* has a mixed-mating system possibly facilitated by rove-beetles (Weiblen and Brehm 1996). Savile (1975) hypothesized that pollination in *Chrysosplenium* was facilitated, at least in part, by a splash mechanism involving water drops from the canopy. In *Lithophragma*, diversity in ovary position may be related to coevolutionary interactions between the flowers and the assemblage of pollinators visiting them (Thompson 1994). Importantly, considering the variable ovary position in the family (Kuzoff et al. 2001; Soltis and Hufford 2002), ovary position may have evolved in consonance with pollinator preferences (e.g., Thompson and Pellmyr 1992; Thompson 1994; Segraves and Thompson 1999).

Fruit and Seed. The fruit is dry, dehiscent, most often dehiscent along the ventral sutures of the carpels above their level of union; seeds are generally numerous, small, with a small embryo embedded in copious endosperm. The seed is winged in several genera (*Sullivantia* and *Leptarrhena*); the surface texture is various, ranging from smooth to warty or spinulose.

The seed coat is exotestal(–endotegmic), the testa often reduced to the tanniniferous outer epidermis with often thickened cell walls, and the tegmen usually crushed, but sometimes, as in *Astilbe*, *Rodgersia*, *Heuchera*, provided with a thickened inner epidermis (Corner 1976; Takhtajan 1996).

Dispersal. Morphological adaptations to seed dispersal supply many generic characters in Saxifragaceae; there is marked variation in seed dispersal mechanisms.

Chrysosplenium, occupying moist forest floors and stream banks, has a flaring, erect capsule, which functions as a splash-cup (Fig. 148F): seeds are thrown out by the rebound of a falling water drop (Savile 1975). Some species of *Mitella* occurring in moist forests also have a splash-cup (Fig. 151C), independently evolved from that in *Chrysosplenium*. *Tiarella* has a horizontal capsule with a long lower valve, and the seeds are ejected by a springboard mechanism that also relies on falling water drops (Savile 1975). In many species of *Heuchera*, dispersal is thought to be by a censer mechanism, with flexible inflorescence stems swung by wind or passing animals; in other Heucheras, a more rigid inflorescence stem is present in which high wind speed induces vibration, bouncing seeds out. Censer or vibrator mechanisms also appear to be present in *Saxifraga*, *Conimitella*, *Suksdorfia*, *Tellima*, *Telesonix*, and *Lithophragma* (Savile 1975). Some taxa, such as *Tolmiea menziesii* and several species of *Heuchera*, have bristly seeds that may be spread by birds or mammals. *Leptarrhena* and *Sullivantia* have small seeds with a loose, strongly bitailed (or winged) coat that facilitates aerial and aquatic transport. There is evidence for long-distance dispersal in *Chrysosplenium* and other genera in the family, from Asia to South America and also from North America to South America (Soltis, Tago-Nakazawa et al. 2001).

Phytochemistry. Saxifragaceae are characterized by high contents of tannins, amounting to 20% in *Bergenia* and *Heuchera*, and comprising both condensed and hydrolysable tannins, the former based on procyanidin and prodelphinidin, the latter containing ellagic and gallic acids. Bergenin, a C-glycoside of gallic acid, is known from several genera; some members of the family are weakly cyanogenic (Hegnauer 1973, 1990). Saxifragaceae may be one of the best studied groups of flowering plants for flavonoid compounds (e.g., Bohm and Wilkins 1976, 1978; Bohm et al. 1977, 1986, 1988; Bohm 1979; Bohm and Collins 1979; Bohm

and Bhat 1985). The major flavonoids of Saxifragaceae are kaempferol, quercetin, and myricetin, all of which occur as 3-O-mono-, 3-O-di-, 3-O-tri- and 3,7-O-triglycosides; flavones typically constitute a small proportion of the total flavonoid chemistry of members of the family. 6-oxygenation and O-methylation are uncommon structural features that have clearly evolved several times in the family (Soltis et al. 1993). Gallyated flavonoid glycosides also appear in some members of the family. Although most members of the family have a rich array of flavonoid glycosides, several taxa have extremely simple profiles; phylogenetic data suggest that these are examples of flavonoid reduction.

Family Circumscription. Saxifragaceae have been variously defined. Engler (1930) took a very broad view of the family, in which he included 15 highly diverse subfamilies, and included not only herbaceous genera, but also woody genera now segregated into other families such as Hydrangeaceae, Grossulariaceae, and Escalloniaceae. Other authors, starting with Hutchinson (1924), found the Englerian concept too broad to be useful, and therefore defined the family more narrowly. A series of molecular systematic studies (Soltis et al. 1993, 2000; Soltis and Soltis 1997; Hoot et al. 1999; Savolainen, Chase et al. 2000) revealed a well-defined and strongly supported family Saxifragaceae s. str. that corresponds to the Saxifragoideae of Engler, and is identical to the family circumscriptions of Takhtajan (1987, 1997) and Thorne (1992). Molecular phylogenetic studies also demonstrated that groups considered part of a broadly defined family Saxifragaceae such as hydrangeoids, escallonioids, *Penthorum*, *Parnassia*, *Lepuropetalon*, *Francoa*, *Vahlia*, and *Eremosyne* are only distantly related to core Saxifragaceae.

Subdivision and Relationships Within the Family. Engler (1930) considered Saxifragaceae s. str. (his tribe Saxifrageae, which was part of the very broadly defined Saxifragaceae s. l.) to consist of four subtribes: Astilbinae, Leptarrheninae, Saxifraginae, and Vahliinae. Later, Schulze-Menz (1964) recognized three tribes: Astilbeae, Leptarrheneae, and Saxifrageae. Klopfer (1973), in contrast, recognized two large groups, one centered around *Heuchera* having parietal placentation, another centered around *Saxifraga* having axile placentation. Data from diverse sources, including morphology, cytology, flavonoid chemistry, as well as molecular phylogenetic studies (reviewed in Soltis et al. 1993; Soltis, Kuzoff et al. 2001) indicate clearly that these groups are not monophyletic.

Phylogenetic and systematic studies rather suggest the presence of six well-marked clades, which are informally recognized as the *Boykinia*, *Heuchera*, *Darmera*, *Chrysosplenium*, *Astilbe*, and *Leptarrhena* groups. Relationships within some of them, such as the *Boykinia* and *Heuchera* groups, have also been studied in detail from a molecular phylogenetic standpoint (e.g., Soltis and Kuzoff 1995; Soltis et al. 1997). Molecular phylogenetic studies also demonstrate that the genus *Saxifraga* comprises two well-separated lineages: *Saxifraga* s. str., and *Micranthes* (Soltis et al. 1996b). Phylogenetic relationships within other genera have been studied, too, including *Chrysosplenium* (Soltis, Tago-Nagazawa et al. 2001), *Micranthes* (Mort and Soltis 1999), *Saxifraga* (Conti et al. 1999; Vargas et al. 1999), and *Lithophragma* (Kuzoff et al. 1999). Other studies have focused on the *Boykinia* and *Heuchera* groups (Soltis and Kuzoff 1995; Soltis et al. 1996a).

Soltis, Kuzoff et al. (2001) demonstrated that Saxifragaceae comprise two major lineages, one with *Saxifraga* s. str. (including *Saxifragella*), and another with all remaining genera of the family (the heucheroids). This major split is accompanied by general biogeographical and morphological differences. Whereas *Saxifraga* is largely arctic to alpine in occurrence, the heucheroid clade is largely temperate in distribution. *Saxifraga* has a relatively uniform floral morphology (generally actinomorphic; 5 sepals, 5 petals, 10 stamens, 2 carpels), whereas the heucheroid clade encompasses actinomorphic and zygomorphic forms, as well as variation in the number of sepals, petals, stamens, and carpels. The affinities of two monotypic genera (*Saxifragella* and *Saxifragodes*) endemic to Tierra de Fuego were also elucidated using DNA sequence data. *Saxifragella* is an early branching member of the primarily north temperate genus *Saxifraga* s. str.; *Saxifragodes* is sister to *Cascadia*, a genus endemic to Oregon and Washington. Long-distance dispersal from East Asia or western North America to South America may have played an important role in forming these and other similar disjunctions in the family involving North America and South America.

Although relationships among genera within the family are generally well-known, the relationships of two genera that are rare and/or restricted to remote locations are still unclear (i.e., *Hieronymusia*, and in particular, *Saniculiphyllum*).

Affinities. Saxifragaceae are part of a well-supported Saxifragales clade (sensu Soltis and Soltis 1997). The immediate sister group of Saxifragaceae is *Ribes*, followed by a clade of *Itea* and *Pterostemon* (Soltis et al. 1996b; Soltis and Soltis 1997; Fishbein et al. 2001). Other members of Saxifragales include Crassulaceae, Haloragaceae, Tetracarpaeaceae, Hamamelidaceae, and Cercidiphyllaceae. However, the position of Saxifragales within the eudicots remains unclear. In some multigene analyses, Saxifragales are sister to the rosids; other analyses place Saxifragales following Gunnerales as sister to all other core eudicots. However, no placement of Saxifragales receives strong bootstrap support (Soltis et al. 2000).

Distribution and Habitats. The family is nearly cosmopolitan in distribution, but with limited representation in the tropics in Africa and Australia, and in New Zealand. The vast majority of genera and species is found in the Northern Hemisphere, particularly in mountainous areas, with centers of diversity in western North America, eastern Asia and the Himalayas, and Europe. The greatest number of genera occurs in North America, especially the western Cordillera. Habitats are variable, but include moist woodlands, damp meadows and bogs, alpine areas, wet to extremely dry cliffs and rocky slopes, and grasslands.

Parasites. Savile (1954, 1975) has studied the taxonomy of a group of microcyclic rusts of the genus *Puccinia* that uses the leaves of several genera of Saxifragaceae as host (these include *Mitella*, *Tiarella*, *Bergenia*, *Saxifraga*, *Chrysosplenium*, *Heuchera*, *Tolmiea*, and *Tellima*). Savile suggests that the rusts are "mostly of a single evolutionary group" that probably originated in the Himalayan region and there parasitized an underived saxifragaceous host-complex.

The angiosperm genus *Orobanche* (Orobanchaceae) parasitizes the roots of several Saxifragaceae in western North America, including *Suksdorfia* and *Lithophragma* (Taylor 1965).

Paleobotany. The early fossil history of Saxifragaceae is unsatisfactorily documented. Muller (1981) did not adduce any pollen record of the family, and two fossil flowers from the Upper Cretaceous of, the one Sweden and the other North America (see Friis and Skarby 1982; Gandolfo et al. 1995, 1998) also show similarities with Hydrangeaceae or other families now excluded from Saxifragaceae s. str., so that they cannot provide a precise starting point of the fossil history of the family.

Economic Importance. Species of *Astilbe*, *Bergenia*, and *Heuchera* (e.g., *H. sanguinea*, coral bells) are frequently cultivated as garden-ornamentals. Many of the species of *Saxifraga* are considered choice ornamentals, particularly in Europe, and are often grown in rock gardens. Other garden-ornamentals include *Tiarella cordifolia*, as well as an intergeneric hybrid known as *Heucherella* involving *Tiarella cordifolia* and a species of *Heuchera*. *Tolmiea menziesii* (the piggyback plant) and *Saxifraga stolonifera* are common house plants. Leaves of *Chrysosplenium* have been used as salad greens; leaves of *Astilbe* were used in the Philippines for smoking; species of *Boykinia*, *Tiarella*, and *Heuchera* were of medicinal value to native peoples. Rhizomes of *Astilboides* contain tannin and starch, and can be used to make tannin extract and wine.

Key to the Genera

1. Placentation parietal — 2
– Placentation axile — 12
2. Petals 0; sepals 4; stamens 4 or 8 — **5. *Chrysosplenium***
– Petals +; sepals 5; stamens 5 or 10, rarely 3 — 3
3. Fruit consisting of 2 very unequal dehiscent parts (carpels); stamens 10; petals entire, linear — **20. *Tiarella***
– Fruit consisting of 2 or 3 essentially equal parts; stamens 3, 5, or 10; petals entire to laciniate — 4
4. Stylodia 3; petals white or pink, laciniate, sometimes entire; plants bearing bulbils in leaf axils or on the underground parts — **13. *Lithophragma***
– Stylodia 2; petals variously colored, petals entire or three-lobed to pinnately divided; plants not bulbil-bearing — 5
5. Petals entire — 6
– Petals trifid to pectinately or pinnately lobed — 10
6. Inflorescence paniculate, spicate, or thyrsoid; seeds finely echinulate in longitudinal rows; stamens 5; calyx never narrowly turbinate — **15. *Heuchera***
– Inflorescence racemose; seeds rarely echinulate, but if so, then the calyx narrowly turbinate; stamens 3, 5, or 10 — 7
7. Stamens 3; calyx greenish-purple to reddish-brown, split much more deeply on one side than between the rest of the lobes; petals linear-subulate, reddish-purple — **18. *Tolmiea***
– Stamens 5 or 10; calyx typically green, not split much more deeply on one side than between the rest of the lobes, usually saucer-shaped to campanulate-turbinate; petals not linear-subulate, white to green — 8
8. Flowers and fruit elongate; racemes loosely 5–12-flowered; leaf margins ciliate — **16. *Conimitella***

– Flowers and fruit saucer-shaped; racemes closely 10–45-flowered; leaf margins not ciliate 9
9. Flowers slightly irregular **14. *Bensoniella***
– Flowers regular **19. *Mitella***
10. Calyx (including that portion adnate to the ovary) usually only 2–4 mm long, in one species up to 4–6 mm long but then the petals trilobed; stylodia less than 1 mm **19. *Mitella***
– Calyx (including the adnate portion) (6)7–10 mm long; stylodia over 1 mm long 11
11. Stamens 10 **12. *Tellima***
– Stamens 5 **17. *Elmera***
12. Leaves compound, sometimes unifoliate 13
– Leaves simple, entire to lobed but not compound 14
13. Rhizome slender; basal leaves often twice or three times ternately divided; petals usually present, 1–5 **28. *Astilbe***
– Rhizome large, thick; basal leaves pinnately or palmately compound; petals often 0 or occasionally 1, 2, or 5 **8. *Rodgersia***
14. Sepals and petals 4 or 5; stamens 8 **7. *Astilboides***
– Sepals and petals usually 5, rarely 0; stamens usually 5 or 10 15
15. Stamens generally 10 16
– Stamens 5(–7) 28
16. Perennial from thick, well-developed rhizome or corm, generally 1 cm or more in diameter 17
– Perennial from slender rhizome, much less that 1 cm in diameter 21
17. Petals 0 **10. *Oresitrophe***
– Petals + 18
18. Leaf blades not peltate 19
– Leaf blades peltate, nearly orbicular 20
19. Plants from thick, creeping rhizome; flowers homostylous; flowering in spring **11. *Bergenia***
– Plants from fleshy corm; flowers heterostylous; flowering in fall **22. *Jepsonia***
20. Inflorescence axis naked; petals white **6. *Darmera***
– Inflorescence axis bearing a single leaf; petals pale yellow **4. *Peltoboykinia***
21. Stems slender, weak, prostrate 22
– Stems erect 23
22. Ovary not much longer than wide, nearly completely inferior; petals not much longer than sepals, and with pink to purple specks **2. *Saxifragodes***
– Ovary elongate, 1/2–2/3 inferior; petals distinctly longer than sepals, without pink to purple specks **1. *Cascadia***
23. Carpels distinct almost to the base, adnate to the calyx for less than 1/5 their length; leaves leathery; anthers bisporangiate, dehiscing terminally by broad opening 24
– Carpels usually fused or adnate to the calyx for at least 1/5 their length; leaves not leathery; anthers tetrasporangiate, opening by longitudinal slits 25
24. Leaves slightly crenate; flowers apetalous **30. *Leptarrhena***
– Leaves serrate; flowers with petals **31. *Tanakaea***
25. Leaf blade jointed to and falling before petiole **29. *Saxifragopsis***
– Leaf blade not jointed to or falling before petiole 26
26. Plants glandular pubescent; stylodia partially connate; petals pink to deep red or purple; calyx campanulate, usually reddish, (5)6–10 mm long; leaves alternate, petiolate **21. *Telesonix***
– Plants usually not glandular pubescent; stylodia free above the ovuliferous portion of the ovary; petals usually white, but if (rarely) pink or red (to purple), then either the calyx not immediately campanulate, red, nor as long as 6 mm, or the leaves sessile and opposite 27
27. Flowering stem leafless, sometimes with large bracts (all leaves arranged in basal rosette); pollen surface reticulate; ovules unitegmic; leaf crystals present **3. *Micranthes***
– Flowering stem generally leafy; pollen surface granular or striate, never reticulate; ovules bitegmic; leaf crystals generally 0 **32. *Saxifraga***
28. Leaves all basal (scape leafless); carpels 2–3 29
– Leaves basal and cauline; carpels 2 30
29. Carpels 2; bracts and disc 0 **9. *Mukdenia***
– Carpels 2–3; bracts and disc + **33. *Saniculiphyllum***
30. Calyx campanulate, the sepals lanceolate-acuminate; ovary appearing nearly superior **23. *Bolandra***
– Calyx not campanulate, various as to size and shape, the sepals not lanceolate-acuminate; ovary with an obvious inferior region 31
31. Plants bulbiferous at the root stock, neither stoloniferous nor conspicuously rhizomatous; flowering stems rarely over 2 dm tall; upper cauline leaves conspicuously stipulate; petals white, rose, or violet **25. *Suksdorfia*** (see also **26. *Hieronymusia***)
– Plants not bulbiferous at the root stock, usually either stoloniferous or with evident rhizomes; flowering stems either well over 3 dm tall or else the upper cauline leaves without conspicuous stipules; petals white 32
32. Petals 1.5–2.5 mm long, withering persistent; calyx mostly 2.5–3.5 mm long; stems rarely 25 cm tall **24. *Sullivantia***
– Petals mostly 4–7 mm long, deciduous; calyx rarely less than 4 mm long; stems (15)20–80(100) cm tall **27. *Boykinia***

Genera of Saxifragaceae

I. Heucheroids

I.1. Cascadia Group

Perennials with slender, prostrate stems. Leaves alternately inserted along the length of the stem. Flowers borne at tips of stems on short peduncles; calyx lobes 5; petals 5; stamens 10; carpels 2; placentation axile.

1. *Cascadia* A.M. Johnson

Cascadia A.M. Johnson, Amer. J. Bot. 14:38 (1927).

Stems weak, frequently branching from below the middle. Leaves petiolate, alternate, ovate-lanceolate to lanceolate, leaves of inflorescence branches reduced to bracts. Flowers with well-developed hypanthium; petals distinctly longer than sepals; ovary elongate, 1/2–2/3 inferior; seeds spiny. One species, *C. nuttallii* A.M. Johnson, from a small area of western Oregon and Washington.

2. *Saxifragodes* D.M. Moore

Saxifragodes D.M. Moore, Bot. Notiser 122:324 (1969).

Stems slender, branched at base. Leaves suborbicular to ovate-elliptical, entire or three-lobed; petals 5, varying from slightly shorter than to slightly longer than the sepals, elliptic to oblanceolate, white with pink to purple flecks; fertile stamens 6; ovary nearly completely inferior. Capsule ovoid, compressed, deeply bifid; seeds tuberculate, brown. One poorly understood species, *S. albowiana* D.M. Moore, from Tierra del Fuego.

I.2. Micranthes Group

3. *Micranthes* Haworth Fig. 147

Micranthes Haworth, Syn. Pl. Succ.: 320 (1812).
Saxifraga sects. *Micrantha* and *Merkianae*, Engler & Irmscher, Pflanzenreich IV, 117:1–448 (1916).

Herbaceous perennial. Leaves primarily or exclusively basal, entire, toothed, or lobed, petiolate to sessile, glabrous to glandular-hairy, with calcium oxalate crystals. Inflorescence cymose, leafless (sometimes with conspicuous bracts). Flowers regular, perfect, calyx saucer-shaped to conic or campanulate; calyx lobes 5; petals commonly 5, white to greenish, yellow; stamens 10, inserted with the petals on or at the top of the hypanthium (if any); carpels 2(3), ranging from only basally fused to connate well above the ovuliferous portion; ovary nearly superior to more than half inferior; placentation axile; ovules unitegmic. Fruit capsular and dehiscent for at least half its length; seeds numerous, smooth to variously wrinkled, winged, crested, muricate, or tuberculate. $2n$ = 10–120. About 70 species, primarily of north temperate to Arctic regions.

See comment under *Saxifraga*.

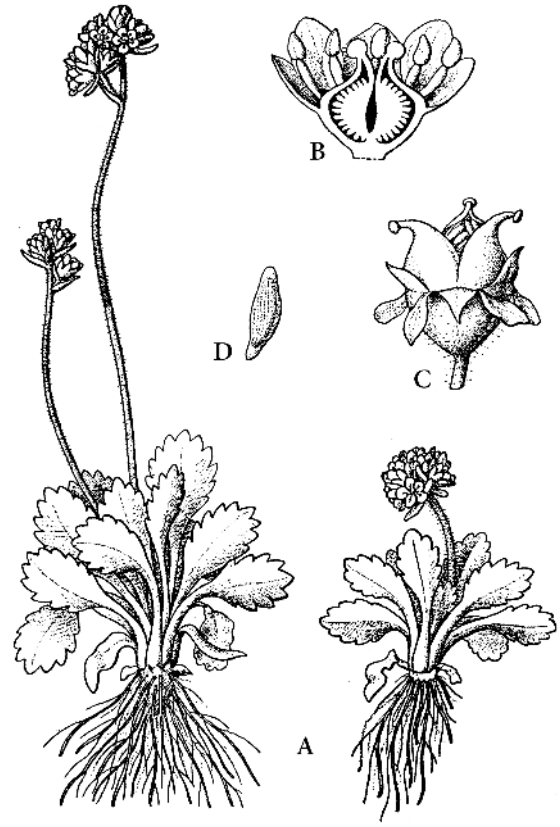

Fig. 147. Saxifragaceae. *Micranthes nivalis*. **A** Habit. **B** Flower, vertically sectioned. **C** Dehiscing tricarpellate fruit. **D** Seed. (Engler 1930)

I.3. Peltoboykinia Group

Perennials. Leaves basal and cauline (cauline leaves few and alternate). Flowers regular; carpels 2; fruit capsular; x = 11.

4. *Peltoboykinia* (Engler) H. Hara

Peltoboykinia (Engler) H. Hara, Bot. Mag. (Tokyo) 51:251 (1937); Gornall & Bohm, Bot. J. Linn. Soc. 90:1–71 (1985), rev.

Large, erect herb from short, thick, creeping rhizome. Leaves chiefly basal, long-petioled, large, peltate, palmately lobed, stipules membranous. Inflorescence a few-leaved, terminal cyme; calyx-tube shallowly campanulate, adnate to the ovary on lower half, lobes 5; petals 5, pale yellow, toothed, glandular-dotted, ascending, deciduous; stamens 10; ovary nearly superior but with a short inferior region; placentation axile. Capsules enclosed in the somewhat inflated calyx-tube; seeds numerous, longitudinally tuberculate. $2n$ = 22. One species, *P. tellimoides* (Maxim.) H. Hara, Japan.

5. *Chrysosplenium* L. Fig. 148

Chrysosplenium L., Sp. Pl.: 398 (1753); Hara, J. Fac. Sci. Univ. Tokyo, Bot. 7:1–90 (1957), rev.

Plants stoloniferous. Leaves glabrous to pilose, small, opposite or alternate, petiolate, crenate, estipulate. Inflorescence a few-flowered terminal or apparently axillary cyme, or flowers solitary. Flowers greenish, yellow, or white, often inconspicuous; calyx adnate to the lower half of the ovary, broadly campanulate, the lobes 4, spreading; petals 0; stamens 4 or 8, alternating with small,

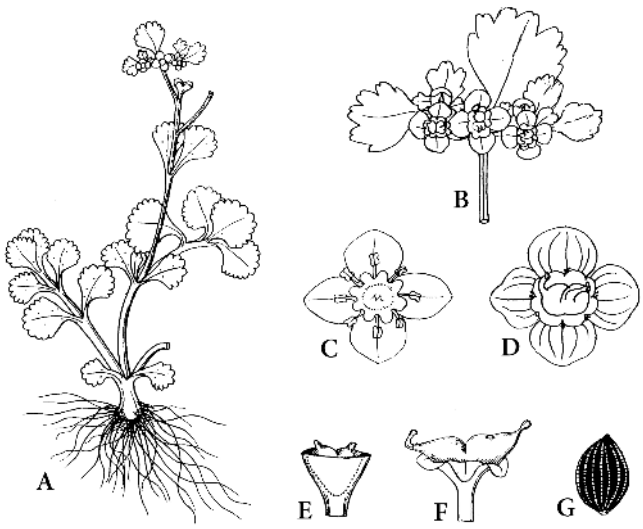

Fig. 148. Saxifragaceae. *Chrysosplenium biondianum*. **A** Flowering plant. **B** Inflorescence. **C** Male flower. **D** Female flower. **E** Pistil. **F** Fruit. **G** Seed. (Wu and Raven 2003)

fleshy glands forming a minute disc-like margin around the ovary; ovary slightly to more than half inferior, the 2 short stylodia protruding through the disc; placentation parietal. Capsule 2-lobed and dehiscent throughout the superior portion; seeds small, several to numerous, smooth; the most common chromosome numbers are $2n = 22$ and 24, other numbers include $2n = 8$, 14, 16, 18, and 42. Approximately 55 species, in moist areas of temperate to arctic North America and Eurasia, several in South America; most species occur in Asia.

Molecular data (Nakazawa et al. 1997; Soltis, Tago-Nakazawa et al. 2001) support the traditional division of the genus into opposite- and alternate-leaved species (see Franchet 1890; Hara 1957).

I.4. Darmera Group

Perennials from large, thick, sometimes scaly, horizontal rhizome. Leaves sometimes only basal, or with few, alternate, cauline leaves much smaller than basal leaves. Inflorescence sometimes leafless, cymose. Flowers numerous, regular; carpels generally 2; placentation axile. Fruit follicular, opening between the stylodia; $2n = 30$ or higher, generally $2n = 34$.

6. *Darmera* (Torrey) A. Voss

Darmera (Torrey) A. Voss, Gart. Zentral-Bl. 1:625 (1899). *Peltiphyllum* Engler (1890).

Large herb, rhizome scaly, typically submerged. Leaves only basal, large, peltate, developing later than inflorescence. Inflorescence large, leafless. Flowers showy; calyx adnate to the base of the ovary, deeply 5-lobed; petals 5, white to bright pink, entire; stamens 10; carpels 2, free above the point of adnation with the calyx; ovary nearly superior, but with short inferior region; seeds cellular-rugulose; $2n = 34$. One species, *D. peltata* (Torr.) A. Voss, occurring along fast-flowing streams in northern California and southern Oregon.

7. *Astilboides* Engler

Astilboides Engler in Nat. Pflanzenfam., ed. 2, 18a:116 (1930); Jintang et al., Fl. China 8:269–452 (2001).

Large herb, rhizome scaly. Leaves primarily basal, large, nearly round or ovate, with short and stiff hairs on both surfaces, shallowly palmately lobed, stem leaf one, similar to the basal leaf, but smaller. Inflorescence with one leaf similar to the basal leaf, but smaller. Flowers numerous, small, white; calyx bell-shaped, 4–5-lobed, the lobes broad ovate; petals 4–5, obovate-oblong; stamens 8; carpels 2; ovary with short inferior region; seeds winged; $2n = 34$, 36. One species, *A. tabularis* (Hemsl.) Engler, northeastern China (provinces Liao-ning and Ji-ling) and Korea, in mountain forests and along valley streams.

8. *Rodgersia* A. Gray

Rodgersia A. Gray, Mem. Amer. Acad. Arts II, 6:389 (1858).

Large herb with short, stout, scaly rhizome. Leaves primarily basal, palmately or pinnately compound, long-petiolate; leaflets 3–9(10), toothed. Inflorescence large and few-leaved, the ultimate branches scorpoid-cymose. Flowers numerous, white, small; calyx-tube shallow, short, the lobes (4)5(–7), spreading, white at anthesis; petals narrowly linear, small, often 0 or occasionally 1, 2, or 5; stamens usually 10(–14); carpels 2(3); ovary nearly superior but with a short inferior region. $2n = 30$, 60 (Fedorov 1969). Five species, from the Himalayas to East Asia (Japan), in mountain forests.

9. *Mukdenia* Koidzumi

Mukdenia Koidzumi, Acta Phytax. Geobot. 4:120 (1935). *Aceriphyllum* Engl. (1890).

Herbs from large rhizome. Leaves basal, palmately 5-lobed. Inflorescence scapose, partial inflorescences cincinnate. Flowers showy; calyx

adnate to the base of the ovary, deeply 5–6-lobed, white, longer than the petals; petals white, 5–6(7); stamens 5–6(7); carpels 2, basally connate; ovary nearly superior but with a short inferior region. Fruit a capsule. $2n = 34$. One species, *M. rossii* (Oliver) Koidzumi, from northern China and Korea, on rocky slopes and in ravines.

10. *Oresitrophe* Bunge

Oresitrophe Bunge, Enum. Pl. China Bor. 31 (1833).

Herbs from short, thick, rhizome. Leaves 2–3, basal, petiolate, blade ovate to cordate, dentate, nearly glabrous. Inflorescence cymose with dense glandular hairs. Flowers small, hypanthium bowl-shaped; calyx lobes 5–7, oblong-ovate, pink and petaloid; petals 0; stamens 10–14, with thin, thread-like filaments and purple anthers; carpels 2; ovary with a short inferior region, nearly superior, cone-shaped. One poorly known species, *O. rupifraga* Bunge, from mountains near Beijing, China.

11. *Bergenia* Moench Fig. 149

Bergenia Moench, Methodus: 664 (1794); Yeo, Kew Bull. 26:113–148 (1966), rev.

Herbs from large, scaly rhizome, forming dense clumps or colonies. Leaves basal, with immersed glands, thick, waxy, simple, persistent, entire, toothed, or crenate. Inflorescence large, bractless. Flowers showy; calyx 5-lobed, green, not fused with ovary; petals 5, entire, white, pink, red, or purple; stamens 10 with pointed filaments and short ovate anthers opening to the side; carpels 2(3), connate at base; ovary with a short inferior region, nearly superior; seeds dark brown. $2n = 34$. Ten species from the Himalayas, northern Mongolia, Siberia, and China.

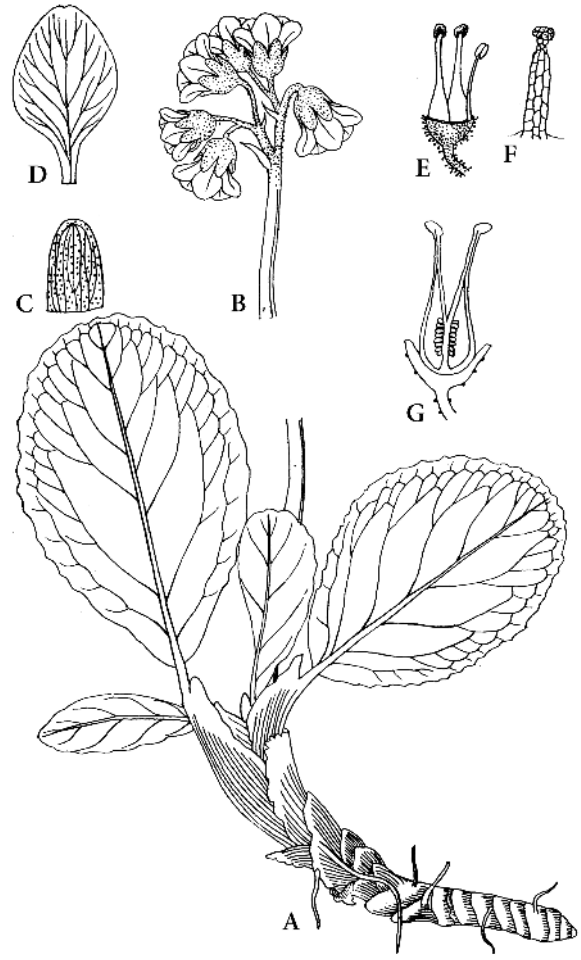

Fig. 149. Saxifragaceae. *Bergenia purpurascens*. **A** Habit. **B** Inflorescence. **C** Sepal, adaxial view. **D** Petal. **E** Stamen and pistil. **F** Glandular hair. **G** Gynoecium, vertically sectioned. (Wu and Raven 2003)

I.5. Heuchera Group

Perennials. Leaves basal and cauline (cauline leaves few, sometimes 0), alternate, rarely opposite or 0, simple, long-petiolate, reniform, palmately veined, stipules small, membranous; calyx lobes 5; petals 5(4, 0); stamens 3, 5, or 10; carpels 2(3); placentation parietal; $x = 7$.

12. *Tellima* R. Br.

Tellima R. Br. in Franklin, Narrat. J. Polar Sea app.: 765 (1823).

Plants from short, stout rhizome, coarsely hirsute. Leaves cordate-ovate, slightly lobed. Inflorescence an elongate, minutely bracteate raceme. Flowers showy, hypanthium well-developed, campanulate-tubular; petals 5, short-clawed, the blade pinnately divided, white; stamens 10; carpels 2; ovary about 1/4 inferior. Capsule dehiscent along the sutures of the beaks, seeds brown, ellipsoid-ovoid. $2n = 14$. One species, *T. grandiflora* R. Br. from northern California to southeastern Alaska.

13. *Lithophragma* Nutt.

Lithophragma Nutt., J. Acad. Philadelphia 7:26 (1834); Taylor, Univ. Calif. Publ. Bot. 37:1–122 (1965), rev.

Plants from slender rhizome bearing numerous bulblets. Leaves orbicular-reniform to reniform, palmately parted or cleft, the petioles slender, cauline leaves 1–several, reduced, sometimes ses-

sile. Inflorescence a terminal raceme, sometimes with bulblets in the axils of the cauline leaves and the bracts. Flowers showy, rarely replaced by bulblets, hypanthium narrowly cyathiform-obconic to campanulate or cup-shaped; petals 5, white or pink or purplish-tinged, narrowly clawed and with a large, expanded, usually digitately, rarely pinnately cleft or divided to shallowly lobed or sometimes entire blade; stamens 10; carpels 3; ovary position ranging from very slightly inferior [appearing superior] to nearly fully inferior. Capsule 3-valved, seeds slightly wrinkled but otherwise smooth to irregularly reticulate, verrucose, or muricate. $2n$ = 14, 28, 35, 42. Ten species of temperate western North America.

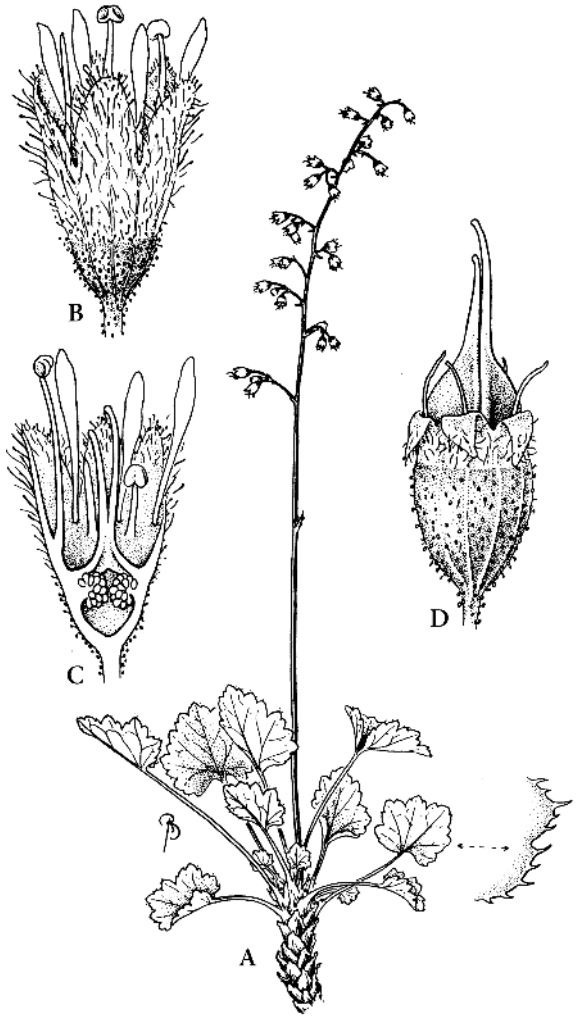

Fig. 150. Saxifragaceae. *Heuchera rubescens*. **A** Habit. **B** Flower. **C** Same, vertically sectioned. **D** Fruit. (Drawing B. Angell; Cronquist et al. 1997)

14. *Bensoniella* Morton

Bensoniella Morton, Leafl. W. Bot. 10:181 (1965).

Plants with long, slender, branching rhizome. Leaves cordate, petioles slender with long brown hairs. Inflorescence a scapiform raceme. Flowers slightly irregular, hypanthium campanulate; petals 5, filiform, entire, whitish; stamens 5, antesepalous; carpels 2, connate for half their length, subcompressed; ovary slightly inferior. Capsule widely dehiscing between the stylodia. $2n$ = 14. One species, *B. oregona* Morton, western USA.

15. *Heuchera* L. Fig. 150

Heuchera L., Sp. Pl. 1:226 (1753); Rosendahl, Butter & Lakela, Monogr. of *Heuchera* (1936); Wells, Syst. Bot. Monogr. 3:45–121 (1984), rev. eastern N. Amer. spp.

Plants usually with thick, scaly rootstocks and erect, naked to bracteate flowering stems, glandular to sometimes glabrous. Leaves primarily basal, palmately lobed and usually deeply once or twice crenate-dentate. Inflorescence with or without leaves, paniculate, spicate, or thyrsoid. Flowers regular, rarely slightly irregular, usually complete, hypanthium greenish, yellowish, or red, from shallowly saucer-shaped to conic or tubular-campanulate, adnate to the ovary; petals 5, sometimes fewer, rarely 0, white to greenish-yellow, or red, mostly distinctly clawed and with an ovate to spatulate or linear, entire blade; stamens 5; carpels 2; ovary from about half to nearly completely inferior, stylodia well-developed to almost 0. Capsule dehiscent along the beaks; seeds spinulose in longitudinal rows, sometimes nearly smooth. $2n$ = 14, 28. About 35 species of North America, ranging from southern Mexico to the Arctic, with most species in western USA.

16. *Conimitella* Rydb.

Conimitella Rydb., N. Amer. Fl. 22:2, 96 (1905).

Plants from short rhizome. Leaves basal, reniform, ciliate. Inflorescence a terminal, inconspicuously bracteate raceme; flowers regular, complete, elongate; calyx turbinate-obconic, adnate to the ovary for about 1/2–1/3 its length, the hypanthium tubular; petals 5, white, with an entire blade and slender claw; stamens 5, antesepalous; carpels 2(3); ovary almost completely inferior, with short stylodia. Capsule dehiscing from small stylar region. $2n$ = 14. One species, *C. williamsii* Rydb., western USA.

17. *Elmera* Rydb.

Elmera Rydb., N. Amer. Fl. 22:2, 97 (1905).

Plants with slender rhizome. Leaves primarily basal, reniform, palmately lobed and once or twice crenate, strongly pubscent, glandular above. Inflorescence a minutely bracteate, simple, terminal raceme. Flowers showy, regular; calyx cup-shaped, adnate to the ovary at the base; petals 5, white, short-clawed, blade 3–7-cleft or entire; stamens 5, opposite to, and shorter than, the calyx lobes; carpels 2; ovary 1/4 inferior. Fruit an ovoid capsule dehiscent on the beaklike upper portion. $2n = 14$. One species, *E. racemosa* Rydb., Pacific Northwest of the USA.

18. *Tolmiea* (Pursh) Torr. & Gray

Tolmiea (Pursh) Torr. & Gray, Fl. N. Am. 1:582 (1840).

Plants from slender rhizome. Leaves primarily basal, often with prominent plantlet at base of blade. Inflorescence a sparingly leafy raceme. Flowers showy, irregular; calyx free of the ovary, greenish-purple to reddish-brown, with a tubular, oblique-based hypanthium; petals 4, linear-subulate, reddish-purple; stamens 3; carpels 2; ovary appearing nearly superior but with a very short inferior region. Fruit a capsule dehiscent along the divergent beaks; seeds dark brown to black, smooth, ovoid. $2n = 14, 28$. Two species, *Tolmiea menziesii* (Pursh) Torr. & Gray, from northern California to southeastern Alaska.

19. *Mitella* L. Fig. 151

Mitella L., Sp. Pl. 1:406 (1753); Rosendahl, Bot. Jahrb. Syst. 50, suppl.: 375–397 (1914), rev.

Plants rhizomatous, rarely stoloniferous, glandular-puberulent and often somewhat hirsute with leafless or 1–3-foliate flowering stems. Leaves cordate or ovate to reniform cordate. Inflorescence an elongate, bracteate, simple raceme. Flowers regular; calyx saucer-shaped to turbinate-campanulate, adnate to the ovary; petals 5, borne with the stamens at, or near the top of, the hypanthium, greenish, white, or pinkish-to purple-tinged, slenderly clawed and with a usually filiformly dissected to trilobed, rarely entire blade; stamens 10, or 5 and then either opposite or alternate with the calyx lobes; carpels 2; ovary from less than half to nearly completely inferior. Fruit a capsule, dehiscent by adaxial, rarely ventral sutures on the free, lobed portion, the dehiscent fruit appearing almost circumscissile; seeds generally black. $2n = 14, 28$. This broadly defined genus comprises 20 species as traditionally circumscribed; these are mostly of the western USA, Japan, and eastern Asia.

The genus is clearly polyphyletic, comprising perhaps four or more distinct lineages most of which ultimately should be recognized as distinct genera (Soltis and Kuzoff 1995).

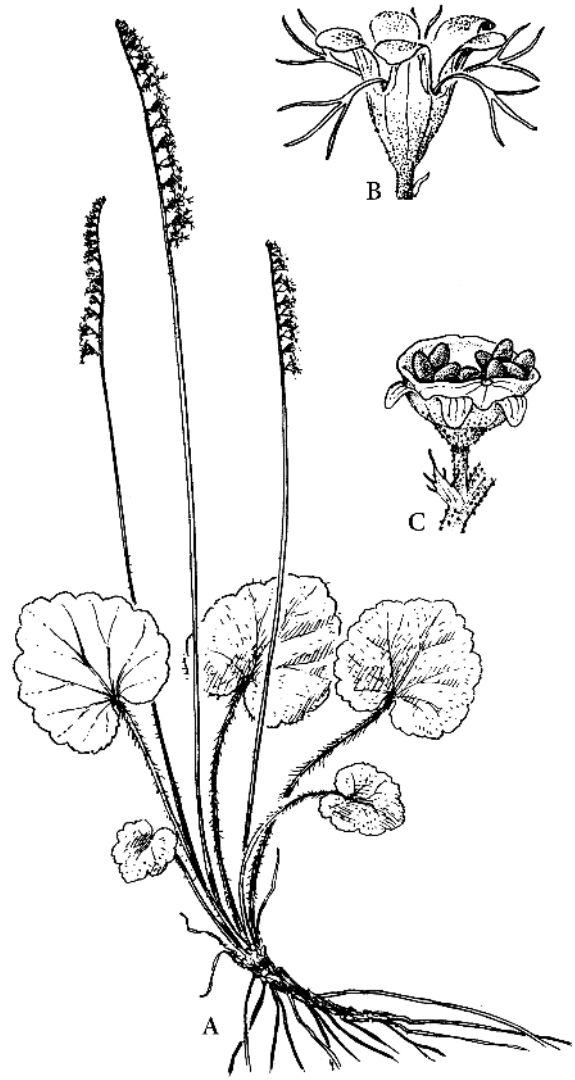

Fig. 151. Saxifragaceae. *Mitella stauropetala*. **A** Habit. **B** Flower. **C** Dehisced splash-cup capsule. (Cronquist et al. 1997)

20. *Tiarella* L.

Tiarella L., Sp. Pl. 1:405 (1753); Lakela, Amer. J. Bot. 24:344–351 (1937), rev.

Plants from slender (sometimes spreading) rhizome. Leaves primarily basal, cordate and palmately lobed to 3-foliolate, variously toothed to cleft, leaves on infloresence 2–3-foliate. Inflorescence an elongate raceme. Flowers showy, slightly irregular; calyx irregular, hypanthium campanulate, free or nearly so of the ovary; petals 5, white, linear to subulate, very similar to the filaments; stamens 10; carpels 2, unequal at anthesis; ovary appearing nearly superior but with a very short inferior region. Fruit dehiscent along the unequal sterile valves above the fertile basal portion; seeds nearly black, shining and almost smooth. $2n = 14$. Three species, one each in Asia, and western and eastern North America, the western North American species, *T. trifoliata* L., comprising three varieties sometimes treated as three distinct species.

I.6. Boykinia Group

Perennials. Leaves basal and cauline (cauline leaves few, alternate, usually much smaller than basal leaves), simple, reniform, palmately veined, and long-petiolate with small, membranous stipules. Inflorescence cymose. Flowers perfect, regular; calyx lobes 5; petals 5; carpels 2; placentation axile; fruit a loculidal capsule. $x = 7$.

21. *Telesonix* Raf.

Telesonix Raf., Fl. Tell. 2:69 (1836).

Plants glandular-pubescent, from short, thick rootstocks. Leaves reniform, doubly crenate; inflorescence compact, terminal, few-flowered, bracteate. Flowers showy; calyx turbinate-campanulate, adnate to the lower part of the ovary, with a somewhat expanded, tubular, free hypanthium, the lobes ovate-lanceolate; petals pink to deep red or purple, ovate to spatulate; stamens 10, inserted at the top of hypanthium, from barely as long to nearly twice as long as the calyx lobes; ovary about half inferior, tapered above into the somewhat beaklike stylodia. $2n = 14$. Two species, western USA.

22. *Jepsonia* Small

Jepsonia Small, Bull. Torrey Bot. Club 23:18 (1896); Ornduff, Brittonia 21:286–298 (1969), rev.

Plants from distinctive, fleshy corm. Leaves basal, long-petiolate, round-cordate, lobed and toothed. Inflorescence appearing in the fall (basal leaves not present at that time), with multiple inflorescences developing. Flowers heterostylous, hypanthium campanulate, not fused with the ovary; calyx lobes yellow green to pink, short, triangular; petals lanceolate, white with tan or purple veins; stamens 10; ovary with a small inferior region. Capsule thin-walled, opening between the stylodia. $2n = 14$, 28. Three closely related species from southern California, Channel Islands, and Baja California.

23. *Bolandra* Gray

Bolandra Gray, Proc. Amer. Acad. Arts Sci. 7:341, 342 (1867); Gornall & Bohm, Bot. J. Linn. Soc. 90:1–71 (1985), rev.

Plants with short, bulbiferous rhizome. Leaves primarily basal, reniform, palmately veined and long-petiolate, the upper cauline leaves reduced but their stipules becoming larger. Inflorescence terminal, few-flowered, open, conspicuously bracteate; calyx tubular-campanulate, with lanceolate, spreading lobes, greenish and purplish-tinged; petals linear, nearly erect or only slightly spreading, reddish-purple, exceeding the stamens; stamens 5, opposite the sepals; carpels fused only 1/4–1/5 their length, free of the calyx; ovary appearing nearly superior. $2n = 14$. Two species, western USA.

24. *Sullivantia* Torrey & Gray ex Gray

Sullivantia Torrey & Gray ex Gray, Amer. J. Sci. 42:22 (1842); Soltis, Brittonia 43:27–53 (1991), rev.

Plants moderately glandular-pubescent, one species stoloniferous. Leaves cordate-reniform, incised-lobed and sharply toothed. Inflorescence of usually numerous flowers in a modified compound cyme; calyx turbinate, the lobes triangular, about as long (at anthesis) as the lower adnate portion; petals white, persistent; stamens 5, opposite the calyx lobes; ovary 1/2–3/4 inferior. Capsule dehiscent along the ventral suture of the sterile portion of the 2 carpels; seeds linear-fusiform, narrowly wing-margined. $2n = 14$. Three species, USA.

25. *Suksdorfia* Gray

Suksdorfia Gray, Proc. Amer. Acad. Arts Sci. 15:41, 42 (1879); Gornall & Bohm, Bot. J. Linn. Soc. 90:1–71 (1985), rev.

Plants with very short, sparsely to copiously bulbiferous rootstock. Leaves crenate to deeply divided, cordate to reniform, cauline leaves strongly stipulate, glandular-pubescent at least in the inflores-

cence. Inflorescence few- to many-flowered; calyx lobes erect to spreading; petals white, rose, or violet, erect to spreading, entire, spatulate to oval; stamens 5, antesepalous; ovary slightly more than half to nearly completely inferior. Capsule dehiscent along the ventral sutures of the beaks; seeds somewhat prismatic, faintly to prominently warty. $2n = 14$. Two species, Pacific Northwest of North America.

26. *Hieronymusia* Engler Fig. 152

Hieronymusia Engler, Notizbl. Bot. Gart. Mus. Berlin-Dahlem 7:265–267 (1918).

Plants from a slender rhizome. Leaves round-cordate, shallowly lobed and serrate. Inflorescence with distal 3–5-flowered partial inflorescences subtended by leafy bracts with spatulate, toothed stipules; calyx lobes erect, prolonged above into a nearly companulate hypanthium, fused with ovary; petals ovate, sessile with broad base, smaller than sepals; stamens 5; ovary completely inferior. One poorly known species, *H. alchemilloides* (Griseb.) Engl., placed in *Suksdorfia* by Gornall and Bohm (1985); Sierra de Tucuman in Argentina and in Bolivia on damp, shady humus and damp rock cliffs at 3,000–4,000 m.

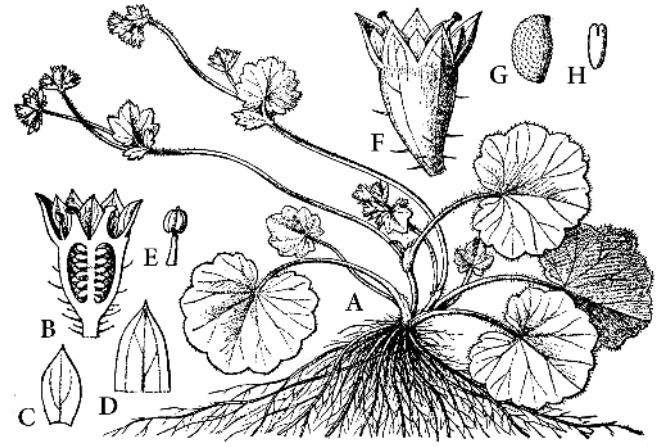

Fig. 152. Saxifragaceae. *Hieronymusia alchemilloides*. **A** Habit. **B** Flower, longitudinally sectioned. **C** Sepal. **D** Petal. **E** Anther. **F** Nearly mature fruit. **G** Seed. **H** Embryo. (Engler 1930)

27. *Boykinia* Nutt.

Boykinia Nutt., J. Acad. Nat. Sci. Philadelphia 7:113 (1834), nom. cons.; Gornall & Bohm, Bot. J. Linn. Soc. 90:1–71 (1985), rev.

Plants glandular-pubescent and often brownish-pilose, from slender to thick, scaly rhizomes. Leaves cordate to reniform, several times shallowly cleft and toothed; stipules varying from well-developed and leaf-like to bristle-like. Inflorescence terminal or subterminal; calyx turbinate to campanulate, green, prolonged above ovary as a tubular hypanthium, the lobes equal, lanceolate; petals white, spatulate or obovate to oblong-ovate, short-clawed, caducous; stamens 5, inserted with the petals at the top of the hypanthium opposite the calyx segments; ovary 1/3 to 3/4 inferior; seeds minutely tuberculate. $2n = 12, 14, 26, 28, 36, 84$. Six species, four from western North America, one in eastern North America, and one in Japan.

I.7. Astilbe Group

Perennials from slender, woody rhizome. Leaves basal and cauline (cauline leaves few, alternate, and much smaller than the basal leaves), compound, rarely unifoliolate; stipules scarious; leaflets lanceolate to ovate-orbicular, basally cuneate, toothed. Inflorescence a bracteate panicle. Flowers numerous, regular, small; calyx lobes and petals generally 5; carpels 2, connate at the base; ovary appearing nearly superior, but with a short inferior region; placentation axile. Fruit follicular, dehiscing between the stylodia; $x = 7$.

28. *Astilbe* Buch.-Ham.

Astilbe Buch.-Ham. ex D. Don, Prodr. Fl. Nepal.: 210 (1825).

Leaves ternately compound, rarely unifoliolate. Flowers white or rose purple, bisexual or unisexual, plants sometimes dioecious; calyx-tube short, adnate to base of ovary, lobes 5(7–11); petals persistent, linear, (0)1–5; stamens 5, 8, or 10. $2n = 14, 28$. About 25 species, one or perhaps two endemic to the southern Appalachians in North America, and about 23 in eastern Asia from Japan through China into the Himalayan region and extending southward into New Guinea.

29. *Saxifragopsis* Small

Saxifragopsis Small, Bull. Torrey Bot. Club 23:19 (1896).

Leaves unifoliolate, blade jointed to and falling before petiole. Flowers bisexual, showy; hypanthium campanulate, partly fused with the base of the ovary; calyx lobes 5, ovate to ovate-lanceolate, recurved; petals 5, white; spatulate, pointed, 1.5 times longer than the sepals, recurved; stamens 10, with

pointed, basally winged filaments. $2n = 14$. One species, *S. fragaroides* (Greene) Small, in northern California and southern Oregon. Sometimes erroneously placed in *Saxifraga*; it is, in fact, the sister group to *Astilbe*.

I.8. Leptarrhena Group

Perennials; strongly rhizomatous. Leaves leathery, persistent or evergreen, short-petiolate, estipulate, primarily basal, cauline leaves few, much smaller than basal leaves. Inflorescence paniculate. Flowers numerous, regular; calyx lobes typically 5; stamens 10; anthers bisporangiate, dehiscing terminally; carpels 2, fused only at the base; ovary only slightly inferior; placentation axile. Capsule ventrally dehiscent. $2n = 14$.

30. *Leptarrhena* R. Br.

Leptarrhena R. Br., Chlor. Melvill.: 15 (1823).

Leaves persistent but not evergreen. Inflorescence sparsely leafy, slightly glandular-pubescent. Flowers numerous, tightly aggregated; hypanthium deeply saucer-shaped; calyx lobes 5, erect; petals 5, white, small, persistent. One species, *L. pyrolifolia* R. Br., Pacific Northwest of USA to Alaska.

31. *Tanakaea* Franchet & Savat.

Tanakaea Franchet & Savat., Enum. Pl. Jap. 2:352 (1878).

Plants stoloniferous. Leaves primarily basal, oblong, irregularly serrate, evergreen. Inflorescence with small linear bracts; flowers white, functionally unisexual and plants dioecious; calyx-tube short, shallow, the lobes (4)5(–7); petals 0. One species, *T. radicans* Franchet & Savat., in China and Japan.

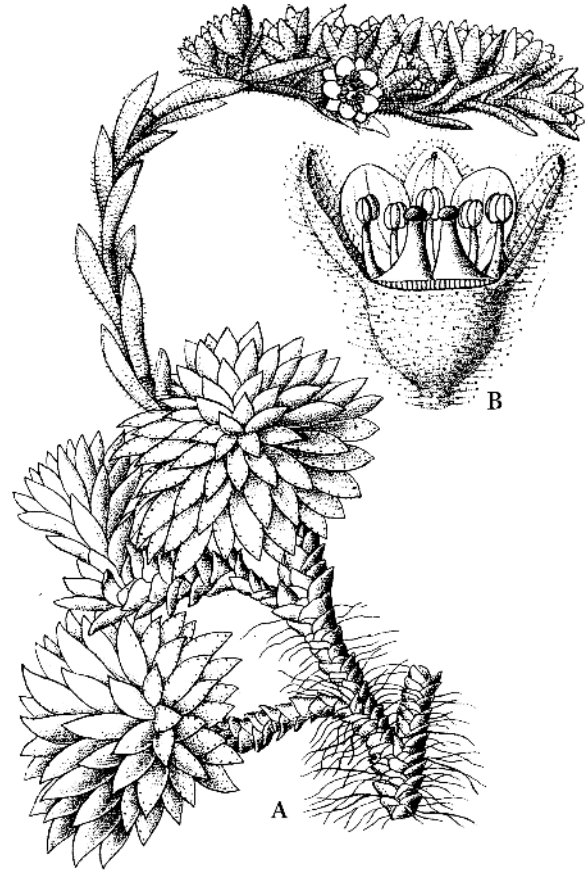

Fig. 153. Saxifragaceae. *Saxifraga media* Gouan. **A** Habit. **B** Flower. (Engler and Irmscher 1919)

II. Saxifragoids

32. *Saxifraga* L. Figs. 153, 154, 155

Saxifraga L., Sp. Pl. 1:398 (1753), excl. sects. *Micranthes* and *Merkiana*, Engler & Irmscher in Pflanzenreich IV, 117 (1919).
Zahlbrucknera Reichb. (1832).
Saxifragella Engler (1890).

Perennials or more rarely delicate annuals or biennials. Leaves entire to toothed, lobed, or pinnatifid, simple, alternate, rarely opposite, petiolate to sessile, glabrous to usually glandular-hairy, sometimes with bulbils in the leaf axils or in the inflorescence, generally without calcium oxalate crystals

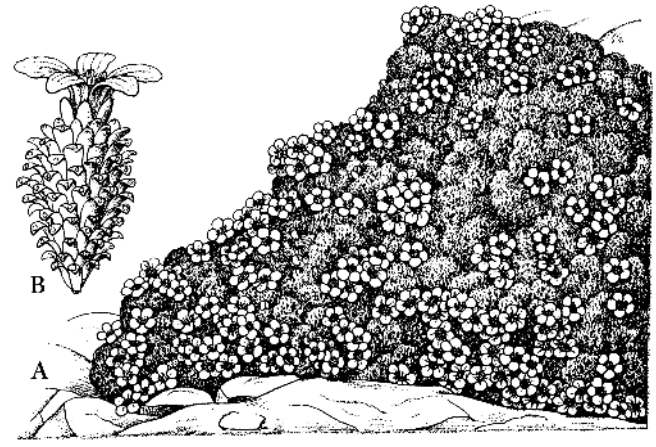

Fig. 154. Saxifragaceae. *Saxifraga imbricata* Royle. **A** Cushion. **B** Flowering branch. (Engler and Irmscher 1919)

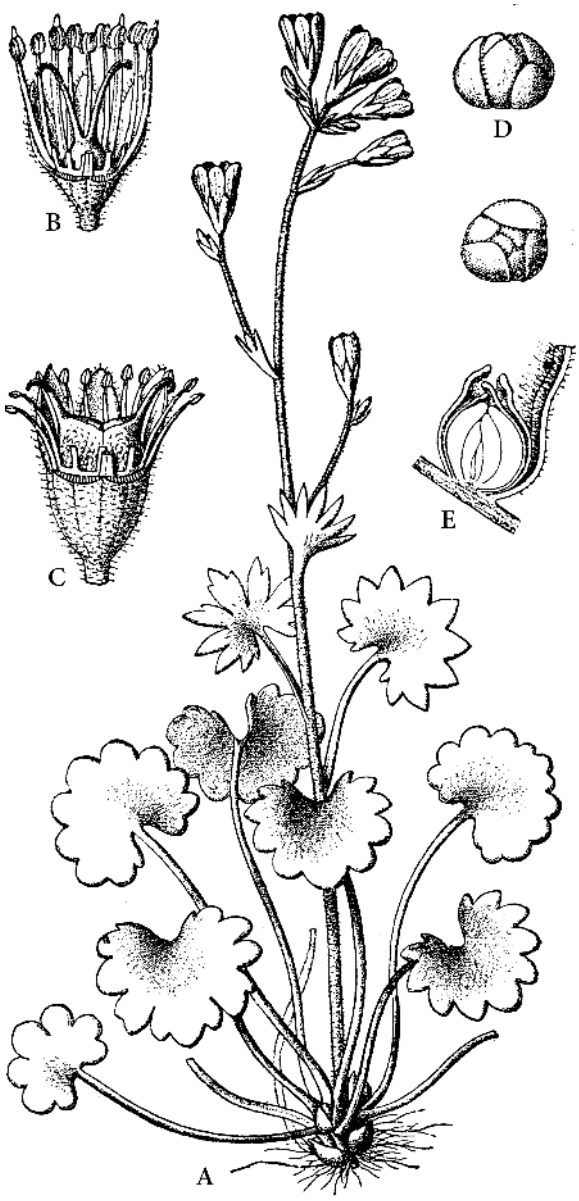

Fig. 155. Saxifragaceae. *Saxifraga granulata*. **A** Habit. **B** Flower. **C** Fruit. **D** Bulbils. **E** Bulbil vertically sectioned. (Engler and Irmscher 1919)

(these present in section *Irregulares*). Inflorescence cymose, generally leafy. Flowers generally regular but conspicuously irregular in section *Irregulares*, usually perfect; calyx lobes 5, saucer-shaped to conic or campanulate; petals commonly 5, white [spotted or flecked with yellow or reddish-purple] to greenish, yellow, or violet-purple, usually alike, clawless or with a distinct and often slender claw, deciduous or persistent; stamens 10, inserted with the petals on or at the top of the hypanthium, if any, or on the calyx around the ovary; pollen surface granular or striate, not reticulate; carpels 2, rarely 3, 4, or even 5, from distinct and joined at base to connate well above the ovuliferous portion; ovary ranging from nearly superior in appearance to completely inferior; placentation axile. Fruit from plainly capsular and dehiscent across the top by the ventral sutures of the stylar beaks to follicular and dehiscent the full length; seeds numerous, with two integuments, from smooth to variously wrinkled, muricate, or tuberculate. $2n = 10$ to more than 200. *Micranthes* has been considered part of a broadly defined *Saxifraga*, but the former is clearly a distinct lineage that should be recognized as a distinct genus. *Saxifraga* in the narrow sense is a morphologically diverse genus that comprises about 370 species, widely distributed but primarily of temperate or Arctic regions of the Northern Hemisphere; many of the species are circumboreal.

Placement unknown

33. *Saniculiphyllum* C.Y. Wu & T.C. Ku

Saniculiphyllum C.Y. Wu & T.C. Ku, Acta Phytotax. Sin. 30: 194 (1992).

Perennial from long, horizontal, thick rhizome. Leaves all basal, palmately deeply lobed, petiolate, stipules 0. Inflorescence cymose; flowers small, green; sepals 5, imbricate with round tips; petals 5, ovate-triangular, entire, imbricate; stamens 5, antesepalous, on thick disc, filaments short; carpels 3(2); ovary inferior with short stylar beaks. One poorly known species, *S. guangxiense* Y.C. Wu & T.C. Ku, from southeastern Yunnan and northwestern Guangxi, China.

The thick rhizomes and palmately lobed leaves suggest that the genus belongs in the *Darmera* group, but until the single species (known from one collection) is examined more closely, it is appropriate to consider the placement of this taxon as unknown.

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22609 Hamburg
Germany

Library of Congress Control Number: 2006928744

ISBN-10 3-540-32214-0 Springer Berlin Heidelberg New York
ISBN-13 978-3-540-32214-6 Springer Berlin Heidelberg New York

Springer is a part of Springer Science+Business Media
springer.com

Cover design: WMXDesign, Heidelberg, Germany
Typesetting and production: LE-TEX Jelonek, Schmidt & Vöckler GbR, Leipzig, Germany

Printed on acid-free paper 31/3150/YL – 5 4 3 2 1 0