Grossulariaceae

Grossulariaceae DC. in Lam. & DC., Fl. Franç., ed. 3., 4, 2:405 (1805), nom. cons.

M. Weigend

Shrubs, sometimes dioecious, 0.1–7 m tall, erect, prostrate or lianescent with regular and very short internodes, unarmed or with simple or ternate nodal and/or simple internodal spines, stem initially with white pith, terete, bark dark brown to black, later often exfoliating in strips; horizontal underground stems often present; indumentum of subsessile and/or unicellular and pluriseriate, glandular or eglandular trichomes on young shoots, leaves, flowers and fruits. Leaves deciduous or evergreen, alternate, petiolate, rarely subsessile; stipules usually dry, brown and fimbriate; bud scales dry and brown, rarely membranaceous, usually pubescent and/or glandular; lamina ovate to subcircular, rarely flabellate, membranaceous to coriaceous, 0.5–25 cm in diameter, base cuneate to deeply cordate, usually trilobate, or subpalmately lobed, rarely undivided; margin irregularly lobulate and coarsely serrate with hydathode teeth, rarely subentire, usually pubescent at least abaxially, sometimes densely covered with resin or wax; venation palmate with usually three major veins; ptyxis mostly plicate, rarely convolute. Inflorescences usually on short shoots, racemose, pendulous, or rarely erect, (1–)5–50-flowered, axis sometimes with very short, sometimes distally contracted and inflorescence appearing corymbose, each flower with a pubescent and often fimbriate bract and usually two smaller prophylls, rarely with a single, amplexicaul prophyll. Flowers hermaphroditic or unisexual, chasmogamous, proterandric or protogynous, erect or pendulous, actinomorphic, (4)5-merous; hypanthium distinct, patelliform to long-cylindrical and usually persistent in fruit; calyx lobes usually oblong-acuminate, erect, spreading or reflexed, rarely erect with reflexed apex, green, white, yellow or red; petals distinct, rarely absent, erect or spreading, margin entire, ovate or oblong with narrowed base, rarely filiform or flabellate, flat or sometimes involute, membranaceous, green, white, yellow or red, aestivation apert; androecium haplostemonous, stamens antesepalous, all fertile or all staminodial; filaments filiform, insertion episepalous; anthers included or long-exserted, basifixed, with 4 microsporangia; connective undifferentiated or with distal nectary, staminodia undifferentiated with poorly developed thecae, or fully developed thecae but without viable pollen; nectary a well-developed, often 5-lobed disc; ovary in hermaphroditic and female flowers well developed, completely inferior to 1/3 superior, conical to globose, glabrous to densely glandular and/or pubescent, with 2 parietal, slightly intrusive placentae, in male flowers very small, undifferentiated or with poorly developed ovules; style conical to filiform with two stigmatic branches and two papillose stigmas, included or exserted, basally often densely pubescent; ovules numerous, anatropous, bitegmic, crassinucellar with well-developed chalazal haustoria. Fruit a soft berry crowned with the persistent perianth, often covered with unicellular or glandular trichomes, yellow, orange, red, black, rarely white and/or covered with waxy bloom, acidic or insipid; seeds (3–)10–60, with outer mucilaginous layer and a hard, brown to black seed coat; embryo small, straight, embedded in copious starch-free, oily endosperm; seedlings with 2 ovate to elliptical cotyledons, these apically emarginate with midvein ending in hydathode tooth, often pubescent and glandular.

One genus with 150–200 species in the northern temperate zone and South America, with outliers in northern Africa, Southeast Asia and Central America.

Vegetative Morphology. *Ribes* consists exclusively of shrubs typically differentiated into short shoots and long shoots. The vast majority of taxa branches at the base and has numerous strong, self-supported, widely spaced branches. Prostrate stems or underground runners are occasionally found in all major groups of *Ribes* but are particularly typical of subg. *Symphocalyx* and subg. *Ribes* sect. *Heritiera*. Many species form large clonal

stands in this way. Species with this type of growth are especially abundant in riparian forests and swamps (*R. glandulosum*, *R. nigrum*) and in alpine habitats (e.g. *R. nitidissimum* in Patagonia). At least one species forms dwarf shrubs only c. 15 cm high in high Andean habitats, some species have very dense and squarrose branching (i.e. many short shoots: *R. cuneifolium*), while others make very long internodes on thin shoots and thus climb in cloud forests (*R. incarnatum* and allied South American taxa). The epidermis of the shoots often exfoliates in long strips in the second year, and is then replaced by a well-developed periderm. Exfoliation is particularly striking in many species of subg. *Ribes* (sect. *Berisia* and sect. *Ribes*). *Ribes* subg. *Ribes* sect. *Berisia*, subg. *Grossularioides* and subg. *Grossularia* have spines, which are usually found at the leaf nodes (nodal spines) but also scattered over the entire shoot (internodal spines, e.g. *R. horridum*). Spines seem to have evolved twice independently, once in the *Berisia* lineage and once in the *Grossularioides*/*Grossularia* lineage. They are typical emergences developing from the epidermis and the subjacent parenchyma; internodal spines are sometimes gland-tipped (especially in *R.* subg. *Grossularioides*) and are derived from conical setae (see below).

Foliage of *Ribes* is mostly deciduous, rarely evergreen. Evergreen species are found in alpine habitats in the Himalayas (*R. laurifolium*, *R. davidii*) and in Mediterranean habitats in California (*R. viburnifolium*), semi-evergreen species in South America (*R. cuneifolium*, *R. ovalifolium*) and East Asia (*R. fasciculatum*). Evergreen and semi-evergreen taxa generally have coriaceous and undivided or shallowly lobed leaves, while most *Ribes* have 3–5-lobed laminas. This leaf type is found in all infrageneric groups and can be considered as plesiomorphic. Leaf venation is always palmate with three veins entering the lamina, irrespective of leaf outline.

Vegetative Anatomy. The plants are usually covered with different types of trichomes, some of which are informative in classification (Weigend and Binder 2001). Unicellular trichomes are usually white and lack a glandular apex. Glandular trichomes are very widespread and always have a pluricellular head. Sessile glands are disc-shaped, rarely globose, and are found in two different subtypes: sessile resin glands (surrounded by a persistent layer of resinous secretion) and non-resinous sessile glands (lacking any visible secretion in the dry stage and with at most a clear secretion at their tip in the living stage; Fig. 55). Subsessile glands are non-resinous and have a short, pluriseriate stalk which is shorter than or equal in length to the diameter of the glandular head of the trichome; they are often characteristic of certain species (cf. ovary of *R. andicola*). Stalked glands are pluriseriate trichomes c. 1 mm long with a well-developed secretory head. Conical setae differ in having a conical stalk 2–10 mm long. The tip of the conical setae is usually glandular, but the development of the apical gland can be retarded or suppressed. They are not usually found on leaf surfaces but are frequently present on stipules and stems, and the entire distal margin of the stipule can be laciniate and divided into conical setae. Plumose setae are conical setae which are densely covered with unicellular trichomes and are thus compound trichomes. There is a more or less gradual transition from conical setae to internodal spines in a few species (e.g. sect. *Grossularioides*, sect. *Berisia*). Nodal spines are apparently of different derivation, but their ontogeny has not been studied so far.

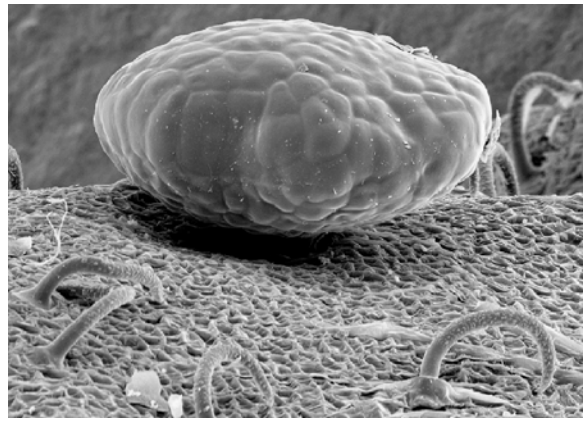

Fig. 55. Grossulariaceae. *Ribes viburnifolium*. Sessile non-resinous gland and unicellular trichomes from inferior portion of ovary, SEM micrograph. (Orig.)

The nodes are always trilacunar, and three veins enter the lamina. The lamina is usually hypostomatic, very rarely amphistomatic (*R. cereum*); stomata are anomocytic. Both the adaxial and abaxial epidermis is uniseriate. The mesophyll has usually 1–2, rarely up to 4 layers of palisade parenchyma with a few interspersed tanniniferous cells. Crystal druses 6–35 µm in diameter are found in the spongy and palisade parenchyma and the collenchyma along the leaf veins. Hydathodes are universally present at the leaf teeth.