
Crassulaceae

Crassulaceae DC. in Lam. & DC., Fl. Franç., ed. 3, 4, 1: 382 (1805), nom. cons.

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Perennial or rarely annual or hapaxanthic herbs to (sub)shrubs, rarely aquatics, treelike, epiphytic or scandent, with \pm succulent leaves, sometimes with succulent stems, rhizomes, underground caudices or succulent roots; indumentum of uni- or multicellular, often glandular hairs, or plants glabrous. Leaves (sub)sessile or rarely petiolate, usually alternate and spiral, or opposite-decussate or rarely whorled, frequently aggregated into rosettes, simple, rarely compound, usually entire or crenate to lobed, rarely dissected, estipulate. Inflorescences usually terminal, bracteate, usually many-flowered, basically thyrsoids, also pleio-, di- or monochasia (cincinni) or rarely true panicles, racemes or spikes. Flowers hermaphrodite, rarely unisexual, actinomorphic or very rarely zygomorphic, usually proterandrous, (3–)5(–32)-merous; sepals free or connate at base, sometimes distinctly unequal in size; petals free or connate to a short to long corolla tube; stamens as many as or usually twice as many as petals; filaments free or \pm connate with a tubular corolla; anthers basifixed in basal pit, 4-sporangiate, 2-locular at anthesis, dehiscence latrorse or slightly introrse by longitudinal slits; ovary usually \pm superior to semi-inferior; carpels as many as petals, usually free or almost so, sessile or sometimes stipitate, tapering gradually to abruptly into short to long, erect to divergent stylodia, basally with a small to conspicuous dorsal nectary scale; stigma small, (sub)apical, often poorly differentiated; ovules usually many, rarely few to one, anatropous, crassi- or tenuinucellate, bitegmic, on parietal to marginal placentae. Fruits usually follicles, and usually \pm completely dehiscent along the ventral suture, rarely few-seeded, indehiscent and nutlike; seeds smallish, usually 0.5–1 mm long, elongate-fusiform, longitudinally ridged (costate) or papillate (uni- or rarely multipapillate), rarely

(nearly) smooth, usually brownish; embryo small, straight; endosperm cellular, scanty.

A family of 34 genera with c. 1,410 species distributed worldwide, usually in arid and/or rocky habitats, with centres of diversity in Mexico and South Africa.

VEGETATIVE MORPHOLOGY. Crassulaceae are usually perennial herbs to (sub)shrubs, rarely small trees (the Malagasy *Kalanchoe beharensis* and *K. dinklagei* reach 8–10 m). The epicotyl is usually well developed; rarely does it remain very small ('t Hart 1982). In most perennials, the whole shoot system and at least some leaves survive unfavourable periods (frost, drought). Leaves are shed only when additional storage organs are present: succulent, \pm elongated stems (e.g. *Tylecodon*) or small, tuber-like swollen stems (e.g. *Dudleya* subg. *Hasseanthus*). Rhizomes are usually sympodial, rarely monopodial (*Rhodiola*). In *Aeonium*, the modular growth form correlates with sectional classification (Jorgensen and Olesen 2000). Some highly reduced annual *Crassula* are morphologically aberrant: flowers of *C. pageae* are embedded in a short 'disc' derived from connate side shoots (coenosom, described in detail by Jäger-Zürn 1989), and *C. aphylla* forms leafless, \pm globular shoots reaching maturity at about 3 mm Ø; it may represent the smallest succulent plant. Few *Sedum* from the Mediterranean and the Mexican Sierra Madre (Clausen 1977) are strictly biennial. Facultative annuals to perennials are found in Mediterranean *Sedum* and Macaronesian *Aichryson* and *Monanthes ictERICA*.

Root apices often contain anthocyanins and are reddish. Roots are usually fibrous, rarely thickened-fusiform (*Villadia* p.p., *Hylotelephium* p.p.) or tuberous. Tuberous rhizomes or rootstocks may develop from the hypocotyl (*Rhodiola rosea*), the upper part of the main root and hypocotyl (*Dudleya caespitosa*), or the hypo- and epicotyl (*Umbilicus*). *Sedum obtusifolium* forms subter-

¹ U. Eggle provided the key and generic descriptions extracted from Eggle (2003) which were largely revised here.

ranean runners with tuberous thickenings, and *S. amplexicaule* forms propagules from the swollen leaf bases clasping the stems. Secondary growth in roots and root tubers of *Sedum* and *Hylotelephium* is described by 't Hart (1994a). Adventitious roots are formed by many prostrate to suberect shoots (e.g. many *Sedum*) or \pm upright shoots of shrubs, especially under conditions of high air humidity (e.g. *Aeonium*); this ability is used for vegetative propagation in horticulture. Thickened short roots in *Sempervivum*, *Sedum* and some other genera which are inhabited by mycorrhizal symbionts (hyphomycetes, Berger 1930) need re-study. The root-nodules recently reported for *Sinocrassula* (Akiyama et al. 2001) may belong here.

Germination is epigeal and cotyledons are fleshy, usually petiolate and long persistent. Adult leaves are usually simple and only rarely pinnately compound (some *Kalanchoe*, e.g. *K. pinnata*), palmately lobed (*Crassula alcicornis*), lacinate (*Kalanchoe laciniata*) or peltate (*Umbilicus* sect. *Umbilicus* and a few *Kalanchoe*). The leaves are \pm flat to subulate and often \pm flat above and semi-terete below, partly with a \pm developed keel. The leaf margin is usually entire or \pm crenate (e.g. *Umbiliceae*), partly with cilia (e.g. many *Aeonium*). Heterophylly is found in some *Orostachys* and *Rosularia* (summer vs. winter rosette; Eggli 1988; Ebel et al. 1991a) and in *Sedum diversifolium* and *S. greggii* (sterile vs. flowering). Leaves typically break off easily and form adventitious shoots at the place of separation, a means of vegetative propagation in nature (e.g. *Adromischus*) which is widely used in horticulture. Many *Kalanchoe* species of sect. *Bryophyllum* form adventitious shoots (gemmae) on leaf margins. *Sedum viviparum* and *S. gemmiferum* form gemmae in the vegetative region, and *Crassula multicava*, *Kalanchoe miniata*, etc. within the inflorescences.

The leaf arrangement is usually alternate (most *Kalanchoideae* and *Sempervivoideae*) or decussate (most *Crassuloideae*), rarely whorled (e.g. a few *Sedum*). Leaf aggregation in \pm dense rosettes evolved independently in many genera of nearly all major clades (except *Umbiliceae*), especially within *Sempervivoideae*. In spirally arranged rosettes, the number of spirostichies may be of systematic value (e.g. *Monanthes*; Nyffeler 1992). The rosettes may be \pm stem-less, with the leaves remaining attached to the stem at least for some time, or terminal at the shoot tips of (sub)shrubs, with dried leaves being usually shed. Stolons are a means of vegetative propagation in some rosettes (e.g. *Semper-*

vivum, *Orostachys*). The rosettes become 'closed' and form bud-like structures ('resting rosettes') during drought periods in some *Aeonium* (Ebel et al. 1991b), *Orostachys* (Ebel et al. 1991a) and *Rosularia* (Eggli 1988).

VEGETATIVE ANATOMY. A detailed account was provided by Gregory (1998, with many references), from which data were taken if not cited otherwise. Soil root hairs are usually unicellular; those of aerial adventitious roots may be uni- or biserially multicellular.

The leaves are generally bifacial, succulent (weakly so in some *Crassula* (*Tillaea*) and few *Sedum* with small and thin scale-like leaves) and typically centric or intermediate between centric and dorsiventral. Palisade parenchyma is normally absent; the adaxial cells are sometimes palisade-like. Most leaves are thickish and exhibit a mesophyll with continuous transition from outer chlorenchyma to inner water-storage parenchyma with large achlorophyllous, highly vacuolated cells. Thinner leaves lack this differentiation and are chlorenchymatous throughout. Vascular bundles are collateral and in flat leaves in one row, in terete leaves in a circle, or irregular. Tissues often contain copious tannin. Solitary crystals and druses are common; crystal sand is found in *Adromischus*, *Cotyledon*, *Kalanchoe* and *Umbilicus* (also within secondary growth). The nodes were studied for few species only and vary even within genera (1-lacunar:1-trace; 1:2 or 1:3; 3:3, 3-multi:3-multi, or multi:3-8). Hydathodes of the 'epithem' type are present in many (all?) *Crassulaceae*. *Crassuloideae* typically have numerous hydathodes along the margin and/or on the leaf surface of one or both faces (Toelken 1977; Martin and von Willert 2000; see also under Physiology). *Kalanchoideae* and *Sempervivoideae* typically have one (sub)apical hydathode only (e.g. *Rosularia*, Eggli 1988); marginal hydathodes are rare, e.g. *Aichryson* p.p. (Caballero and Jiménez 1977) or *Phedimus* ('t Hart and Bleij 2003). The venation is pinnate or palmate and campodromous or reticulate, usually with a distinct intramarginal vein. In \pm flat leaves, the midvein typically protrudes at least on parts of the lower face.

The leaf epidermis is usually one-, occasionally two- (to three)-layered. Outer walls are thin (mesomorphic) to extremely thick (xeromorphic), the anticlinal walls straight (especially in xeromorphic types) or wavy to markedly sinuous (especially in mesomorphic types). Some *Crassula*, *Monanthes*