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Crassulaceae

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

J. THIEDE AND U. EGGLE¹

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 stylochia, 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 \varnothing ; 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?) Crassuloideae. 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 camptodromous 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*

and *Tylecodon* species exhibit enlarged epidermal cells (bladder-cell idioblasts).

The cuticle is usually smooth or with fine striations (e.g. *Aichryson*) or distinct ridges (e.g. *Aeonium*). Epicuticular wax deposits are in rods, irregularly lobed platelets, threads, smooth platelets or a very thick layer fissured into platelets (Fehrenbach and Barthlott 1988). Stomata are usually superficial to somewhat sunken (some *Crassula*) or raised (some *Sedum*), and usually anisocytic or rarely helicocytic (*Kalanchoe* and *Sedum*) and mesogenous with 3–8(–10) subsidiary cells. Stomata are usually \pm equally numerous on both faces, or more numerous abaxially (rarely adaxially) and usually irregularly orientated. The stomatal density is low, similarly to other leaf succulents, and about 5–80 per mm². Cystoliths are reported for *Orostachys japonicus*.

Hairs occur usually on both leaf surfaces when present, with six types: (1) unicellular, simple, thick-walled; (2) unicellular swollen bladder-cell idioblasts with constricted base sometimes covering the epidermis completely; (3) most common are multicellular simple hairs with biseriate stalk which may be non-glandular or glandular with \pm spherical heads of 2–12 secretory cells; (4) multicellular stellate hairs with 3(–6) apical arms (only in Malagasy *Kalanchoe* with dense-felty tomentum, e.g. *K. beharensis*; Boiteau and Allorge-Boiteau 1995); (5) multicellular sessile hairs with 2–3 basal cells and small head; and (6) multicellular uniseriate, simple or capitate hairs.

On young stems, the periderm arises usually in the subepidermis, also in the epidermis or more deeply in the cortex and forms continuous rings or separate groups of cork cells. Additional cambia from the outer cortex sometimes lead to thick periderms (e.g. *Kalanchoe beharensis*). The cork is impregnated with resin in some Malagasy *Kalanchoe*. A peeling outer bark occurs in stem-succulent pachycauls (*Tylecodon* p.p., *Aeonium smithii*, some *Sedum*). The epidermal cells are thin-walled. Subepidermal collenchyma layer(s) are reported for some genera. The cortex is parenchymatous, sometimes with chlorophyll, and aerenchymatous in the semi-aquatic *Crassula inanis* (Moteetee and Nagendran 1997). A distinct endodermis is recorded for some genera.

Secondary growth typically yields vessels, parenchyma and lignified fibres in distinct bands, layers, or as ground mass. The pith is parenchymatous, later sometimes lignified. Medullar bundles

are reported for some genera. Stem succulents often have secondary growth dominating in the parenchyma of cortex and pith. Growth rings are absent. The phloem is poorly developed. The wood structure is rather similar between unrelated genera and conspicuous in its juvenile features (raylessness, short vessels without variation in length and shape within the radius, and with secondary thickenings characteristic of the primary xylem), and differs strongly from the secondary wood of 'normal' woody plants. These differences were interpreted by 't Hart and Koek-Noorman (1989) as resulting from pedomorphosis and were thought to indicate secondary woodiness derived from a primarily herbaceous ancestor (see also Phytochemistry). Vessel elements are moderately short (100–229 μ m) with slightly inclined end walls. Perforation plates are simple (rarely reticulate in *Sedum*). Vessels have helical and annular lateral wall thickenings and/or scalariform(-reticulate) pitting. Libriform fibres are non-septate with simple pits and thin to thick walls, and form the major part of the wood in most species. Axial parenchyma is usually scanty paratracheal, but may rarely constitute the entire ground tissue, as in *Crassula arborescens* and some *Monanthes*. Cortical bundles are reported for some thick-stemmed taxa but are merely leaf-traces running \pm vertically for some distance. The rhizome anatomy of *Sedum tuberosum* and *Rhodiola rosea* was described by 't Hart (1982, 1994b).

ULTRASTRUCTURE. Crassulaceae exhibit the S₀ type of sieve element plastids (without protein inclusions and without starch) not found elsewhere in Saxifragales (Behnke 1991). Chloroplast ultrastructure differs between C₃ and CAM species (Teeri and Overton 1981).

INFLORESCENCE STRUCTURE. Detailed data can be found in Troll (1964, 1969) and especially in Troll and Weberling (1989). Inflorescences are usually thyrsoids (monotelic, i.e. with a terminal flower). Rarely, the terminal flower may be reduced, partly together with the distal part of the inflorescence (*Adromischus*, *Umbilicus*). The partial inflorescences are dichasia (frequent in Crassuloideae, Kalanchoideae, Telephieae, Umbiliceae), monochasia (double or simple cincinni; frequent in Semperviveae, Aeonieae and Sedeae) or thyrsoids. They are sometimes concaulescent and thus branch off above their subtending bracts (e.g.

Aeonium), or the bracts are recaulescently shifted onto the partial inflorescences (e.g. *Tylecodon reticulatus*). Rarely, intercalary inhibition zones with bracts not subtending partial inflorescences are found (*Aichryson*, some *Crassula*).

Some species produce pleiochasia (pseudo-whorls of three or more distal partial inflorescences below the terminal flower); proximal partial inflorescences are absent or consist of few to single flowers only (e.g. *Sempervivum tectorum*). Cymoids with one cincinnus or two cincinni below the terminal flower are also frequent. In uniflowered species, only the terminal flower is developed. Obligately uniflowered inflorescences appear to be rare (e.g. *Sedum humifusum*).

In *Kalanchoe*, all intermediates from many-flowered thyrsoids over racemes to solitary flowers occur. True panicles (some *Adromischus* and *Umbilicus*), racemes (some *Umbilicus*), double racemes (*Umbilicus oppositifolius*) or spikes (some *Adromischus*) are rare. The presence of prophylls, as in the botryoids (e.g. *Villadia imbricata*), is interpreted as derived from thyrsoids. Lateral inflorescences occur in some *Sedum*, *Aichryson*, *Aeonium*, *Rosularia*, *Prometheum* and throughout in *Afrovivella*, *Meterostachys*, *Rhodiola*, *Dudleya* and the *Echeveria* group.

FLOWER STRUCTURE. Pedicels are distinct to (nearly) wanting. Either two, one or no prophylls are present. The flowers are usually upright to spreading, rarely pendent (then, again upright in the fruiting stage) and nearly always hermaphrodite (plants dioecious in *Rhodiola* p.p.). The length of the flowers ranges from a few mm (some *Crassula* [*Tillaea*]) to 140 mm (*Kalanchoe marmorata*). Flowers are actinomorphic, slightly zygomorphic only in *Tylecodon grandiflorus*, *Kalanchoe elizae* and *K. robusta*, (3–)5(–32)-merous, and differ strongly in the degree of sympetaly (see, for instance, Figs. 28, 30).

The sepals are usually green, (nearly) free or \pm connate and usually much shorter than the corolla. They are usually equal and basally connate with the receptacle, or (in *Sedum* subg. *Sedum*) often free and \pm spurred at base and unequal in size.

Petal aestivation is quincuncial, cochlear, or contorted in *Sedum* ('t Hart 1990), imbricate or contorted in *Crassula*, convolute in *Dudleya*, imbricate in *Sedella*, *Thompsonella* and most *Echeveria*, and valvate in a few *Echeveria*. The petals are typically thin-textured (rarely membranous in annual *Crassula*), rarely thickish-succulent (e.g. *Echeve-*

ria), frequently dorsally keeled and sometimes papillose to hairy, and completely free or slightly to nearly completely connate to a corolla tube. Sympetaly is found in all Kalanchoideae and is frequent in many Sempervivoideae where it is of multiple origins ('t Hart et al. 1999; Mort et al. 2001). Petals are yellow, red, white, greenish to brownish with intermediates, very rarely blue (e.g. *Sedum caeruleum*), often unicoloured, partly bi- to rarely tricoloured (e.g. many *Echeveria*), sometimes with dots (some *Pachyphytum*) or irregular spottings (most *Graptopetalum*). Petals rarely have subapical unifacial precursory tips ('Vorläuferspitzen'; e.g. *Crassula* subg. *Crassula*, many *Sedum*, some *Villadia*). Leinfellner (1954) studied the basal petal scales of *Pachyphytum*, which are also found in some *Echeveria*.

The androecium is obhaplostemonous (Crasuloideae; then, antesealous stamens only) or more frequently obdiplostemonous (most Kalanchoideae and Sempervivoideae). In obdiplostemonous androecia, the antesealous stamens are typically longer. In sympetalous corollas, the stamens are \pm connate with the tube; the antepetalous (always?) inserted somewhat higher than the antesealous ones. The filaments are free from each other, usually \pm thin-filiform, rarely broadened or thickened. The anthers are usually about 1 mm long, but are longer in long-tubed flowers. Anther colours are usually yellow or red, but also orange, purple, brown, black, white, pink and green with nearly all intermediates and partly infraspecific variation; they are of some taxonomic value (Thiede, unpubl. data). The gynoecium is nearly exclusively isomerous with the perianth (oligomerous only in *Sedum tricarpum* and *S. bonnierii*). The ovary is usually superior and the carpels are (nearly) completely free, rarely connate higher up and completely connate only in *Crassula pageae* (Jäger-Zürn 1989). Soltis et al. (2003) suggested that the ovary in Crassulaceae is secondarily superior, according to a character-state reconstruction based on molecular data. The carpels narrow gradually to abruptly into separate, erect to divergent stylodia which are usually short to very long in long-tubed flowers. The stigma is small, often poorly differentiated, usually terminal (lateral in some *Crassula*, Toelken 1977). A compitum is recorded from some *Echeveria*. The carpels nearly always exhibit nectary scales at their dorsal bases (absent in a few *Crassula*, *Sedum* and *Aeonium*), which are usually less than 1 mm long and very diverse in shape and colour.

In *Monanthes*, *Sedum surculosum*, *S. longipes* and *S. pentastamineum*, the large, petaloid nectary scales are more obvious than the petals.

FLORAL DEVELOPMENT AND ANATOMY. Floral anatomy, vasculature and development have been described in general by Wassmer (1955), Jensen (1966) and Quimby (1971), for *Sedum*, *Crassula* and *Phedimus* by Eckert (1966), for *Kalanchoe* by Tillson (1940), for *Hylotelephium* by 't Hart (1985c) and for *Crassula pageae* by Jäger-Zürn (1989). During ontogenesis, sepals develop much earlier than petals (Wassmer 1955). The haplostemonous *Crassula dejecta* lacks antepetalous (outer) stamens and otherwise develops as the obdiplostemonous *Sedum acre*, thus indicating that flowers in Crassulaceae are probably basically obdiplostemonous (Eckert 1966). The anthers are median-sagittate in shape (transverse-sagittate in other Saxifragales studied by Endress and Stumpf 1991). Anthers are basifixed, and the filament is attached to the connective with its very thin upper end in the basal pit (dorsifixed only in *Rhodiola hobsonii*). Anthers are usually latrorse, slightly introrse only in *Crassula*, *Sinocrassula yunnanensis* and *Umbilicus rupestris* (as *U. pendulinus*; Wassmer 1955) and usually caducous. The anther epidermis is astomate and shows different types (Endress and Stumpf 1991). Apical connective protrusions with different shapes were found in several genera (Wassmer 1955; Endress and Stumpf 1991); in *Kalanchoe* they may function as secretory glands (Raadts 1979). The carpels are open in early developmental stages and postgenitally connate and are mainly plicate. Carpels within a flower are congenitally connate at least for a short distance below and postgenitally above; completely free carpels have not been found. Ontogenetic studies suggest that the nectary scales represent emergences of the carpels (Wassmer 1955). They exude nectar through stomata (Said 1982).

EMBRYOLOGY. Embryology was studied especially by Mauritzon (1930, 1933), and also by Rocén (1928), Souèges (1936) and Fétré and Lebègue (1964). Reviews are by Davis (1966) and Johri et al. (1992), from which most data were taken. The anther wall comprises a persistent epidermis, a one-layered fibrous endothecium, two ephemeral middle layers, and the secretory, uninucleate tapetum. Microsporogenesis is simultaneous. Pollen is shed in monads. It is binucleate and sometimes contains starch grains. The ovules are

anatropous, bitegmic and crassinucellate in Kalanchoideae and Sempervivoideae, and tenuinucellate in Crassuloideae. The micropyle is usually formed by both integuments which are both 2-layered. The embryo sac is usually of the normal Polygonum type. In *Hylotelephium*, an embryo sac of the bisporic Allium type develops from the chalazal dyad. In *Prometheum*, haustoria are given off from the megaspores and pass through the nucellus into the integuments; such megaspore haustoria are a rather unusual feature. The embryo sac generally contains starch grains. Endosperm formation is ab initio cellular, usually with a chalazal endosperm haustorium, and differs between Crassuloideae and Kalanchoideae/Sempervivoideae (Mauritzon 1933). The endosperm is scanty, fleshy and typically reduced to a 1-layered cap surrounding the hypocotyl (Krach 1976). The zygote divides into embryo, suspensor and a suspensor-haustorium within the nucellus (Mauritzon 1933). The embryogeny conforms to the Caryophyllad type. The embryo is small, long and straight, without a plumula, and stores aleuron as well as oil (Krach 1976).

POLLEN MORPHOLOGY. The pollen is usually 3-colporate and subspheroidal to prolate in equatorial view, \pm convex-triangular in polar view, and 13–38 μm long. Apertures are lalongate. The sexine is about as thick as the nexine. The tectum is complete and usually striate, reticulate, rugulate or cerebroid (Hideux 1981). The striae have a straight or rarely irregular margin (*Monanthes*). More rarely, the tectum is (nearly) completely smooth (*Sempervivum* sect. *Jovibarba*; *Rosularia* p.p., *Prometheum*) or has a fine OL-pattern. Colpi are tenuimarginate, with the thin exine usually protruding at the equatorial part of the colpi (Erdtman 1952). Pollen morphology may vary within the same inflorescence and is thus of restricted systematic applicability (Kim 1994). Data are based on an overview SEM study by Hideux (1981), more focused SEM studies for *Sempervivum* (incl. *Jovibarba*; Parnell 1991), European *Sedum* ('t Hart 1975), *Rosularia* and *Prometheum* (Eggli 1988), *Monanthes* (Nyffeler 1992), Korean *Sedum* (Kim 1994) and Korean Crassulaceae (Sin et al. 2002), and on light microscopy for *Aeonium* (Pérez de Paz 1980). Pollen morphology of Crassulaceae is similar to that of Saxifragaceae (Erdtman 1952).

KARYOLOGY. Crassulaceae display an extensive variation in chromosome numbers among and often within genera and often among species,

and possibly represent the karyologically most diverse family of angiosperms. The base number for the family and subfamilies Crassuloideae and Sempervivoideae, $x(n) = 8$, is also found in outgroups (Penthoraceae, Haloragaceae). The basic chromosome numbers for the major clades have been reconstructed by Mort et al. (2001). Many studies have been conducted on North American taxa (*Graptopetalum* and *Thompsonella*, Uhl 1970; *Pachyphytum*, Uhl and Moran 1973; *Sedum*, Uhl 1976–1992; *Echeveria*, Uhl 1994–2005; intergeneric hybrids, Uhl 1993–1995; *Lenophyllum*, Uhl 1996; *Villadia*, Uhl and Moran 1999), on European *Sedum* by 't Hart (especially 1985a, 1991), on European and Macaronesian *Semperviva* by Uhl (1961), on *Rosularia* by 't Hart and Eggli (1998), on *Crassula* by Merxmüller et al. (1971) and Friedrich (1973), and on Kalanchoideae by Uhl (1948). The Asian taxa are less thoroughly studied (Uhl and Moran 1972; Wakabayashi and Ohba 1999). Karyotypes are typically rather symmetrical and the chromosomes small (less than 1 or 2 μm), so that pairs and structural details can hardly be recognised. Satellites are present in *Crassula* subg. *Crassula* (Friedrich 1973) and some other genera (Sharma and Gosh 1967).

Most larger and also some smaller genera exhibit different base numbers and few to many polyploids, partly including high polyploids. Closely related genera often, but not always, exhibit different base numbers. Karyological variability reaches an extreme in *Sedum* and especially in the *Echeveria* group (Uhl 1992). Among the 62 studied European/Mediterranean *Sedum* species, about 140 cytotypes with all base numbers from 5 to 18 and some higher ones (20, 22, 24, 25, 29, 37) have been found. The data show that 64% of these cytotypes are polyploid, and nearly half of the species exhibit polyploids among diploids, some of them high polyploids (*S. rubens*: 20 \times) or complete series (*S. forsterianum*: 2 to 8 \times), partly also dysploids ('t Hart 1991). The high degree of polyploidy is attributed at least partly to allopolyploidy ('t Hart 1991), which was demonstrated experimentally ('t Hart et al. 1993). The Mexican *Sedum suaveolens* exhibits the highest chromosome number in angiosperms, $n = 320 (= 40\times)$. See also under Reproductive Systems.

POLLINATION AND REPRODUCTIVE SYSTEMS. Flower induction in *Kalanchoe* is under short-day conditions (Engelmann 1960), whereas *Hylotelephium telephium* is a long-day plant ('t Hart and

van Arkel 1985). In *Echeveria*, short- as well as long-day plants are found (Rünger and Wehr 1969). Flowers are usually protogynous, with the anthers of the antesepalous (inner) stamens releasing pollen before the anthers of the antepetalous (outer) ones. Sometimes, anthers dehisce already within the floral bud (Wassmer 1955). Proterogyny and homogamy are rare (e.g. some European *Sedum*). Differentiation among the two whorls for allogamy (stamens of outer whorl bending over petals) and autogamy (inner whorl remaining erect or bending over styloids), respectively, is common in European *Sedum* and *Sempervivum* (Günthart 1902). Stamen movements are extreme in *Graptopetalum*, where the stamens curve back towards the sepals and petals during anthesis (Moran 1949). *Crassula (Tillaea) muscosa* is autogamous, and *C. aquatica* appears to be cleistogamous and autogamous (Berger 1930); some tendency towards cleistogamy has also been observed in *Sempervivum* sect. *Jovibarba* (Günthart 1902:61).

Crassulaceae appear to be usually self-incompatible but *Sedum* sect. *Gormania* shows self-compatibility in varying degrees (Denton 1979). Fecundity in *Echeveria gibbiflora* is limited by pollen and resource availability (Parra et al. 1998). In *Hylotelephium telephium*, di-, tri- and tetraploid cytotypes are sympatric ('t Hart 1985b).

Studies on the conservation genetics of *Rhodiola integrifolia* subsp. *leedyi* (Olfelt et al. 1998, 2001) and *Dudleya multicaulis* (Marchant et al. 1998) revealed a high intrapopulation genetic variation, indicating little gene flow among the isolated populations.

Floral biology is poorly studied and largely restricted to the establishment of floral types and pollination syndromes. The carpellary nectary scales exude nectar in large quantities, which often forms glistening droplets. The few Crassulaceae without nectary scales may have deceptive flowers. Five major pollination syndromes are found (mostly taken from Vogel 1954).

1. Melittophily is assumed for taxa with a free, rotately spreading (e.g. most *Sedum*, many Telephieae and Umbiliceae, *Aeonium*, *Sempervivum*) or short tubular corolla (e.g. many *Crassula* species, *Kalanchoe* p.p., *Tylecodon* p.p. (Gess et al. 1998), *Umbilicus*). It represents the most frequent and least specialised, possibly plesiomorphic syndrome in Crassulaceae.
2. Psychophily corresponds to long-tubed salver-shaped flowers (*Adromischus*, *Pistorinia*,

Kalanchoe, e.g. *K. rotundifolia*) or flowers with at least connivent petals forming a tube-like structure (e.g. *Crassula coccinea*) and intensive colouration (red, yellow) and scent production over the day. This floral type has earlier led to artificial generic segregations (e.g. *Rochea* for long-‘tubed’ *Crassula* species such as *C. coccinea*).

3. The sphingophilous syndrome (long, whitish corolla tubes, nocturnal scent) appears to be restricted to a few *Crassula* (e.g. *C. fascicularis*; detailed study by Johnson et al. 1993) and some *Kalanchoe* (e.g. *K. marmorata*), and thus to Africa.
4. Ornithophilous flowers (red, long-tubed corollas, lack of odour, abundant nectar production, exerted anthers) are found in species of *Kalanchoe*, *Cotyledon*, *Tylecodon*, *Echeveria* (Parra et al. 1993) and *Dudleya*. There appears to be a gradual transition from psycho- or melittophily to ornithophily. The psychophilous *Crassula coccinea* is also visited by nectar birds (Vogel 1954). In *Dudleya*, the gradual shift from bee to hummingbird pollination has been demonstrated to be accompanied by changes in nectar amount, increase in tube length, colour shift to reddish corollas, and shift from low to high auto-fertility (Levin and Mulroy 1985).
5. Myophily is assumed for *Monanthes* (open flowers with darkish colours, freely accessible nectar produced by large nectary scales; Vogel 1954). Carrion flies are possible pollinators for the fade-coloured and foetid flowers of most *Graptopetalum* (Moran and Meyrán 1974). In both genera, the darkish to fade flower colours are accompanied by corresponding anther colours (Thiede, unpubl. data). Some *Crassula* and *Sedum* species with small, insignificant whitish flowers with a musky scent are probably also fly-pollinated. The report of effective ant pollination for *Sedum pusillum* is one of the few known cases of ant pollination in angiosperms (Wyatt and Stoneburger 1981). When exploiting the freely accessible nectar from the nectary scales, the ants ‘accidentally’ transfer pollen over the dense stands of the plant, but bee pollination also occurs. Flower visits by ants were also reported for *Kalanchoe* (Bahadur et al. 1986) and may be more frequent, at least accidentally. Melittophily is widespread and dominates in the northern temperate region, whereas psycho-

sphingo- and ornithophily are restricted to (sub)tropical or southern temperate regions. Pollination syndromes in southern Africa are more diversified than in North America. The derived pollination syndromes are certainly of multiple origin within Crassulaceae, possibly from the plesiomorphic melittophily.

Hybridisation patterns in European Sedae are strictly correlated with the presence or absence of four morphological character states (see Subdivision). Species can be hybridised only when they agree in all four character states, but not all hybrids are possible (’t Hart and Koek-Noorman 1989). In Aeonieae, hybridisation patterns correspond to present generic boundaries between *Aichryson*, *Monanthes* and *Aeonium* (incl. *Greenovia*): no hybrids between genera, but many within these genera are possible. The c. 200 species of the *Echeveria* group appear to be fully interfertile (though natural hybrids are rare) and form the largest comparium known among angiosperms (Uhl 1992).

FRUIT AND SEED. Fruits are usually many-seeded follicles which dehisce xerochastically; hygrochastic opening is rare (e.g. *Sedum acre*). Fruit dehiscence is sometimes reversible under humid conditions (*Phedimus aizoon*; Huber 1961) or, vice versa, the suture opens fully only under humid conditions but closes again when drying out (*Sedum acre* and *S. annum*; Stopp 1957). The ripe follicles either remain upright (orthocarpic) or become divergent to stellate-patent (kyphocarpic). An earlier classification of *Sedum* based on these features (Fröderström 1930–1935) proved to be artificial. Follicles of most genera dehisce completely along the ventral suture; other types are more rare: the suture mainly opens apically or basally only, or the plicate carpel part breaks off as a whole (*Aeonium* sect. *Greenovia*). Some species of *Crassula* sect. *Glomeratae* have only 1- or 2-seeded follicles from which the upper part breaks off with circumscissile splits and encloses one or two seeds (Stopp 1957; Toelken 1977). Similar fruits are found in *Hypogophytum* and some *Sedum*. *Sedella* and *Sedum microcarpum* have one-seeded, non-dehiscent nut-like fruits, and the fruits of *Sedum smallii* dehisce with a tear-shaped flap unique within the family (Clausen 1975). In European *Sedum*, kyphocarpic follicles usually exhibit carpel walls broadened to \pm distinct ‘lips’ (possibly favouring splash-cup dispersal by rain), whereas orthocarpic follicles are without lips (’t Hart 1991).

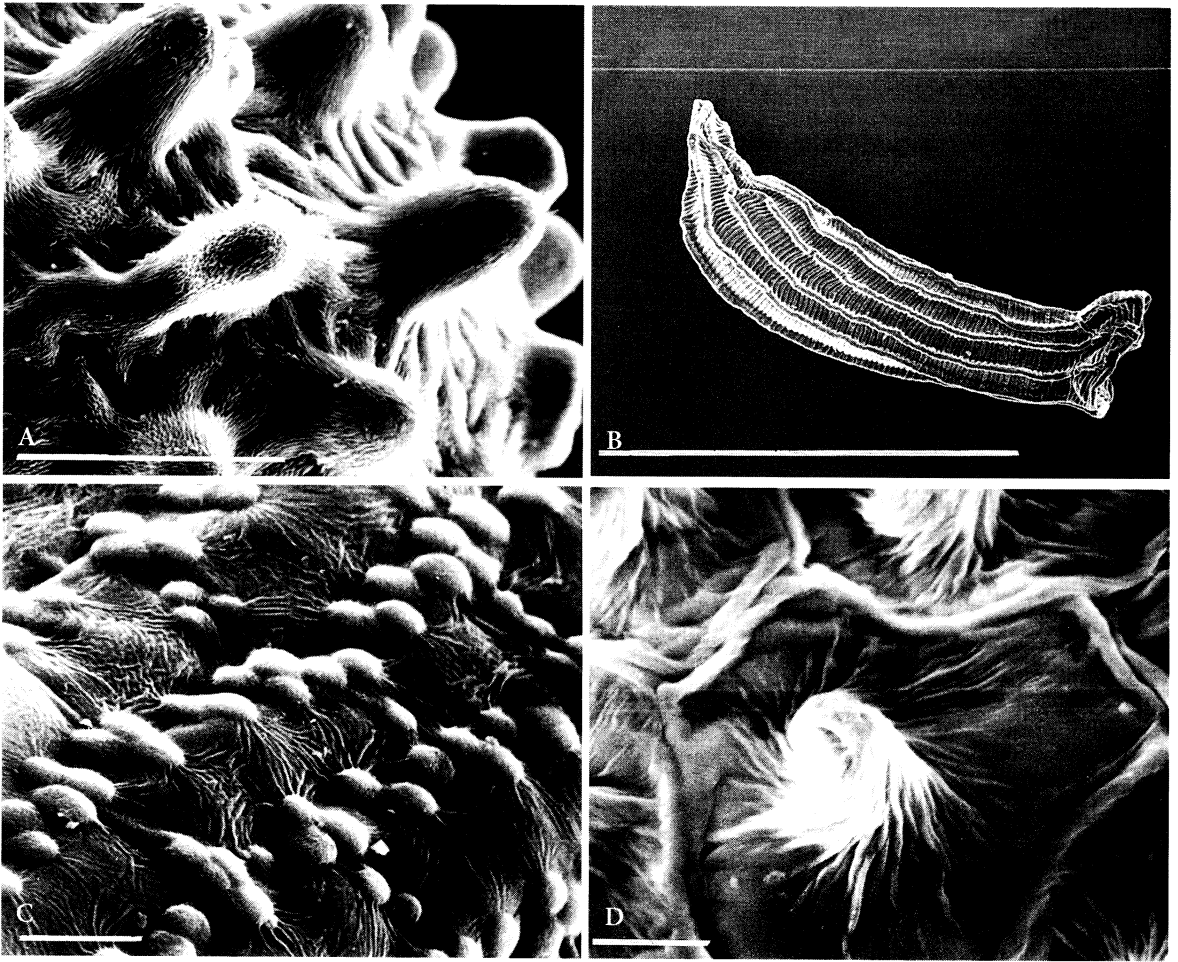


Fig. 26. Crassulaceae. Seed surface structures. A *Crassula streyi*. Sinuate (unipapillate) ('Puzzle-Modell' of Knapp 1994): anticlinal walls sinuate, periclinal walls usually convex to centrally papillate or rarely almost smooth (Crassuloideae). Types B–D Anticlinal walls straight. B *Kalanchoe brachyloba*. Costate (bipapillate) ('Leitermodell'): cells with two papillae at each distal end. The papillae remain \pm free or are mostly fused to form distinct costae with those of the neighbouring cells, partly with transverse connections (Kalanchoideae and all Sempervivoideae,

except for the following). C *Umbilicus horizontalis*. Multipapillate ('Warzenmodell'): cells with 2–3(–5) small papillae which are usually unequal in size and form small groups with those of adjacent cells (only genus *Umbilicus* within tribe Umbiliceae). D *Sedum wrightii*. Reticulate (unipapillate) ('Wabenmodell'): the lateral cell-walls are always thickened and form a distinct reticulate pattern, usually with a central papilla (Acre clade). Scale: A 100 μ m, B 1,000 μ m, C, D 10 μ m. (A, C From Knapp 1997 and B, D from Knapp 1994)

The seeds are \pm oblong-fusiform, \pm brownish, usually 0.5–1 mm long and weighing c. 0.02 mg (*Sempervivum*). The East African *Sedum epidendrum* and the Mexican *S. botteri* and related species exhibit seeds up to 3 mm in length, a possible adaptation to their epiphytic habitats (Clausen 1959: 46; Gilbert 1985). The seed coat is 4-layered: the exotestal cells have a \pm thickened outer wall, the inner exotegmic cell layer is pigmented, and the two middle layers are completely crushed (Krach 1976). The chalazal region is obtusely

rounded or elongated to acute (apiculate; Fig. 26B; Knapp 1994: 163). The micropylar region is partly surrounded by the outcurved testa which forms a distinct corona (Fig. 26B; Kalanchoideae, some *Sedum*; 't Hart and Koek-Noorman 1989; Knapp 1994: 163). In SEM studies of testa structures ('t Hart and Berendsen 1980, for *Sedum*; Knapp 1994, 1997), four main types are distinguished, differing mainly in the number and position of papillae and concurring well with phylogenetic patterns (Fig. 26A–D): A sinuate-unipapillate with

sinuate anticlinal walls, or **B** costate-bipapillate, **C** multipapillate and **D** reticulate-unipapillate with straight anticlinal walls. Specific SEM datasets have been published for *Crassula* (Bywater 1980; Wickens and Bywater 1980; Bywater and Wickens 1983), *Sedum* sect. *Ternata* (Calie 1981), *Sedum* sect. *Gormaniana* (Denton 1982), *Rosularia* and *Prometheum* (Eggl 1988), *Monanthes* (Nyfeler 1992) and East Asian taxa (Gontcharova 1999).

DISPERSAL. The follicles usually release the seeds immediately after ripening. The seeds are dispersed by gravity and wind, but are much larger than typical anemochorous dust seeds (e.g. orchids, many parasites). Nakanishi (2002) recorded splash-cup dispersal by raindrops for the divergent follicles of two Japanese *Sedum* spp.; this mechanism may be more frequent. The seed number in Crassulaceae may be very high (an old inflorescence of *Aeonium nobile* was estimated to produce about 50,000 flowers (Burchard 1929) and 500,000 or even much more seeds). Most seeds are dispersed over short distances as anemochorous seed rain around the mother plant (Parra et al. 1993). Anemochorous long-distance dispersal appears to be rare, as evidenced, e.g. by the closely related island vicariants on the Canary Islands, and the rarity of pronounced disjunctions. Evidence for long-distance dispersal comes from molecular data (van Ham and 't Hart 1998; Mort et al. 2001). Berger (1930) suggested the possibility of secondary dispersal by water and ants, but evidence is wanting. Ripe seeds typically remain viable for a few years only or even less. On wet soil, seeds typically germinate within a few days (in cultivation) and generally in light. Studies on the germination ecology of the winter annuals *Sedum pulchellum* and *S. smallii* from the eastern USA revealed after-ripening of the seeds during summer, which is interpreted as an adaptation to summer-dry habitats (Baskin and Baskin 1972, 1977).

PHYTOCHEMISTRY. Reviews are given by Hegnauer (1964, 1989) and Stevens (1995a, b). Crassulaceae accumulate large amounts of sedoheptulose, which is the most abundant sugar in most species. In contrast to many other succulents, nearly all species investigated to date contain isocitrate (Hegnauer 1964).

Proanthocyanidins (condensed tannins) have been found in all clades, except for the Acre clade

where they are absent or at least rare and replaced by alkaloids (Stevens et al. 1992, 1995; Stevens 1995a). Proanthocyanidins are widespread both in woody and herbaceous Crassulaceae. The lack of exclusivity in the woody representatives supports the hypothesis that Crassulaceae are primarily herbaceous (Stevens 1995a), which is also supported by wood anatomy (see there). Galloyl esters are common, but ellagitannins are absent, in contrast to Saxifragaceae and Penthoraceae (Jay 1971).

Flavonols and flavones, both unmethylated and methylated, are known to occur in Crassulaceae, but myricetin is rare (Denton and Kerwin 1980; Hegnauer 1989; Stevens et al. 1996).

Wax composition (in particular, alkane and triterpene profiles) has been studied by Eglinton et al. (1962), Manheim et al. (1979), Bowman (1983) and Stevens et al. (1994). Since the isolation of sedamin from *Sedum acre* in 1939, many different pyrrolidine and piperidine alkaloids have been detected in *Sedum* subg. *Sedum* (several studies on *Sedum acre*; see Hegnauer 1989; Stevens et al. 1993) and in *Echeveria*. Alkaloids thus seem to be restricted to the Acre clade, but they are absent in its more derived members (except *Echeveria*; Stevens et al. 1992, 1995).

Cyanogenic substances have been found in some, but not all Crassulaceae studied. Cyanogenesis is weak especially in *Sedum*, and several species appear to be polymorphic in this respect (Hegnauer 1989).

The South African *Tylecodon paniculatus* contains toxic bufadienolides which may cause a lethal cattle disease ('krimpsiekte'). Structurally similar poisons occur in *Tylecodon grandiflorus*, *Cotyledon* and *Kalanchoe* (incl. *Bryophyllum*; Hegnauer 1989). Bufadienolides from *Kalanchoe* (*Bryophyllum*) are reported as potent, novel antitumor agents (Yamagishi et al. 1989) and insecticidal compounds (Supratman et al. 2001).

SUBDIVISION AND RELATIONSHIPS WITHIN THE FAMILY. The infrafamilial classification is under debate over the last 200 years (review by 't Hart and Eggl 1995). Most classifications relied heavily on a few trivial characters such as habit, leaf arrangement, number of floral parts, degree of petal fusion, number of stamens, and position of ripe follicles. However, most of these characters are of restricted value due to extensive homoplasy ('t Hart 1995; van Ham and 't Hart 1998; Mort et al. 2001). Molecular data ('t Hart et al. 1999) indicated

that sympetaly originated six times independently in European Crassulaceae of the Leucosedum clade. The widely accepted classification by Berger (1930) suffered strongly from such inadequacies. For instance, subfamily Cotyledonoideae, which includes Berger's African/Eurasian sympetalous Crassulaceae, has long been revealed as artificial (e.g. Uhl 1948). 't Hart and Koek-Noorman (1989) and 't Hart (1991) discovered hitherto largely unrecognised characters of considerable systematic value in European *Sedum* and related genera: interspecific crossbreeding is possible only between species which agree in the character states for testa ornamentation (costate vs. reticulate-papillate), shape of the micropylar region (coronate vs. apiculate), sepal insertion (free vs. connate at base), and presence or absence of glandular hairs. Groups characterised by these long-overlooked characters usually agree well with those of molecular studies. Many other, such more cryptic characters have been established as synapomorphies for the major clades by Thiede (unpubl. data).

Molecular data (cpDNA *trnL-trnF* spacer sequences: 't Hart 1995; cpDNA RFLPs: van Ham and 't Hart 1998; cpDNA *matK* sequences: Mort et al. 2001) led to the recognition of seven major clades; an eighth clade has recently been found (nuclear ITS and *trnL-trnF* sequences; Mayuzumi and Ohba 2004). From the six subfamilies of Berger, only the largely monogeneric Crassuloideae (*Crassula*) and Kalanchoideae (*Kalanchoe* s.l.) were found to be monophyletic. Here, the revised classification of Thiede (unpubl. data) is adopted, which largely follows the sequencing convention (Fig. 27), i.e. it assigns the same rank to clades which branch off subsequently (three major clades: subfamilies; five major clades within Sempervivoideae: tribes). This contrasts with a previous proposal by 't Hart (1995), who followed the ranking convention and classified the two sister-clades of subsequent di-

chotomies with formal ranks in descending order. Here, three subfamilies are recognised, as suggested earlier by Thorne (1983, 1992): the two morphologically well-supported *Crassula* and *Kalanchoe* clades are recognised as Crassuloideae (*Crassula* clade) and Kalanchoideae (*Kalanchoe* clade) respectively, and the remaining six clades are subsumed as Sempervivoideae (formerly Sedoideae). Within the latter, five tribes are recognised (Fig. 27): the Hylotelephium clade as tribe Telephieae, the Rhodiola clade as tribe Umbiliceae, the Sempervivum "clade" as tribe Semperviveae, the Aeonium clade as tribe Aeonieae, and the Leucosedum and Acre clades together as tribe Sedeae.

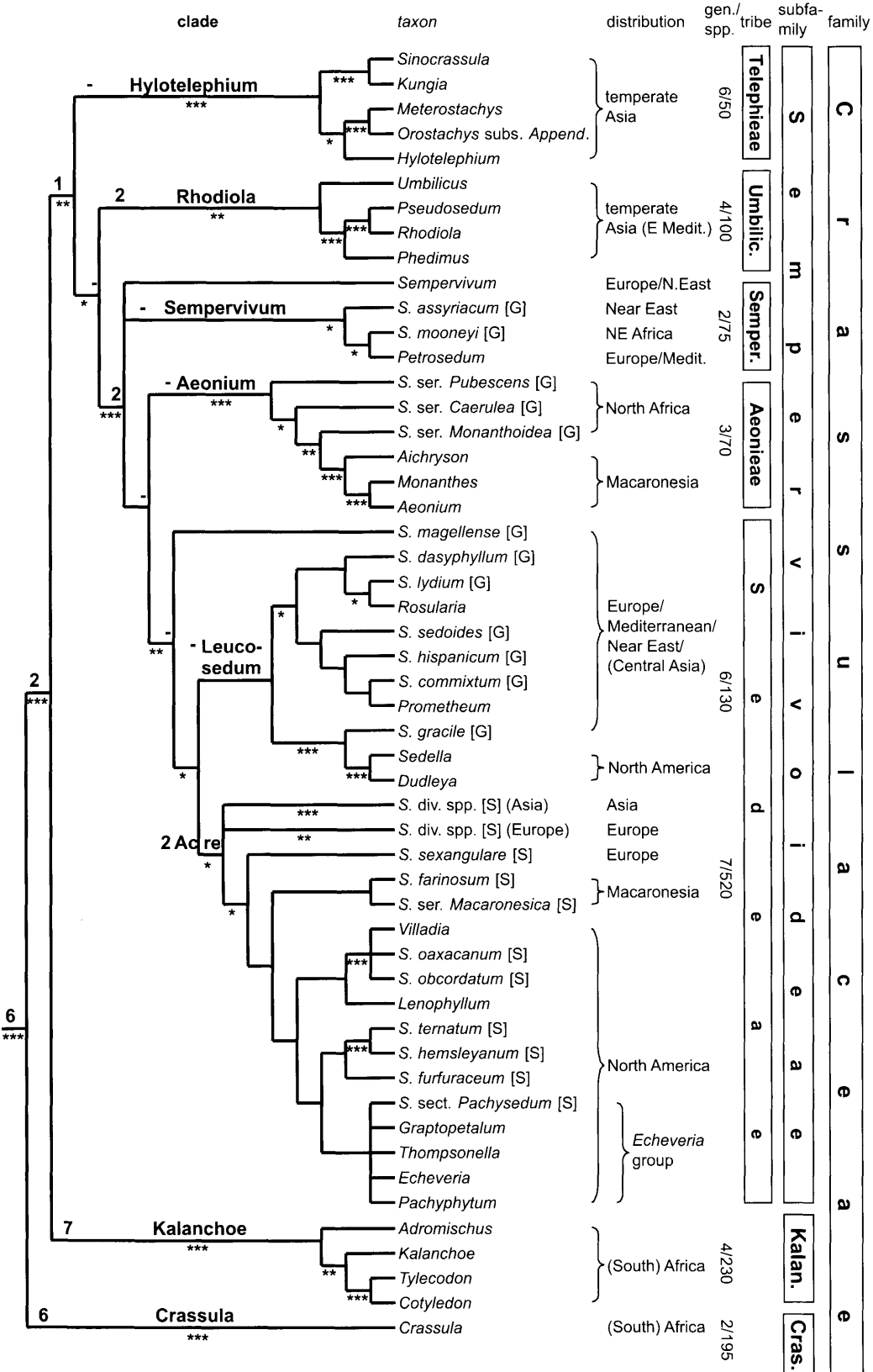
It should be noted that the *Crassula* and *Kalanchoe* clades, which preferentially are (sub)tropical, are morphologically highly derived (see diagnoses of subfamilies Crassuloideae and Kalanchoideae), whereas the predominantly temperate Sempervivoideae largely retain the basic features of the family which have been recognised by outgroup comparison. For this reason, the taxonomic treatment starts with subfamily Sempervivoideae characterised by the basic features of the family.

Molecular data ('t Hart 1995; van Ham and 't Hart 1998; 't Hart et al. 1999; Mort et al. 2001) indicated that *Sedum*, by far the largest genus of Crassulaceae, is highly paraphyletic. *Sedum* encompasses the least specialised species groups within the Semperviveae, Aeonieae and Sedeae, and is definable with plesiomorphic features only. *All other genera in these tribes are derived from within Sedum and form a monophyletic lineage together with the latter.* This implies that many segregates of *Sedum* are closely related to other genera in the Sempervivum, Aeonium, Acre and Leucosedum clades.

In order to reflect phylogenetic relations within Semperviveae, Aeonieae and Sedeae, the segregates of *Sedum* identified to date by molecular studies are placed according to these molecular data. For most segregates, no generic names other than *Se-*

Fig. 27. Summary tree of Crassulaceae, showing the eight major clades, their number of genera/species (incl. *Sedum*), their main distribution, and the formal classification. The number of synapomorphies for the major clades (if any) is indicated above the branches; bootstrap support below the branches (* = 50–70%; ** = 71–90%; *** = 91–100%). The genus *Pistorinia* of tribe Sedeae is not included. Further explanations are provided in the text. Combined from molecular data of van Ham and 't Hart (1998), cpDNA restriction sites, Sempervivum clade; Mayuzumi and Ohba (2004) and

Mayuzumi (unpubl. data), ITS and *trnL-F* sequences, Hylotelephium and Rhodiola clades; Mes et al. (1995), *trnL-F* sequences, Aeonium clade; Mort et al. (2002), *matK*, *trnL-F*, *psbA-trnH* and ITS sequences, Aeonium clade; and Mort et al. (2001), *matK* sequences, all other clades. Abbreviations: Appendic. = subsect. *Appendiculatae*, S. = *Sedum* with [G] = subg. *Gormanina* and [S] = subg. *Sedum*, Medit. = Mediterranean, Eur. = Europe, N. East = Near East, Umbilic. = Umbiliceae, Semper. = Semperviveae, Kalan. = Kalanchoideae, Cras. = Crassuloideae



dum are available (except for *Petrosedum* or perhaps *Oreosedum*, *Amerosedum*, etc.). However, the phylogenetic status of most of these segregates is insufficiently known, not to mention the dearth of morphological characters which could define them. Therefore, they are all classified here under *Sedum* but mentioned in the respective clades along with the genera most closely related to them. It is unlikely, and not intended, that any of these segregates will ever be elevated to generic status.

The inclusion of all genera derived from within *Sedum* into a broadly defined, then monophyletic *Sedum* would be highly impractical because of the dramatic morphological heterogeneity of the resulting taxon. The other course, splitting *Sedum* into numerous constituent monophyletic taxa, would result in a tremendous increase of very small genera usually ill-defined morphologically; most of these can not be identified with present knowledge. A third option would be the inclusion of the segregates of *Sedum* into the existing, cladistically contiguous genera. Again, apart from presently insufficient knowledge and lack of morphological characters of these clades, several consist only of species of *Sedum* and do not contain a genus with which these could be united taxonomically (see particularly the molecular data for European *Sedum* by 't Hart et al. 1999). Here, we follow 't Hart's (1995) suggestion to accept *Sedum* as a paraphyletic grouping. Genera derived from within *Sedum* should be monophyletic and for practical reasons not monospecific, and morphologically well defined (cf. 't Hart 1995: 165), but this is not yet achieved for all genera (see especially the *Echeveria* group).

A molecular clock model dates the origin of Crassulaceae at 69–77 Ma B.P., of the Crassuloideae/Kalanchoideae+Sempervivoideae split at 39–41 Ma B.P., of the Kalanchoideae/Sempervivoideae split at 25–29 Ma B.P., and of the split between the *Leucosedum* and *Acre* clades at 13–18 Ma B.P. (Wikström et al. 2001; cf. Fig. 27). A complete species-level taxonomic synopsis is provided by Eggli (2003).

AFFINITIES. Crassulaceae were usually placed next to Saxifragaceae and the monogeneric Penthoraceae, either within Rosales (Cronquist 1968; Thorne 1968) or Saxifragales (Takhtajan 1969; Thorne 1992). The circumscription of Crassulaceae is nearly undisputed, except for the inclusion of *Penthorum* by some authors (de Candolle 1828; Torrey and Gray 1838; Schönland 1894; Hutchinson

1973). Molecular data (Morgan and Soltis 1993; Soltis and Soltis 1997; Fishbein et al. 2001) establish the monophyly of Crassulaceae. Putative morphological synapomorphies are leaf succulence, aniscocytic stomata and carpellary nectary scales. Homoplasious synapomorphies are thyrsoid inflorescences, papillate seeds and obdiplostemony, which are shared with Saxifragaceae; papillate seeds are also found in Penthoraceae. *Penthorum*, formerly included in Crassulaceae, approaches some *Phedimus* species and its peculiar fruit is similar to that of *Sedum* (*Diamorpha*), but it differs clearly from Crassulaceae in its non-succulent leaves with anomocytic stomata, its vessel and fibre structure, its diplostemonous flowers, in having the follicles connate almost to the middle, the lack of carpellary nectary scales, the presence of an operculum, and in its chemistry (see Penthoraceae, this volume). Saxifragaceae differ primarily in their oligomeric gynoecium, the presence of a nectariferous disc and of non-succulent leaves with stipules or sheathing leaf bases, and usually anomocytic stomata (see Saxifragaceae, this volume).

According to molecular data, Crassulaceae belong to a distinct clade within Saxifragales, from which Crassulaceae, Aphanopetalaceae, Tetracarpaeaceae, Penthoraceae and Haloragaceae branch off successively. Stevens (2005) lists an axis with endodermis, nodes 1:1 and the lack of stipules as putative morphological synapomorphies. This clade is in turn sister to a clade which includes Saxifragaceae, Grossulariaceae, Iteaceae and Altingiaceae (Savolainen, Chase et al. 2000; Savolainen, Fay et al. 2000; Soltis et al. 2000; Fishbein et al. 2001).

DISTRIBUTION AND HABITATS. Crassulaceae occur almost worldwide. General distribution patterns and centres of diversity are described by 't Hart (1997a); for North America, a detailed survey is given by Thiede (1995), and climatic correlations are presented by Teeri et al. (1978). More focused datasets have been published for *Sedum* (Böttcher and Jäger 1984), European taxa (Meusel et al. 1965; Jalas et al. 1999), Mediterranean *Sedum* ('t Hart 1997b), *Crassula* (Jürgens 1995), *Tylecodon* and *Cotyledon* (van Jaarsveld 1994), and *Rhodiola* (Ohba 1989).

Crassulaceae are often viewed as a typical northern temperate element, but species diversity is concentrated in Mexico (about 325 species) and South Africa (about 250 species). The taxa of the eastern USA and especially the Mexican upland regions represent a distinct terminal clade within

the Acre clade, including the majority of North American Crassulaceae (van Ham and 't Hart 1998; Mort et al. 2001). Southern African Crassulaceae belong exclusively to Crassuloideae (*Crassula*) and Kalanchoideae (van Ham and 't Hart 1998; Mort et al. 2001). Genera of the latter are predominantly distributed in either the winter-rainfall (*Tylecodon*, *Adromischus*) or the summer-rainfall region (*Kalanchoe*). *Cotyledon* and *Crassula* are distributed in both regions, but many sections in the latter are specialised (Jürgens 1995).

Diversity centres of secondary importance are the wider Californian winter-rainfall region (lineage within the Leucosedum clade with *Sedella*, *Dudleya* and the American *Sedum* subg. *Gormania*), Macaronesia (Aeonieae and a few *Sedum* species of the Acre clade), the Mediterranean (mainly Leucosedum clade: *Sedum* subg. *Gormania*, *Pistorinia* and *Rosularia*, and a few *Sedum* subg. *Sedum* in the Acre clade), the wider Himalayan region (Telephieae and Umbiliceae and the Asian *Sedum* subg. *Sedum*), East and Northeast Africa (*Crassula*, *Kalanchoe*, *Sedum*, *Cotyledon*, *Hypogophytum*, *Afrovivella*), and Madagascar (*Kalanchoe*, *Perrierosedum*, a few *Crassula*). All these centres, except for the Himalayan one, exhibit at least one or two (near-)endemic genera. Crassulaceae are poorly represented in the humid tropics as well as in South America (Thiede 1995) and Australia (Toelken 1986). Most genera are confined to a single continent. Exceptions are *Sedum*, *Kalanchoe*, the circumboreal *Rhodiola* and *Hylotelephium*, and the semi-aquatic *Crassula* (*Tillaea*), the worldwide distribution of which is attributed to long-distance dispersal by birds (Bywater and Wickens 1983). Of the genera restricted to the New World, only *Echeveria* and *Villadia* extend to South America, separated by a broad gap in Central America; all others are confined to North America and Guatemala (Thiede 1995).

Migration and diversification of Crassulaceae principally followed the route (southern) Africa → Asia → Europe-Mediterranean → (northern) America (Fig. 27; see also van Ham and 't Hart 1998 and Mort et al. 2001). Since Crassuloideae and Kalanchoideae are mainly southern African (Fig. 27), a first major diversification in southern Africa is assumed. The next branching clades, Telephieae and Umbiliceae, are mainly Asian, with *Umbilicus* and *Phedimus* extending to the eastern Mediterranean. Semperviveae extend from the Middle East to the Mediterranean and parts of Europe. Aeonieae and Sedeae are basically

European-Mediterranean. Aeonieae are diversified in Macaronesia, and Sedeae include distinct northern American lineages within the Leucosedum and Acre clades. The northern temperate clades are poor in species; whereas northern American and southern African lineages are highly diversified (Fig. 27). Growth form zonation reflects the climatic conditions: hemicryptophytes (*Hylotelephium*, many Umbiliceae) are restricted to northern temperate regions, annuals occur in climates with short vegetation periods, especially in winter-rainfall regions ('t Hart 1997b) and in alpine regions especially in East Asia, and subshrubs are restricted to regions without severe frosts. In contrast, small, often rooting and/or mat-forming herbs as well as stem-less rosette plants occur nearly throughout all regions (cf. also Böttcher and Jäger 1984 for *Sedum*).

Crassulaceae generally prefer azonal sites, usually with more moderate temperatures and higher air humidity. Most taxa grow in arid habitats such as rocks and rock fissures under otherwise more humid climatic conditions, or in mountain regions in moderately arid areas, and are largely absent from hot deserts and arid lowlands. An exception is the arid coast of California, where many *Dudleya* species occur under moderate temperatures on coastal rocks exposed to sea breezes and fog (Thiede 2004), and the arid southern African Succulent Karoo, which exhibits a considerable species richness. Many rock plant communities with Crassulaceae have been described for Tenerife (Rivas-Martínez et al. 1993), Europe (Ellenberg 1996), Africa (Knapp 1973) and Arabia (Deil 1991). More unusual habitats are wet bogs (e.g. *Sedum villosum*), ephemeral water ponds where many *Crassula* (*Tillaea*) occur nearly hydrophytic, seasonally wet rock pools (e.g. *Sedella*), or moist forests with a few epiphytic *Echeveria* (Mexico, Central America), *Sedum* (Central and East Africa) and *Kalanchoe* (Madagascar). Edaphic specialisation is rare, e.g. *Sempervivum dolomiticum* is found only on dolomite, and *Sedum alpestre* occurs on siliceous and *Sedum atratum* on calcareous soil (Huber 1961). Germination and seedling establishment in rock habitats often occur within lichen or moss covers (e.g. *Dudleya*; Riefner et al. 2003). Crassulaceae frequently represent a first pioneer vegetation on shallow soils (e.g. Braun-Blanquet and Sutter 1982).

PARASITES. Specific crassulacean fungal parasites, the powdery mildews *Erysiphe sedi* and

Microsphaera umbilici (Braun 1987) and the rusts *Puccinia umbilici* and *P. rhodiolae* and *Uromyces sedi*, are all restricted to Telephieae and/or Umbiliceae. For further data on specific *Puccinia*, see Huber (1961). The rust fungi *Endophyllum sempervivi* and the mildews *Fusarium solani* and *Phytophthora nicotianae* var. *parasitica* occur on *Sempervivum* leaves (Ph. Neeff; in litt. 2004). The mildew *Oidium kalanchoeae* is known only from cultivated *Kalanchoe* (Braun 1987). Within angiosperms, *Cuscuta campestris* (Convolvulaceae) and *Tapinanthus oleifolius* (Loranthaceae) are unspecific parasites on *Cotyledon* (Visser 1981). *Cuscuta* spp. are occasionally found on European/Mediterranean *Sedum*, *Petrosedum* and *Aeonium* (U. Eggli, pers. obs.). Several mining insect larvae feed specifically on Crassulaceae: *Sandia xami* (Lepidoptera) on Mexican species (Jiménez and Soberón 1989), *Phytomyza sedi* (Diptera) and *Glyphipteryx equitella* (Lepidoptera) on European *Sedum*, and *Phytomyza rhodiolae* (Diptera), *P. sedicola*, *Yponomeuta vigintipunctatus* (Lepidoptera) and *Apion sedi* (Coleoptera) on European Telephieae and/or Umbiliceae (Huber 1961; Bland 1995). *Thuleaphis sedi* is a specialist aphid on *Rhodiola rosea* (Jacob 1964).

PHYSIOLOGY. Nocturnal CO₂ fixation based on the Crassulacean acid metabolism (CAM) pathway was first detected in Crassulaceae and named after this family, although it is now known to occur in many succulent taxa and a few non-succulents. CAM is expressed in many Crassulaceae and is either constitutive or facultatively induced under certain environmental conditions, especially under drought stress, and is found even in the weakly succulent semi-aquatic *Crassula* (*Tillaea*; Keeley 1998). Detailed data on CAM have been published for *Sedum* and *Aeonium* (Pilon-Smits 1992), Macaronesian Aeonieae (Lösch 1990), and *Kalanchoe* (Kluge and Brulfert 1996). Crassulaceae and other CAM plants are often highly endopolyploid (de Rocher et al. 1990), but the reason for this is unknown. Most *Crassula* studied by Martin and von Willert (2000) absorb water deposited on the leaf surfaces via hydathodes (see Vegetative Anatomy), which may subsequently stimulate CO₂ fixation rates.

PALAEOBOTANY. Probably no fossil remains are known (Thomas Bolliger, pers. comm.); leaf fossils ascribed to Crassulaceae (e.g. *Crassulaceophyllum*) are doubtful.

ECONOMIC IMPORTANCE. Apart from their horticultural value, Crassulaceae have minimal economic importance. *Kalanchoe blossfeldiana* cultivars are annually produced in large quantities as popular pot plants. Species of *Hylotelephium*, *Phedimus*, *Sedum* and *Sempervivum* are frequently cultivated in rock gardens and increasingly used for 'green roofs'. Most perennial taxa of the family are choice collectors' plants and commonly grown by succulent plant enthusiasts. Overviews of genera and species of horticultural importance are given by Cullen (1995) and Huxley et al. (1997). Several species, especially *Kalanchoe pinnata*, are aggressive invaders in the tropics.

Nowadays, Crassulaceae are not used for food, although especially *Petrosedum rupestre* (vernacular name 'Trip-Madame') was recommended for salad in medieval herbals ('t Hart 1997a) and has locally been used as salad or pot-herb (Lippert 1995). The fleshy leaves may appear appealing in arid environments, but they are completely tasteless or bitter and are generally avoided even by cattle ('t Hart 1997a).

Rhizomes of *Rhodiola rosea* have some use in folk medicine and were used officinally ('Rose Root'; Radix *Rhodiolae*); an ethnobotanical review for Norway lists many uses (Alm 2004). For further data on folk uses and folk names of Central European taxa, see Huber (1961).

Several Asian species of *Rhodiola* have been the subject of intense phytochemical and pharmacological studies (e.g. Kurkin and Zapesochayna 1986; many older Russian references listed by Clausen 1975: 531). The medicinal properties of their rhizomes were known for a long time, and recent investigations have identified a vast array of different chemical compounds (e.g. Yoshikawa et al. 1996). There exist attempts for the large-scale cultivation of at least *R. sachalinensis* for the improved production of certain bioactive compounds (e.g. Xu et al. 1998).

CONSERVATION. Most Crassulaceae occur in rocky places not prone to habitat destruction ('t Hart 1997a). Narrow endemics (frequent in California, Mexico, Africa, Madagascar and Macaronesia) may be seriously threatened by land development and tourism. For example, two of three accessible populations of the Madeiran *Sedum fusiforme* have been destroyed during the construction of tourist accommodations ('t Hart 1997a). Legal and illegal trade and collecting of wild plants do occur but appear to be rather restricted,

compared to other succulents, due to low demands and easy vegetative and generative propagation (data for South Africa: Newton and Chan 1998).

Genera popular in horticulture are typically protected under state laws (e.g. *Sempervivum*, *Aeonium* and *Aichryson*). *Sedella leiocarpa* and eight *Dudleya* taxa are listed as endangered in the USA (U.S. Fish and Wildlife Service 2004). Many data (general and per country listings with IUCN categories) are included in Oldfield (1997). Golding (2002) lists the IUCN Red Data List categories for many southern African species per country.

Studies on the conservation biology (reproduction, life history, population genetics) are available for *Rhodiola integrifolia* and *Dudleya multicaulis* (see Reproductive Systems). Special ex situ propagation programs have been initiated for some endangered local endemics (e.g. the Madeiran *Aichryson dumosum*, Fernandes 1997). Most genera and species of horticultural appeal appear to be cultivated in specialised public and private collections.

CONSPECTUS OF CRASSULACEAE

I. Subfam. Sempervivoideae Arn. (1832).

1. Tribe Telephieae ('t Hart) Ohba and Thiede ined. (= Hylotelephium clade).

Genera 1–5

Incertae sedis: genus 6

2. Tribe Umbiliceae Meisn. (1838) (= *Rhodiola* clade).

Genera 7–10

3. Tribe Semperviveae Dumort. (1827) (= *Sempervivum* clade).

Genera 11–12 and *Sedum* subg. *Gormaniana* p.min.p. (*S. assyriacum*, *S. mooneyi*)

4. Tribe Aeonieae Thiede ined. (= *Aeonium* clade).

Genera 13–15 and *Sedum* subg. *Gormaniana* p.min.p. (series *Caerulea*, *Pubescens* and *Monanthoidea*)

5. Tribe Sedeae Fr. (1835).

a. Leucosedum clade

Genera 16–21 and *Sedum* subg. *Gormaniana* p.maj.p.

b. Acre clade

Genera 22–28 and *Sedum* subg. *Sedum*

II. Subfam. Kalanchoideae A. Berger (1930)

(= *Kalanchoe* clade).

Genera 29–32

III. Subfam. Crassuloideae Burnett (1835)

(= *Crassula* clade).

Genera 33–34

STAMENS EQUAL IN NUMBER TO PETALS

2. Leaves usually decussate, rarely verticillate; with hyathodes along margins and/or leaf face; seeds sinuate-papillate (*Crassula* type) 3
 - Not as above; leaves spiral 4
3. Perennial tuberous herbs, flowers 10–12-merous; fruits 2-seeded, breaking transversely (Ethiopia)
 - 34. *Hypagophytum*
 - Not as above; when plants tuberous or flowers polymorous, then fruits not few-seeded 33. *Crassula*
 - 4. Plants with persistent or monocarpic rosettes 5
 - Plants without rosettes 7
 - 5. Monocarpic rosette-forming herbs (Asia) 6
 - Perennial shrublets with lax rosettes at branch tips (Mexico) 25. *Graptopetalum* p.p.
 - 6. Inflorescences broad, flat-topped, corymboid thyrsoids
 - 1. *Sinocrassula*
 - Inflorescences narrow-elongate thyrsoids 2. *Kungia*
 - 7. Plants tuberous; leaves peltate; inflorescences elongate racemes 7. *Umbilicus* p.p. (*U. heylandianus*)
 - Not as above, annual to perennial herbs 8
 - 8. Annual to perennial herbs; fruits many-seeded follicles (N hemisphere) 22. *Sedum* p.p. (e.g. *S. rubens*)
 - Minute annual herbs; fruits 1-seeded nutlets (USA: California) 20. *Sedella* p.p.

STEMS FRAIL OR LEAVES CADUCOUS

9. Perennials, but leaves or aboveground stems annually caducous 10
 - Annual or biennial, or perennial and then with at least some perennating leaves 17
10. Stems perennial, succulent, ± elongated; leaves crowded at branch tips (southern Africa)
 - 31. *Tylecodon*
 - Stems annual, not succulent; perennials with underground tubers, rhizomes or thickened roots (usually outside Africa) 11
 - 11. Plants with tuberous stems 12
 - Plants with rhizomes, caudices or thickened roots 13
 - 12. Leaves not peltate; inflorescences axillary, cymose (W USA and Baja California)
 - 21. *Dudleya* p.p. (*D.* sect. *Hasseanthus*)
 - Leaves usually distinctly peltate; inflorescences terminal, racemes or panicles 7. *Umbilicus* p.p.
 - 13. Plants with thickened roots; leaves terete-subulate (America) 23. *Villadia* p.p.
 - Plants with rhizomes or caudices; leaves flat 14
 - 14. Carpels narrowed at base (stipitate-attenuate)
 - 5. *Hylotelephium*
 - Carpels with broad base 15
 - 15. Rhizomes thin; inflorescences pleiochasia
 - 10. *Phedimus* p.p.
 - Plants with very thick rhizome; inflorescences thyrsoids 16
16. Petals free; flowers often unisexual (plants monoecious or dioecious) 9. *Rhodiola*
 - Corolla connate at base for 1/3–2/3 8. *Pseudosedum*

PERENNIALS WITH MONOCARPIC ROSETTES

WITH TERMINAL INFLORESCENCES

17. Plants with perennial monocarpic rosettes with terminal inflorescences 18

KEY TO THE GENERA

1. Stamens equal in number to petals 2
 - Stamens double in number to petals 9

- Plants annual (rarely biennial or triennial), or perennial and then not with monocarpic rosettes with terminal inflorescences 24
- 18. Nectary scales larger than the insignificant petals (Canary Islands)
 - 14. *Monanthes* p.p. (*M.* sect. *Monanthes*)
 - Nectary scales inconspicuous, much smaller than the showy petals 19
- 19. Flowers 5 (rarely 6)-merous; inflorescences corymboid to much elongated and spike-like thyrsoids 20
 - Flowers (5)6-32-merous; inflorescences corymboid to dome-shaped thyrsoids or with several cincinni, never spike-like 22
- 20. Inflorescences flat-topped, corymboid thyrsoids, or cymose, few-flowered (eastern Mediterranean, W Asia)
 - 18. *Prometheum* p.p.
 - Inflorescences elongate, many-flowered 21
- 21. Partial inflorescences helicoid (Turkey, Iraq, Turkmenistan) 17. *Rosularia* p.p. (*R. elymaitica*)
 - Partial inflorescences never helicoid (C to E Asia)
 - 4. *Orostachys*
- 22. Leaves semi-terete, not apiculate; flowers 5-merous; white (Europe/Mediterranean)
 - 22. *Sedum* p.p. (e.g. *S. hirsutum*)
 - Leaves usually flat and apiculate; flowers 6-32-merous 23
- 23. Rosettes sessile, usually < 10 cm; inflorescences pleiochasia; flowers 6-18-merous, often pink to purple, rarely white or yellow; carpels (sub)erect (Europe to Caucasus) 11. *Sempervivum*
 - Rosettes sessile or at branch tips, often > 10 cm; inflorescences thyrsoids or pleiochasia; flowers (6-)10-32-merous, often yellow or whitish, rarely reddish; carpels spreading (mainly Macaronesia, also N and NE Africa and SW Arabia) 15. *Aeonium*
- 24. Leaves decussate throughout length of stems 25
 - Leaves alternate at least in upper stem parts, or in rosettes, rarely verticillate 32

LEAVES DECUSSATE

- 25. Annual to biennial, glabrous to glandular-hairy herbs, to 15 cm; flowers (4)5-merous, white, pink or purplish; petals 4-5 mm (Mediterranean) 26
 - Perennial herbs (rarely monocarpic), or shrubs or small trees, or lianas; flowers 4-6-merous; petals > 5 mm, in various colours 27
- 26. Annual glabrous herbs; inflorescences to 5 cm
 - 10. *Phedimus* p.p. (*P. stellatus*)
 - Annual to biennial, glandular-hairy herbs; inflorescences to 60 cm 22. *Sedum* p.p. (e.g. *S. cepaea*)
- 27. Flowers 4-merous; herbs (rarely monocarpic) to shrubs or small trees, or lianas 30. *Kalanchoe*
 - Flowers 5- or 6-merous; shrublets or herbs 28
- 28. Flowers (5)6-merous, white 29
 - Flowers 5-merous, not white (Africa, Caucasus, North America) 30
- 29. Shrublets to 80 cm tall (Madagascar)
 - 6. *Perrierosedum*
 - Dwarf herbs to 10 cm tall (Europe/Mediterranean) 22. *Sedum* p.p. (e.g. *S. dasyphyllum*)
- 30. Herbs with creeping stems; leaves petiolate, flat and thin; inflorescences arching over; flowers yellow, narrowly urceolate (Caucasus)
 - 7. *Umbilicus* p.p. (*U. oppositifolius*)

- Not as above 31
- 31. Shrubs; leaves not easily detached; flowers 2-3 cm, usually pendent; corolla connate at base (Africa, Arabia) 32. *Cotyledon*
 - Herbs; leaves often easily detached; flowers to 1 cm, ± upright; petals free (USA, Mexico) 24. *Lenophyllum*
- 32. Leaves verticillate (Africa) 22. *Sedum* p.p. (e.g. *S. epidendrum*)
 - Leaves alternate at least in upper stem parts, or in rosettes 33
- 33. Annual (to rarely biennial or triennial) herbs 34
 - Perennial herbs to shrublets 40

ANNUALS

- 34. Flowers 6-7-merous, dirty white; nectary scales conspicuous, larger than the insignificant petals (Canary Islands) 14. *Monanthes* p.p. (*M. icterica*)
 - Flowers 5-12-merous; nectary scales inconspicuous and never larger than the showy petals 35
- 35. Flower 5-merous; corolla distinctly connate (Iberian Peninsula, N Africa) 36
 - Flower 5-12-merous; petals (nearly) free 36
- 36. Filaments inserted at the base of the corolla tube; stylopodia ± 1 mm 22. *Sedum* p.p. (*S. mucizonia*)
 - Filaments inserted slightly below the mouth of the corolla tube; stylopodia 2.5-5 mm 16. *Pistorinia*
- 37. Annual to biennial herbs; leaves flat; young plants with conspicuous basal rosettes (E Mediterranean) 22. *Sedum* p.p. (*S. lampusae*, etc.)
 - Young plants without basal rosettes 38
- 38. Fruits 1-seeded nutlets (USA: California) 20. *Sedella* p.p.
 - Fruits many-seeded follicles opening at ventral suture 39
- 39. Annual to triennial herbs; leaves flat, often ± rosulate near branch tips; flowers yellow; nectary scales 2-5-fid (Macaronesia) 13. *Aichryson* p.p. (*A.* sect. *Aichryson*)
 - Annual herbs; leaves ± semi-terete; nectary scales entire (northern hemisphere to E Africa) 22. *Sedum* p.p.

PERENNIALS WITH LARGE NECTARY SCALES

- 40. Nectary scales conspicuous, larger than the insignificant petals 41
 - Nectary scales inconspicuous, much smaller than the showy petals 43
- 41. Leaves with bladder-cell idioblasts (Canary Islands) 14. *Monanthes* p.p.
 - Leaves without bladder-cell idioblasts 42
- 42. Flowers 5-merous; stems elongate, repent (Mexico) 22. *Sedum* p.p. (*S. longipes*)
 - Flowers 5-7-merous; stems short and thick; leaves in rosettes (Morocco) 22. *Sedum* p.p. (*S. surculosum*)
- 43. Inflorescences terminal; leaves not in rosettes 44
 - Inflorescences lateral; leaves usually in distinct rosettes, or at least crowded at branch tips 49

PERENNIALS WITHOUT ROSETTES

AND WITH TERMINAL INFLORESCENCES

- 44. Plants herbaceous, at highest slightly woody at base 45
 - Plants shrubby 47
- 45. Corolla connate (Mexico, Peru) 23. *Villadia* p.p. (*V. imbricata*, etc.)

- Petals free 46
- 46. Leaves \pm densely imbricate and acuminate; flowers yellow(ish); fruits erect (Europe/Mediterranean)

12. *Petrosedum*

- Leaves not densely imbricate nor acuminate; fruits erect to spreading (northern hemisphere to E Africa)
- 47. Stems distinctly succulent, with \pm flaking papery bark; inflorescences pleiochasia; petals free

22. *Sedum* p.p. (p.max.p.)

- Stems not distinctly succulent, without flaking papery bark; inflorescences elongate; corolla connate 48
- 48. Leaves usually soft fleshy, semi-terete; inflorescences thyrsoids; filaments glabrous (America)

23. *Villadia* p.p.

- Leaves firmly fleshy; inflorescences thyrses or spikes without terminal flower; filaments papillate where connate with corolla (southern Africa)

29. *Adromischus*

PERENNIALS WITH ROSETTES, LATERAL INFLORESCENCES, AND THE COROLLA CONNATE FOR MOST OF ITS LENGTH

- 49. Corolla connate for most of its length; petals distinctly fleshy (America) 50
- Petals free or corolla connate for less than 1/2 of its length; petals membranous 51
- 50. Leaves usually very thick and with strong wax bloom; inflorescences cincinnoid; bracts usually very large and \pm covering the flowers at anthesis; petals with basal scale on each margin (Mexico) **28. *Pachyphytum***
- Inflorescences racemose, cymose-paniculate, spicate thyrsoids, or cincinnoid; petals usually without, rarely with small scales (southern USA to Argentina)

27. *Echeveria*

PERENNIALS WITH ROSETTES, SHRUBBY HABIT AND LATERAL INFLORESCENCES, AND PETALS FREE OR COROLLA CONNATE FOR <1/2 OF ITS LENGTH

- 51. Shrublets; rosettes at branch tips 52
- Stem-less herbs 56
- 52. Leaves glandular-hairy; flowers yellow, 7-8-merous (Canary Islands)
- 13. *Aichryson* p.p. (*A. sect. Macrobia*)**
- Leaves glabrous (America) 53
- 53. Leaves with intensive wax bloom; rosettes typically branching dichotomously; leaves not easily detached; seeds costate (W USA and Baja California)
- 21. *Dudleya* p.p. (e.g. *D. formosa*)**
- Not as above; seeds reticulate-papillate (mainland Mexico, Guatemala) 55
- 54. Petals (almost) free, yellow or white
- 22. *Sedum* p.p. (*S. sect. Pachysedum*)**
- Corolla connate at base 55
- 55. Inflorescences broad thyrsoids with cincinnoid partial inflorescences; inner face of petals usually with \pm red to brown spottings, or whitish to yellowish
- 25. *Graptopetalum* p.p.**
- Inflorescences elongate and narrow, partly spike-like thyrsoids; petals inside \pm purplish-red, unspotted
- 26. *Thompsonella* p.p.**

PERENNIALS WITH STEM-LESS ROSETTES AND LATERAL INFLORESCENCES, AND PETALS FREE OR COROLLA CONNATE FOR <1/2 OF ITS LENGTH

- 56. Leaves glandular-pubescent to glandular-hairy; corolla connate at base 57
- Leaves glabrous; petals free or corolla connate at base 59
- 57. Plants offsetting with long brittle runners; leaf apex mucronate, margins distinctly ciliate (Ethiopia)
- 19. *Afrovivella***
- Plants not offsetting or with short runners; leaf apex not mucronate, margins usually not ciliate 58
- 58. Leaves densely glandular-pubescent; flowers 5-merous, white or pale yellow/reddish; fruits erect or spreading (E Mediterranean to W Asia) **18. *Prometheum* p.p.**
- Leaves glandular-hairy; flowers 5-9-merous, white to pink(ish); fruits erect (E Mediterranean, Near East to E Asia)
- 17. *Rosularia* p.p.**
- 59. Plants with thickened taproot; leaf apex cuspidate to spinulose; carpels connate at base, with only 4-6 ovules each (Asia) **3. *Meterostachys***
- Not as above 60
- 60. Rosettes typically branching dichotomously; leaves usually with intensive wax-bloom, not easily detached; bracts semi-amplexicaul, never spurred (W USA and Baja California) **21. *Dudleya* p.p.**
- Not as above (southern USA, mainland Mexico) 61
- 61. Leaves usually mucronate; inflorescences short and broad thyrsoids; petals usually with \pm red to brown spottings, or bright pink
- 25. *Graptopetalum* p.p. (*G. sect. Graptopetalum*)**
- Leaves not mucronate; inflorescences elongate and narrow, partly spike-like thyrsoids; petals inside \pm purplish-red **26. *Thompsonella* p.p.**

GENERA OF CRASSULACEAE

Basic Features

Herbaceous, arhizomatic perennials, tanniniferous, with solitary crystals or druses; shoots aerial; leaves alternate, scattered (dispersed), succulent*, sessile, \pm flat, entire, with marginal hydathodes, glabrous or with non-glandular indumentum; stomata anisocytic*; inflorescences terminal thyrsoids*, partial inflorescences dichasial; flowers \pm erect, actinomorphic, 5-merous, obdiplostemonous*; sepals \pm appressed to corolla, connate at base; corolla choripetalous, spreading; stamens with filaments free to base; anthers basifixed, latrorse, yellow, without terminal connective appendage; ovary superior; carpels free (nearly) to base, with many crassinucellate ovules and carpellary nectary scales* at their bases; fruits erect follicles, opening along whole suture; seeds small, \pm cylindrically fusiform, \pm brown, testa papillate*. $x = 8$.

Note: these features are valid for all genera of the family, unless modified in the subsequent characterisations of subfamilies, tribes, clades or informal generic groups in which their characters behave correspondingly.

Putative synapomorphies for higher taxa and major clades are marked with asterisks (*). Note the distinction made between taxonomic characters which are valid only for the genera included in the respective taxon (e.g. tribe), thus excluding the formalised segregates of *Sedum*, and cladistic synapomorphies which are valid for all members of a clade, including the segregates of *Sedum*.

The synoptic treatments for all genera included in Eggli (2003) as well as standard flora works are not cited in the descriptions of the genera.

Subfamilies Sempervivoideae and Kalanchoideae

Leaves usually with single (sub)apical hydathode*; seeds costate*.

Genera 1–32.

(Note that basic features for family are further valid.)

I. SUBFAM. SEMPERVIVOIDEAE Arn. (1832).

Flowers (4)5(–32)-merous, flowers obdiplostemonous (rarely haplostemonous, but then leaves never decussate); seeds costate with many (>6, usually c. 10) costae* in side view. Genera 1–28. Largely confined to the northern hemisphere.

I.1. TRIBE TELEPHIEAE ('t Hart) Ohba & Thiede, ined.

Leaves usually in rosettes (except *Hylotelephium*), rosettes usually monocarpic, leaves partly cuspidate; petals often spotted to mottled with red to brown; carpels stipitate or connate at base; flowering mainly in autumn.

Genera 1–5. Mainly in temperate Asia.

1. *Sinocrassula* A. Berger

Sinocrassula A. Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:462 (1930).

Perennial, sometimes annual or biennial herbs, glabrous, papillose or rarely pubescent; leaves obtuse to usually acuminate, often mottled with red; inflorescences broad corymbose thyrsoids, simple

to richly branched; flowers campanulate-urceolate; petals free, connivent to urceolate corolla; \pm whitish, greenish or rose, \pm mottled with red, orange or brown; stamens 5, alternating with and slightly shorter than petals; carpels connate at base; stylodia abruptly narrowed. $n = 11$. Seven species, northern India (Uttar Pradesh), Bhutan, eastern Tibet, south-western China (Yunnan, Szechuan).

2. *Kungia* K.T. Fu

Kungia K.T. Fu in J.N.W. Teachers Coll. (Nat. Sci.) 1:3 (1988).

Orostachys sect. *Schoenlandia* H. Ohba (1978).

Herbs, glabrous or hairy; stolons present; sterile stems usually present; basal leaves in subsessile rosettes, decussate or usually alternate, obtuse; flowering stems erect, very slender but strong; inflorescences many-flowered terminal, narrow, racemiform or paniculiform thyrsoids; sepals lanceolate-triangular, much shorter than petals, spurless; petals connate at base, lanceolate, red or purple; stamens 5, alternating with petals, shorter than petals; anthers oblong-reniform; carpels nearly free, oblong, base attenuate or stalked; stylodia long. Two species, south-western China (northern Szechuan, Gansu, Shaanxi), on rocky slopes from 700–3,100 m.

Sister to *Sinocrassula*, according to molecular data (Hideaki Ohba, unpubl. data, pers. comm. 2004); the two genera share haplostemonous flowers. Formerly classified as sect. *Schoenlandia* within *Orostachys*.

3. *Meterostachys* Nakai

Meterostachys Nakai, Bot. Mag. (Tokyo) 49:74, 210 (1935); Moran, Cact. Succ. J. (U.S.) 44:262–273 (1972); Ohba, J. Fac. Sci. Univ. Tokyo III, Bot. 12:173–174 (1978).

Herbs with thickened taproot; leaves in small rosettes, apex cuspidate to spinulose, often cartilaginous; inflorescences axillary, simple, cymose; flowers (4)5-merous, pedicels often longer than flowers; petals upright, connate at base for 1/3 to 2/5, white, often with reddish hue; stamens distinctly shorter than petals; carpels connate at base, suberect, with only 4–6 ovules each; $n = 16$. Only 1 species, *M. sikokiana* (Makino) Nakai from Japan, Korea and China (Byalt 1997).

Sister to *Orostachys* subsect. *Appendiculatae*, according to molecular data (Mayuzumi and Ohba 2004).

4. *Orostachys* Fischer

Orostachys Fischer, Mém. Soc. Imp. Naturalistes Moscou 2:274 (1809); Byalt, Novost. Sist. Vyssh. Rast. 32:40–50 (2000), rev. (in Russian).

Biennial monocarpic herbs; leaves of first year in solitary rosette, rosettes often dimorphic with compact winter (resting) stage, normally offsetting; leaves linear to ovate, apex cuspidate (ser. *Appendiculatae*) or blunt (ser. *Orostachys*); inflorescences dense, narrowly pyramidal to cylindrical, many-flowered thyrsoids, usually with secondary branches; sepals connate at base; corolla \pm stellate; petals lanceolate, subconnate, white, pink or red; stamens longer than petals; carpels stipitate; stylochia slender. $n = 12$. Eleven species, Russia (East Siberia), Kazakhstan, Mongolia, China, Korea, Japan.

Polyphyletic, according to molecular data (Mayuzumi and Ohba 2004): subsect. *Orostachys* is nested within *Hylotelephium*, and subsect. *Appendiculatae* is sister to *Meterostachys* but differs strongly from that genus and should possibly be given separate generic status. See also under *Kungia*.

5. *Hylotelephium* H. Ohba

Fig. 28

Hylotelephium H. Ohba, Bot. Mag. (Tokyo) 90:46–47 (1977); Fröderström, Acta Horti Gothob. suppl. 5:1–75 (1930), sub *Sedum*; Ohba, J. Fac. Sci. Univ. Tokyo III, Bot. 12:162–166 (1978).

Hemicytrophites with rootstock of fibrous to tuberous, often carrot-shaped roots and short, fleshy or woody rhizome (*H. populifolium* (Pall.) H. Ohba with perennial, woody, frail stems); flowering stems from adventitious buds on rootstock or basal nodes of former years' flowering stems, simple, annual, usually with numerous leaves and visible internodes, some species with additional vegetative shoots; leaves alternate, rarely decussate to 3–5-whorled, broad, flat, margin entire, crenate, or lobed, apex usually blunt; inflorescences thyrsoids, compound or paniculate or umbellate-corymbose in shape, dense and many-flowered; flowers (4)5-merous; petals usually free, white, purple, pink or red, occasionally yellowish or greenish; stamens shorter to longer than petals, those opposite petals basally connate with them; carpels stipitate. $n =$ usually 12, also 11, 23, 24, 25, 46. About 27 species, East Asia, Siberia, Caucasus, Europe, North America.

A relatively recent segregate from *Sedum* s.l. The division into two sections with two series

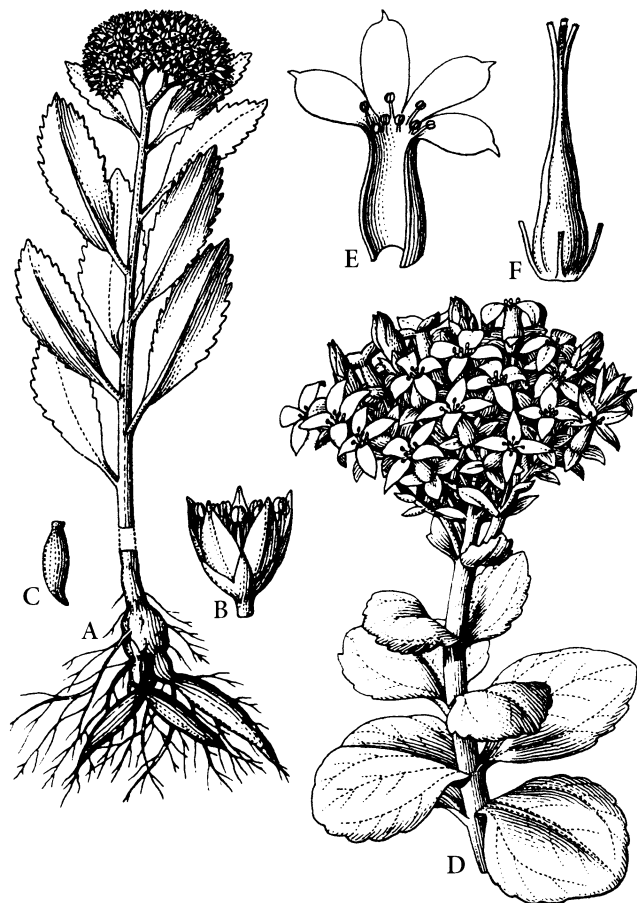


Fig. 28. Crassulaceae. A–C *Hylotelephium telephium*. A Flowering plant with tuberous roots. B Flower seen from side. C Seed. D–F *Kalanchoe grandiflora*. D Flowering shoot. E Flower, opened out. F Ovary with hypogynous scales. (Berger 1930)

(Ohba, l.c.) is not supported by molecular data (Mayuzumi and Ohba 2004). These data also indicate that *Orostachys* sect. *Orostachys* is nested within *Hylotelephium*; the two taxa share blunt leaves, stipitate carpels and $x = 12$. This causes nomenclatural problems, since *Orostachys* antedates *Hylotelephium*. *Orostachys paradoxa* (A.P. Khokhr. & Vorosch.) Czerep. links both taxa (Byalt 1998).

INCERTAE SEDIS:

6. *Perrierosedum* (A. Berger) H. Ohba

Perrierosedum (A. Berger) H. Ohba, J. Fac. Sci. Univ. Tokyo III, Bot. 12:166 (1978).

Branched shrublets 50–80 cm; stems 4-angled; leaves decussate, oblong-spathulate, base long-

attenuate, margins crenulate; inflorescences terminal, corymbose-cymose, 5–10-flowered, pedunculate; flowers (5)6-merous; sepals free; petals free, broadly spatulate, white tinged with red; filaments shorter than petals; nectary scales conspicuous, 3–3.5 mm, tips bifid; carpels free, ventrally straight, tapering towards tip. Only 1 species, *P. madagascariense* (H. Perrier) H. Ohba from Madagascar.

Possibly linking the African Kalanchoideae with the Asian Telephieae.

I.2. TRIBE UMBILICEAE Meisn. (1838).

Rhizomatic hemicryptophytes to tuberous geophytes*; leaves usually crenate to dentate* (except *Pseudosedum*); flowering mainly in spring to early summer.

Genera 7–10. Mainly in temperate Asia.

7. *Umbilicus* DC.

Umbilicus DC., Bull. Sci. Soc. Philom. Paris 3:1 (1801).

Chiastophyllum (Ledebour) Stapf ex A. Berger (1930).

Small herbs with tubers and frail stems (sect. *Umbilicus*) or with short, creeping and rooting rhizomatous stems (*U. oppositifolius*); tissues with crystal sand; leaves alternate (sect. *Umbilicus*) or decussate (*U. oppositifolius*), suborbicular, with distinct petiole, \pm peltate with central dimple (sect. *Umbilicus*) or not peltate (*U. oppositifolius*); inflorescences many-flowered, long terminal panicles or racemes (sect. *Umbilicus*) or double racemes (*U. oppositifolius*), without terminal flower, upright (sect. *Umbilicus*) or arching over (*U. oppositifolius*); flowers usually \pm horizontal or drooping, rarely haplostemonous (usually in *U. heylandianus* Webb. & Berth.); corolla tubular or campanulate; petals connate, white, green or yellow; filaments usually connate with corolla for most of their length; seeds multipapillate, papillae arranged in small groups (sect. *Umbilicus*) or connate (*U. oppositifolius*). $n = 24$. Thirteen species, western, southern and central Europe, Macaronesia, Mediterranean, Near East to Caucasus, Arabia, North, Central and East Africa.

Divided into sect. *Umbilicus*, which exhibits complex patterns of variation probably due to self-pollination and is in need of revision, and sect. *Chiastophyllum* with *U. oppositifolius* (Ledeb.) Ledeb. from the Caucasus, which is also recognised at generic level by some authors.

8. *Pseudosedum* (Boiss.) A. Berger

Pseudosedum (Boiss.) A. Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:465 (1930).

Hemicryptophytes; flowering stems one to numerous, arising from usually well-developed simple or branched sympodial rhizome, old stems usually persistent; leaves usually linear, (sub)obtuse, broadly spurred, subterete, entire, usually fleshy; flowering branches one to many, simple, usually densely leafy, 5–40 cm; inflorescences dense terminal thyrsoids, corymbose or umbellate, rarely paniculate, usually many-flowered; flowers (5)6-merous; corolla campanulate to tubular; petals connate at base for 1/3 to 2/3, lobes \pm divergent, pink to violet or red or pure white; fruits erect or slightly divergent follicles. Twelve species, Central Asia; stony soils in mountainous regions.

Sister to *Rhodiola*, according to molecular data (Mayuzumi and Ohba 2004); the two genera are hemicryptophytes, with usually well-developed rhizomes.

9. *Rhodiola* L.

Rhodiola L., Sp. Pl.: 1035 (1753); Ohba, J. Fac. Sci. Univ. Tokyo III, Bot. 12:139–198 (1978); l.c. 12:337–405 (1980); l.c. 13:65–119 (1981); l.c. 13:121–174 (1982).

Clementsia Rose (1903).

Hemicryptophytes; rhizomes monopodial, massive or slender, apical part with foliage and/or scaly leaves; leaves usually flat; flowering stems sometimes persistent for a while; inflorescences usually broad thyrsoids, partly reduced to solitary flowers or rarely racemes; flowers hermaphrodite or plants dioecious (rarely monoecious), 4–5(6)-merous, pedicellate, when dioecious: petals and ovaries opposite in male but alternate in female plants, when hermaphrodite or monoecious: petals and ovaries always opposite; calyx fleshy, in female plants forming a tube divided into 4–5(6) \pm equal lobes; petals free, white, reddish, deep purplish-red or pale yellow to greenish, always longer than sepals in female plants; carpels superior to semi-inferior, usually connate at base (rarely completely free), straight at anthesis, slightly patent in fruit. $n = 7, 10, 11, 22, 33, 44, 55$. About 58 species, East Asia, Siberia, North America, Europe; especially sub-Arctic and alpine zones.

The subdivision into four subgenera with seven sections (Ohba 1978) is not supported by molecular data (Mayuzumi and Ohba 2004).

10. *Phedimus* Raf.

Phedimus Raf., Amer. Monthly Mag. Crit. Rev. 1:438 (1817); Grulich, Preslia 56:29–46 (1984), sub *Asterosedum*; Chung & Kim, Korean J. Pl. Taxon. 19:189–227 (1989), rev. Korean taxa.

Aizopsis Grulich (1984).

Asterosedum Grulich (1984).

Spathulata (A. Borissova) A. Löve & D. Löve (1985).

Perennial or rarely annual herbs, usually glabrous, sometimes stems woody at base, emerging from thin woody rhizome; leaves decussate or alternate, base narrowed; with several hydathodes on lower face along margins; flowering branches erect or ascending; inflorescences usually dense many-flowered terminal pleiochasia; flowers (4)5–6(7)-merous; sepals usually unequal; petals free, usually spreading, white, pink, red, purplish (subg. *Phedimus*) or yellow (subg. *Aizoon*); anthers red (subg. *Phedimus*) or yellow, orange or reddish (subg. *Aizoon*); fruits follicles, usually spreading; seeds costate-papillate (i.e. papillae incompletely connate to costae), multipapillate in *P. selskianus* (Regel & Maack) 't Hart ('t Hart and Berendsen 1980; Gontcharova 1999). $n = 5, 6, 7, 8, 15-16, c. 32, 33, 34$. Eighteen species, eastern Europe and Asia.

Only recently re-segregated from *Sedum*. Divided into subg. *Phedimus* (stems creeping and rooting, with sterile stems; $x = 5, 6, 7$; 5 spp.; Mediterranean to Caucasus) and subg. *Aizoon* (annual shoots often woody at base, emerging from woody rhizome; follicles with distinct lips along suture; $x = 8$; 13 spp.; China, Japan, Korean and Central Siberia). Subg. *Aizoon* is distinct morphologically, karyologically and according to molecular data (Mort et al. 2001; Mayuzumi and Ohba 2004), and also recognised at generic level as *Aizopsis* by some authors.

All other Sempervivoideae

Plants often glandular-pubescent; leaves basically (semi-)terete* (in derived genera often \pm flat and thick); partial inflorescences typically monochasial* (double or single cincinni).

Genera 11–28. Mainly northern temperate region, also North, Central and East Africa and southern America.

I.3. TRIBE SEMPERVIVEAE Dumort. (1827).

Leaves acuminate; inflorescences pleiochasial; flowers poly(at least 6)-merous; base chromosome numbers high, $n = 12-16$.

Genera 11 + 12.

Sedum assyriacum Boiss. (Near East) and *S. mooneyi* M.G. Gilbert (Ethiopia) of *Sedum* subg. *Gormaniana*, and possibly further species related to these, also come out here according to molecular data ('t Hart 1995; van Ham and 't Hart 1998). These two species do not share the tribal characters but their yellow flowers agree with those in *Petrosedum* and some *Sempervivum*.

11. *Sempervivum* L.

Sempervivum L., Sp. Pl.: 464 (1753); Praeger, Account *Sempervivum* Group (1932).

Jovibarba (A.P. de Candolle) Opiz (1852).

Leaves rosulate, with glandular and non-glandular hairs, reproducing vegetatively through axillary stolons or rarely through rosette division, flattened, glabrous or pubescent, with marginal cilia; inflorescences usually pleiochasia, partial inflorescences dense, with (2)3(4) single or double cincinni; flowers 6–18-merous; petals spreading and pink, purple, yellow to almost white (sect. *Sempervivum*) or erect during anthesis, with fimbriate margins and (pale) yellow to whitish (sect. *Jovibarba*); nectary scales \pm square; carpels (sub)erect. $n = 16-19, 21, 32, 34, 36, 40, 42, 54$. About 63 species, Morocco (Atlas Mts.), Europe to north-western and central Russia, Balkan Peninsula, Carpathians, Turkey, northern Iran, Caucasus.

Divided into sect. *Sempervivum* (flowers 8–18-merous; $x = 16-21$) and sect. *Jovibarba* (flowers 6(7)-merous; $x = 19$; 2 spp.; 't Hart and Bleij 1999). According to molecular data, *Jovibarba* is nested in *Sempervivum* (Philipp Neeff, pers. comm.), or both are sister groups (Mort et al. 2001). Notoriously difficult in its taxonomy, due to reticulate evolution. A revision is being undertaken by Ph. Neeff (University of Essen, Germany). *Sempervivum* shares several features with *Petrosedum*.

12. *Petrosedum* Grulich

Petrosedum Grulich, Preslia (Praha) 56:39 (1984); 't Hart, Biosyst. stud. Acre-group and ser. *Rupestris* of gen. *Sedum* (Crassulaceae); Thesis Univ. Utrecht (1978).

Sedum ser. *Rupestris* A. Berger (1930).

Mat-forming herbs, glabrous, inflorescences also glandular, perennating with branching and rooting non-flowering ascending to repent shoots; leaves (semi-)terete, linear-elliptic, acuminate, spurred,

usually densely imbricate; flowering shoots erect, simple, 10–60 cm, often \pm woody at base; inflorescences usually pleiochasia, partial inflorescences single or double cincinni, at anthesis erect or nodding; flower (sub)sessile, 6–7(–12)-merous; sepals acute to acuminate; petals obtuse, spreading during anthesis, yellow, rarely white; filaments usually yellow; carpels erect, dark brown in fruit; stylodia long. $n = 12, 13, 16, 17, 24, 26, 32, 34, 36, 44, 48, 56$. Seven species, western and central Europe, Balkan, Mediterranean.

Sedum ser. *Rupestris* is here recognised at the generic level, since morphologically it is highly distinct from European-Mediterranean *Sedum*, also in its embryology (Mauritzon 1933), flavonoid patterns (Stevens et al. 1996) and epicuticular triterpenes (Stevens et al. 1994). According to molecular data, *Petrosedum* does not form a clade together with *Sempervivum*, but the two form a polytomy (van Ham and 't Hart 1998; Mort et al. 2001) or place separate from each other ('t Hart 1995).

I.4. TRIBE AEONIEAE Thiede, ined.

Plants glandular-hairy; leaves usually \pm flat, in \pm distinct rosettes; flowers poly(at least 6)-merous; carpels often with glandular hairs, immersed into receptacle; seeds usually costate-papillate (i.e. papillae incompletely connate to costae) to costate. Genera 13–15. Mainly in Macaronesia.

Sedum subg. *Gormanis* ser. *Caerulea*, *Pubescens* and *Monanthoidea* (from North Africa) also belong here, according to molecular data (Mes and 't Hart 1994; Mes 1995; 't Hart 1995; van Ham and 't Hart 1998), but do not exhibit all of the tribal characters.

13. *Aichryson* Webb & Berth.

Aichryson Webb & Berth., *Phytogr. Canar.* 1:180 (1840); Bramwell, *Bol. Inst. Nac. Inv. Agron. (Madrid)* 28:203–213 (1968), synopsis; Fairfield et al., *Pl. Syst. Evol.* 248:71–83 (2004); mol. phylog.

Macrobis (Webb & Berth.) G. Kunkel (1977).

Annual to triennial monocarpic herbs (sect. *Aichryson*) or small perennial shrublets (sect. *Macrobis*); stems densely hairy or glabrous, branches occasionally slightly woody; leaves alternate, often \pm rosulate near branch tips, sessile or petiolate, entire or crenulate, glabrous or (glandular) hairy to viscid; inflorescences few- to many-branched, lax thyrsoids; flowers 6–12-merous; sepals glabrous

or hairy; petals pale or deep yellow; nectary scales 2–5-fid; carpels glabrous or glandular-hairy; fruits erect follicles; seeds costate-papillate to costate. $n = 15, 17, 30$. Fourteen species, from Macaronesia (Canary Islands, Madeira, Azores [Santa Maria]), naturalised in Portugal.

Divided into sect. *Aichryson* and sect. *Macrobis* (2 spp.).

14. *Monanthes* Haw.

Monanthes Haw., *Saxifrag. Enum.*, 2:68 (1821); Nyffeler, *Bradleya* 10:49–82 (1992), rev.; Nyffeler in 't Hart & Eggli, *Evol. Syst. Crassulaceae*: 76–88 (1995); Mes et al., *J. Evol. Biol.* 10:193–216 (1997), mol. phylog.; Cartwright et al., *IOS Bull.* 12:23–24 (2004), mol. phylog. (abstract).

Petrophytes Webb & Berth. (1841).

Herbs or shrublets, perennial, *M. ictERICA* annual; leaves alternate, rarely decussate, usually in rosettes or scattered along stems, glabrous or glandular-hairy, covered with bladder-cell idioblasts; inflorescences terminal from rosette or at branch tips, or lateral shoots, reduced thyrsoids of 1–3(–5) cymes with (1–)3–8 flowers; flowers (5)6–8(9)-merous; petals insignificant in colour and size, pale yellow, variously striped with red; nectary scales larger than petals, bilobed or flabellate, pale yellow to dark red; carpels often with glandular hairs; fruits follicles, rarely breaking off transversally; seeds costate-papillate to costate or almost smooth. $n = 18, 36, 54; 10$ in *M. ictERICA*. Nine species, from Macaronesia (Canary and Selvagens islands).

Divided into four sections (Nyffeler in Eggli 2003). The position of *M. ictERICA* (Webb ex Bolle) Christ (sect. *Annuae*) is equivocal, according to molecular data: sister to *Aichryson* (Mes et al. 1997; Mort et al. 2001; weak to moderate support), between *Aichryson* and *Monanthes* (Mort et al. 2002; strong support), or sister to the rest of *Monanthes* (Cartwright et al. l.c.; weak support). *Monanthes* is sister to *Aeonium*, according to molecular data; the two genera share a chromosome base number of $x = 18$.

15. *Aeonium* Webb & Berth.

Fig. 29

Aeonium Webb & Berth., *Phytogr. Canar.* 1:184 (1840); Liu, *Syst. Aeonium*, *Natl. Mus. Nat. Sci. (Taiwan) Spec. Publ.* 3 (1989), rev.; Mes & 't Hart, *Mol. Ecol.* 5:351–363 (1996), mol. phylog.

Greenovia Webb & Berth. (1840).

Megalonium (A. Berger) G. Kunkel (1980).

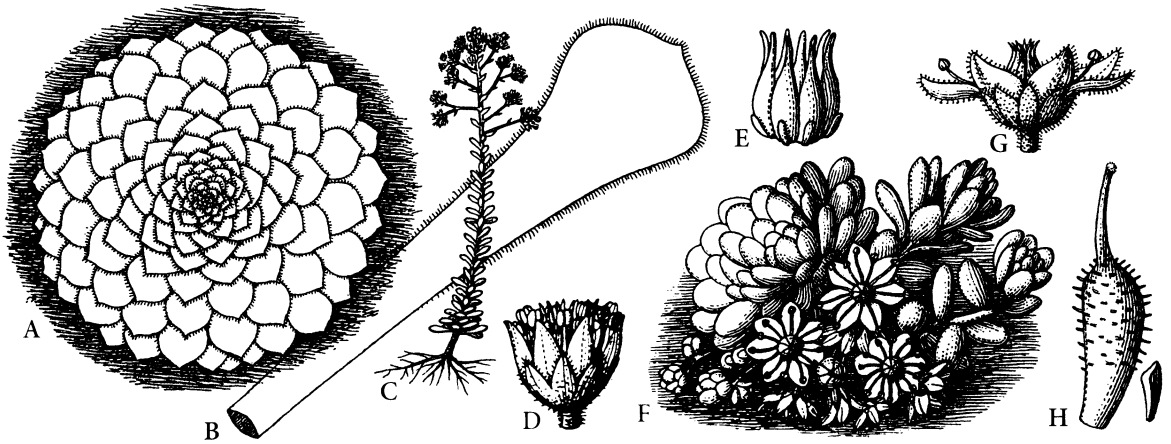


Fig. 29. Crassulaceae. A–E *Aeonium tabulaeforme*. A Rosette. B Leaf from rosette. C Flowering plant. D Flower. E Carpels with hypogynous scales. F–H *Sedum sedoides*.

F Flowering plant. G Flower. H Carpel with detached scale. (Berger 1930)

Perennial, rarely biennial, sometimes monocarpic subshrubs or single or caespitose subshrubby rosette plants; stems glabrous, puberulent, or with reticulate pattern, leaf scars often distinct; leaves glabrous, glabrate, pubescent, or viscid, margins often ciliate; inflorescences terminal (axillary in *A. simsii* (Sweet) Stearn), often large thyrsoids or pleiochasia (esp. sect. *Greenovia*), scape distinct; flowers (6)7–12(–16) or 18–32-merous; sepals connate at base, glabrous or pubescent; petals free, spreading or slightly recurved, usually yellow(ish) or whitish; nectary scales rarely absent; carpels sometimes distinctly immersed in the receptacle, often with glandular hairs; fruits kyphocarpic; seeds costate-papillate or most often costate. $n = 18, 27, 36$. About 36 species, Macaronesia (Canary Islands, Cape Verde Islands, Madeira), south-western Morocco, Northeast and East Africa and Yemen.

According to molecular data (Mes 1995; Mes et al. 1996; Mort et al. 2002), paraphyletic with respect to *Greenovia*; the latter is recognised as one of five sections within *Aeonium* (Nyffeler in Eggl 2003). *Aeonium* is a classic example of adaptive radiation leading to a broad array of growth forms, which has been studied with regard to phylogenetics (Mes 1995; Mes et al. 1997; Mort et al. 2002), adaptive radiation (Jorgensen and Olesen 2001), growth forms (Mes and 't Hart 1996; Mes et al. 1996; Jorgensen and Olesen 2000) and ecophysiology (Lösch 1990). *A. nobile* (Praeger) Praeger may exhibit the largest rosettes in the family, with up to 80 cm Ø.

1.5. TRIBE SEDEAE Fr. (1835).

No tribal characters.

Genera 16–28.

This tribe includes the *Leucosedum* and *Acre* clades which both are well supported with molecular cpDNA restriction-site data (van Ham and 't Hart 1998). With a broader sampling of *matK* sequence data (Mort et al. 2001), both clades are weakly supported only and together sister to *Sedum magellense* Tenore (cf. Fig. 27); this pattern may become even more evident with an exhaustive study. Thus, both clades for the time being are not recognised as distinct taxa but are subsumed as two informal clades within tribe Sedeae.

1.5. A. LEUCOSEDUM CLADE

Plants usually glandular-hairy (not in American taxa).

Genera 16–21. Mainly in winter-rainfall regions.

This clade also includes the major part of *Sedum* subg. *Gormanina*, which is broadly paraphyletic according to molecular data (van Ham 1994; van Ham and 't Hart 1998; 't Hart et al. 1999; Mort et al. 2001).

Genera 16–19

Petals connate. Genera 17 + 18 with rosettes. These taxa are independently derived from within European-Mediterranean *Sedum* subg. *Gormanina*, according to molecular data (van Ham and 't Hart 1998; 't Hart et al. 1999; Mort et al. 2001).

16. *Pistorinia* DC.

Pistorinia DC., Prodr. Syst. Regni Veg. 3:399 (1828).

Small annual herbs; leaves (semi-)terete, often tinged red; inflorescences many-flowered cymes; corolla 5.5–22(–30) mm; petals connate at base for $\geq 1/2$ to distinct corolla tube, lobes spreading, yellow, pink or purple, often finely spotted; filaments inserted below orifice, short; nectary scales long, 1–2 mm; stylodia slender, recurved, 2.5–5 mm; fruits slender follicles, erect. $n = 7$. Three species, from the Iberian Peninsula and North Africa.

According to molecular data (van Ham 1994; 't Hart 1997b), closest to *Sedum* ser. *Monregalensis*.

17. *Rosularia* (DC.) Stapf

Rosularia (DC.) Stapf, Curtis's Bot. Mag. 149: t. 8985, in adnot. (1923); Eggli, Bradleya suppl. 6:1–119 (1988), rev.

Dwarf perennial rosulate herbs, glabrous or glandular-hairy; caudex usually wanting (sect. *Rosularia*) or well developed (sect. *Ornithogalopsis*), often with thickened taproot; rosettes \pm stem-less, solitary or with offsets; leaves oblong to broadly spatulate, glandular-hairy, setate or denticulate, partly dimorphic (summer-winter) and forming 'resting rosettes' (frequent in sect. *Rosularia*); inflorescences lateral or terminal, glabrous or glandular-hairy, slender spicate thyrsoids (sect. *Rosularia*) to corymbiform-paniculate thyrsoids (sect. *Ornithogalopsis*), partial inflorescences cinnoid; flowers 5–9-merous; corolla urceolate, tubular to funnel-shaped, campanulate or stellate; petals connate at base for $1/10$ to $3/4$, white, pale yellow, pink, pinkish-purple or pinkish-brown, dorsally glabrous or glandular-hairy; carpels erect, slender or massive-voluminous, normally glandular-hairy along upper ventral part, completely free or \pm connate at base and sunken into the receptacle; fruits erect follicles. $n = 9, 18$. Seventeen species, eastern Mediterranean, Near East, Inner Asia, Karakorum-Himalaya, Altai.

According to molecular data, *Rosularia* sensu Eggli (1988) is polyphyletic ('t Hart et al. 1999; see also under *Prometheum* and *Sedum*). The genus is divided into sect. *Rosularia* (flowers 5-merous; Mediterranean to Near East) and sect. *Ornithogalopsis* (flowers 5–9-merous; 5 spp.; petals whitish; Inner Asia) which is probably misplaced here.

18. *Prometheum* (A. Berger) H. Ohba

Prometheum (A. Berger) H. Ohba, J. Fac. Sci. Univ. Tokyo III, Bot. 12:168 (1978); Eggli, Bradleya suppl. 6:1–119 (1988), sub *Rosularia*.

Pseudorosularia Gurgeneidze (1978).

Rosularia sect. *Chrysanthae* Eggli (1988).

Perennial or annual to biennial and monocarpic herbs with a narrow taproot and without caudex, usually densely glandular-pubescent; leaves in dense rosettes, flat to semi-terete, usually with subsessile offsets; inflorescences usually terminal or lateral, corymbose thyrsoids or cymose, with two to many cincinni, \pm glandular-hairy; flowers shortly pedicellate; petals connate at base for $\leq 1/2$, outside glandular, lobes spreading or suberect, yellow, cream, white, pink or red; carpels usually slender; fruits stellately patent follicles with distinct lips along suture, or erect or spreading follicles with indistinct lips; seeds with thin, distinct costae. $n = 6, 7, 13, 14, 28, 35, 42, 52$. Eight species, from usually high altitudes in northern Greece, Turkey, Armenia, Caucasus, northern Iran.

Based on different molecular taxon samplings, *Prometheum* appears closest to *Sedum inconspicuum* Hand.-Mazz. (van Ham 1994), or *S.* ser. *Alsinefolium* and *Glaucorubens* ('t Hart et al. 1999), or *S. ince* 't Hart & Alpınar of *S.* ser. *Elegans* ('t Hart and Alpınar 1999). Some species were formerly included in *Rosularia* by Eggli (1988).

19. *Afrovivella* A. Berger

Afrovivella A. Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:466–467 (1930); Eggli, Bradleya suppl. 6:1–119 (1988), sub *Rosularia*.

Perennial herbs with a narrow taproot and without caudex; rosettes sessile, \pm flat, offsetting; leaves spatulate, with short or long mucro, glabrous or shortly glandular-hairy, margins setate; inflorescences lateral, reduced, 1–5-flowered thyrsoids, brownish glandular-hairy; flowers 5–7-merous; corolla campanulate; petals connate at base for $1/3$, outside glandular, tips mucronate, white, outside tinged reddish; nectary scales oblong-acicular; carpels slender; seeds within thin, distinct costae. Only 1 species, *A. semiensis* (J. Gay ex A. Rich.) A. Berger, from shaded rocks in Ethiopian highlands.

Of uncertain status and thus kept separate. Classified as *Rosularia* by Eggli (1988). The thin, distinct costae of the seeds match those of *Prometheum* (Eggli 1988).

Genera 20 + 21

Plants glabrous. According to molecular data (Mort et al. 2001), the two genera form a distinct clade in western North America.

Most probably, the c. 30 American species of *Sedum* subg. *Gormaniana*, i.e. the American *Sedum* with costate seeds, also belong to this clade (= sections *Gormaniana*, *Lanceolata*, *Ternata* and *Tetrorum* (incl. *Diamorpha*); cf. Knapp 1994, 1997). Molecular data are yet sparse ('t Hart 1995).

20. *Sedella* Britton & Rose

Sedella Britton & Rose, Bull. New York Bot. Gard. 3:45 (1903); Clausen, *Sedum* N. Am. (1975), sub *Sedum*; Moran, *Haseltonia* 5:53–60 (1998, '1997'), rev.
Parvisedum Clausen (1946), nom. illegit. (Art. 53.1).

Small annuals < 10 cm; stems usually branching, often red(dish); leaves decussate near base, alternate above, usually caducous before anthesis; inflorescences cymose with several cincinni; sepals erect, almost free; petals imbricate in bud, erect to spreading, connate at very base, bright to pale or greenish-yellow, much longer than sepals; stamens 5 or rarely 10; carpels erect, clavate, with a single basal erect ovule; fruits flimsy, clavate, nutlet-like and indehiscent, each with one erect seed. $n = 9$. Three species, as ephemeral vernal herbs often in rock pools; USA (northern and central California, southern Oregon?).

21. *Dudleya* Britton & Rose

Dudleya Britton & Rose, Bull. New York Bot. Gard. 3:12–13 (1903); Moran, Revision *Dudleya* (1951), unpubl. rev.; Bartel in Hickman, *Jepson Manual* 525–530 (1993), synopsis N. Amer. spp.
Hasseanthus Rose (1903).
Stylophyllum Britton & Rose (1903).

Stems unbranched or branched, usually dichotomously, stems usually short and erect, covered by dry leaf remains at base; leaves in rosettes, united with stem axis with broad or narrow base (subg. *Hasseanthus*), often densely farinose; inflorescences axillary, cymose, usually with 1–3(–10) cincinnoid partial inflorescences; sepals connate at base; petals forming \pm tubular corolla or spreading, usually convolute in bud; carpels \pm erect at anthesis, basally at base; stylodia slender; fruits slightly divaricate to widely spreading follicles. $n = 17$, also 34, 51, 68, 85, \pm 119, 136. About 47 species, western USA (south-western Oregon, southern Nevada, central and western Arizona, California incl. Pacific Islands), Mexico (Sonora, Baja California incl. islands), predominantly coastal, rocky places to 2,200(–3,025) m.

Divided into subg. *Dudleya* (leaves usually broad; petals upright), subg. *Stylophyllum* (leaves usually narrow; petals spreading from middle) and subg. *Hasseanthus* (stems tuberous; leaves vernal; petals broadly spreading). None of these is monophyletic, according to a molecular study (D. Burton, San Diego State University, USA; in litt. 2002). *Dudleya* is not related to *Echeveria*, with which it was united in subfamily Echeverioideae by Berger (1930). Possibly closest to *Sedum* subg. *Gormaniana* sect. *Gormaniana* with which it shares the rosulate habit. The systematics and biology are reviewed by Thiede (2004).

I.5. B. ACRE CLADE

Plants glabrous or with non-glandular trichomes; seeds reticulate-papillate* or reticulate (except for *Sedum litoreum* Guss.); tannins largely absent* and often replaced by alkaloids.
Genera 22–28.

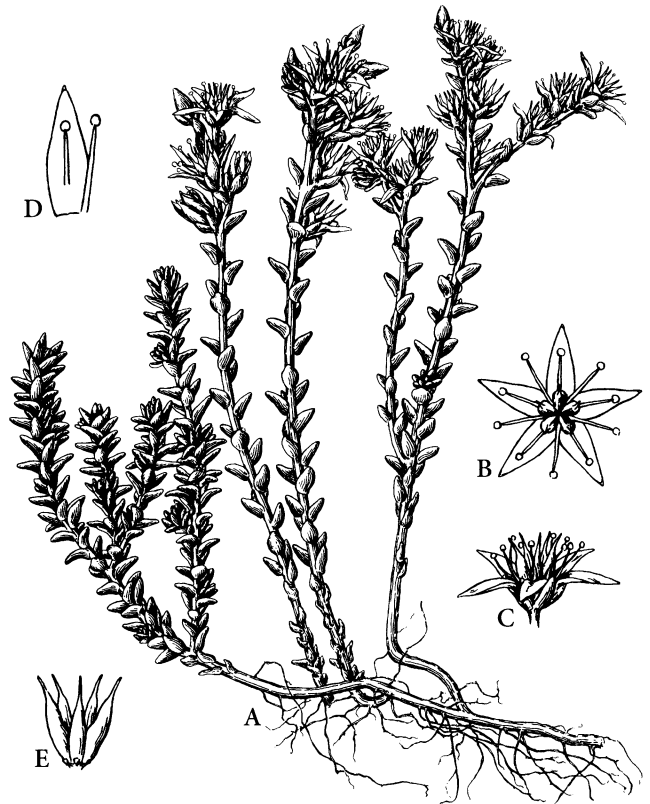


Fig. 30. Crassulaceae. *Sedum acre*. A Flowering plant. B Flower seen from above. C Flower, side view. D Petal with two stamens, the antepetalous stamen epipetalous. E Carpels with hypogynous bracts. (Clausen 1975)

This clade most probably includes all of *Sedum* subg. *Sedum*, i.e. *Sedum* with reticulate-papillate or reticulate seeds. Molecular data are from van Ham and 't Hart (1998) and Mort et al. (2001).

22. *Sedum* L. Figs. 29, 30

Sedum L., Sp. Pl.: 5 (1753); Fröderström, Acta Horti Gothob. suppl. 5–7 (1930–1932) & 10 (1935); Clausen, *Sedum* Trans-Mexican Volcanic Belt (1959); Clausen, *Sedum* N. Am. (1975); 't Hart, Fl. Medit. 1:31–61 (1991).

Diamorpha Nuttall (1818).

Altamiranoa Rose (1903).

Cremnophila Rose (1905).

Sempervivella Stapf (1923).

Mucizonia (DC.) A. Berger (1930).

Rosularia sect. *Sempervivella* (Stapf) Jansson in Jansson & Rechinger (1970).

Amerosedum, *Breitungia*, *Clausenellia*, *Etiosedum* & *Hjaltalinia* A.D. Löve & D. Löve (1984).

Oreosedum Grulich (1984).

Ohbaea Byalt & I.V. Sokolova (1999).

Glabrous or pubescent, perennial or annual herbs to subshrubs with usually much branched non-flowering shoots, rarely rosulate; roots usually fibrous or tuberous or taproots; stems usually without secondary thickening, sometimes (slightly) woody or with subterranean rootstock; leaves usually alternate, rarely decussate or in whorls of 3 or 4, sessile or rarely (semi-)petiolate, usually (semi-)terete, rarely flat, with entire margins; inflorescences terminal or rarely axillary, many-flowered pleiochasia with single or double cincinni, or corymboid or compound thyrsoids with many cincinni, rarely few-flowered cymes with one or two cincinni; bracts usually present, often leaf-like; flowers (3–)5(–12)-merous, rarely haplostemonous, sessile to pedicellate; sepals broadly sessile or free and spurred, equal or strongly unequal, usually smaller than petals; petals usually free, or connate at base for 1/3 to 2/3, usually spreading, or erect, often with distinct, frequently reddish keel and dorsal sub-apical appendage, yellow, white, pink, purple or reddish; filaments usually free, antepetalous stamens connate at base with petals or rarely higher up; nectary scales variable, usually whitish, or yellow or red; carpels usually sessile with broad base and slightly connate at base, or completely free, rarely stipitate; stylodia usually slender and recurved during anthesis, or short and stigma \pm sessile; fruits (sub)erect or stellate-patent follicles, without lips along ventral suture, or

stellate-patent follicles with distinct lips, rarely nutlike (e.g. *S. caeruleum* L.); seeds ovoid to ellipsoid, costate-bipapillate (subg. *Gormanina*) or reticulate-papillate to reticulate (subg. *Sedum*). $n = 4–20$ and many higher polyploids. About 420 species, mainly temperate and subtropical regions of North America, Europe, North Africa, Near East and Asia, a few species in South America and Central to East Africa.

Tremendously variable in its morphology, with numerous exceptions from the generalised description given above which are usually confined to small species groups and have often prompted generic separation. A highly paraphyletic genus, with many segregates phylogenetically basal within Semperviveae, Aeonieae and Sedeeae, but formally preferably to be treated under *Sedum*. See also discussion under Subdivision and Relationships.

Sedum as defined here is divided into **subg. *Gormanina*** which includes the species from the Sempervivum, Aeonium and Leucosedum clades (often glandular-pubescent; sepals broadly sessile and usually of equal length; seeds costate; c. 110 spp., 60 in Europe/Mediterranean (anthers in these usually red), 10 in Asia, 10 in East Africa and 30 in North America), and **subg. *Sedum*** which includes the species from the Acre clade (usually glabrous or rarely with non-glandular hairs; sepals free at base and spurred, or broadly sessile and often distinctly unequal in size; seeds with reticulate-papillate or reticulate testa; c. 320 spp., 30 in Europe/Mediterranean/Near East, 120 in Asia and 170 in the Americas).

Genera 23–28

Genera 23–28 form a distinct American clade, together with the American species of *Sedum* subg. *Sedum* (according to molecular data of Mort et al. 2001).

23. *Villadia* Rose

Villadia Rose, Bull. New York Bot. Gard. 3:3 (1903); Uhl & Moran, Amer. J. Bot. 86:387–397 (1999); Palmer et al., <http://www.botany2002.org/section12/abstracts/189.shtml> (2002), mol. phylog. (abstract).

Herbs or small shrubs; roots fibrous or thickened and fusiform; stems either woody-persistent and \pm erect (then, small shrubs), or herbaceous and decumbent-ascending (then, mat-forming herbs), or herbaceous and \pm annual (then, geophytes or hemicryptophytes with thickened, persistent

roots); leaves usually terete-subulate, \pm conspicuously spurred at base; inflorescences \pm elongate thyrsoids, often spike- or raceme-like, with 6–70(–150) cincinnoid partial inflorescences with 1–5(–8) flowers; sepals (almost) free, (always?) spurred at base; petals connate at base, lobes spreading to reflexed or erect, whitish to pink or reddish; stylodia \pm recurved; fruits erect. $n = 9$ –17, 20–22, 33 and higher. About 21 species in southern USA (south-western Texas), Mexico, Guatemala (Baja Verapaz), Peru, at (600–)1,500–4,000 m.

Divided into seven informal species groups (Thiede in Eggli 2003). Appears to be closest to *Sedum* sect. *Fruticisedum* (Uhl and Moran, l.c.). Taxa formerly classified in sect. *Altamiranoa* are now placed in *Sedum* (Moran 1996; Thiede and 't Hart 1999).

24. *Lenophyllum* Rose

Lenophyllum Rose, Smithsonian Misc. Collect. 47:159 (1904); Moran, *Haseltonia* 2:1–19 (1994), rev.

Herbs, roots fibrous or thickened; leaves decussate in few basal pairs, elliptic, roundish or rhombic; inflorescences thyrsoids with several cincinni, narrow thyrsoids of compact cincinni or reduced to racemes or spikes above or throughout; sepals erect or ascending, nearly equal, \pm as long as open corolla; petals in upper half spreading to recurved, (ob)lanceolate, yellow(ish); stamens slightly exerted; nectary scales subquadrate; carpels erect, narrow, tapering into slender stylodia; fruits erect. $n = 22, 32, 33, 44$. Seven species, from USA (southern Texas) and north-eastern Mexico.

Genera 25–28

Stems at least basally woody, but many taxa with sessile rosettes; leaves usually thick and strongly succulent, in \pm distinct rosettes; inflorescences lateral; petals at least basally connate. $x = 30$ –34 with secondary reductions. Centred in Mexico.

According to molecular data (Mort et al. 2001), these genera form a distinct American clade (= '*Echeveria* group'), together with *Sedum* sect. *Pachysedum*. The latter shares the above characters, except for its choripetalous flowers.

25. *Graptopetalum* Rose

Graptopetalum Rose, Contr. U.S. Natl Herb. 13:296 (1911); Acevedo et al., *Brittonia* 56:185–194 (2004), morph. phylog.; Acevedo et al., *Amer. J. Bot.* 91:1099–1104 (2004), mol. phylog.

Byrnesia Rose (1922).

Tacitus Moran (1974).

Herbs (sect. *Graptopetalum*) to subshrubs (sect. *Byrnesia*); leaves obovate to (broadly) spatulate, usually mucronate in sect. *Graptopetalum*; usually \pm glaucous-pruinose; inflorescences thyrsoids with few to many cincinnoid partial inflorescences, or pleiochasia with few cincinnoid partial inflorescences; flowers (4)5(–10)-merous, stamens diplostemonous, rarely haplostemonous; sepals appressed, free to base and \pm equal in size; petals slightly connate at base, spreading stellately, basically whitish or yellowish (to greenish), usually with reddish to brown cross-band markings or blotches becoming denser towards tips, rarely uniformly coloured; stamens first erect, after anther dehiscence spreading and the antesealous stamens recurved between the petals, after anthesis becoming erect again; carpels shortly connate at base; stylodia normally abruptly offset; fruits ascending to erect; seeds usually reticulate. $n = 30$ –32, 34, 35, 62, 64, 66, 68, ± 93 , ± 170 , ± 175 , 192, ± 204 , ± 208 , ± 244 , ± 270 . Eighteen species, USA (central and southern Arizona), Mexico (widespread from Sonora and Chihuahua to Oaxaca); rocky places, to 2,400 m.

Divided into sect. *Byrnesia* and sect. *Graptopetalum* (incl. *Tacitus*). According to molecular data, *Graptopetalum* and its sections are not monophyletic, and *Tacitus*, *Cremonophila* (= *Sedum*) and selected species of *Sedum* and *Echeveria* are interspersed among its species (Acevedo et al. l.c.).

26. *Thompsonella* Britton & Rose

Thompsonella Britton & Rose, Contr. U.S. Natl Herb. 12:391 (1909); Moran, *Cact. Succ. J. (U.S.)* 64:37–44 (1992), synopsis.

Glabrous herbs or subshrubs; leaves in rosettes, flattish, semi-amplexicaul, often glaucous, margins straight or undulate; inflorescences erect narrow thyrsoids or spicate above or as a whole, with 10–70, 1–12-flowered cincinni; flowers (almost) sessile; sepals free, (sub)equal, clavate; petals shortly connate at base, imbricate in bud, spreading from middle, outer face pale, inner face \pm dark purplish-red; nectary scales minute; carpels shortly stipitate, shortly connate at base; stylodia slender; fruits erect; seeds reticulate with irregular longitudinal rows. $n = 26, 52$. Six species, central and southern Mexico; usually on limestone.

Genera 27 + 28

Petals upright and connate for most of their length; sepals often strongly unequal in size; petals thick-fleshy; anthers (light) yellow; fruits divergent.

27. *Echeveria* DC.

Echeveria DC., Prodr. Syst. Regni Veg. 3:401 (1828); Walther, *Echeveria* (1972), rev.
Oliverella Rose (1903).
Urbinia Britton & Rose (1903).
Oliveranthus Rose (1905).

Glabrous to hirsute herbs to subshrubs; stem none or tall, branching or not; leaves rarely scattered along the stems, usually (ob)lanceolate and mucronate, often glaucous or highly coloured; inflorescences, racemose, paniculate, or rarely spicate thyrsoids, or cymose with one to several cincinni; pedicels usually with one to several minute bracteoles; sepals reflexed to appressed but usually somewhat expanding, almost completely free, equal to strongly unequal; corolla cylindrical to pentagonal to urceolate; petals imbricate (valvate in Ser. *Valvatae*), white through yellow and orange to red, rarely green(ish), inner surface usually with nectar-cavity at base; stamens 10, 5 attached at top of nectar-cavities, 5 at top of corolla tube between petals; carpels connate at base, erect at anthesis; stylodia slender; fruits widely divergent follicles; seeds reticulate or smooth. $n = 12-34$, polyploid from 28–250. About 139 species, centred in (southern) Mexico, also southern USA (Texas) and Central and South America (Venezuela, Colombia, Ecuador, Peru, Bolivia, northern Argentina).

Divided into 17 series (Kimmach in Eggli 2003).

28. *Pachyphytum* Link, Klotzsch & Otto

Pachyphytum Link, Klotzsch & Otto, Allg. Gartenzeitung 9:9–10 (1841).

Subshrubs; stems first erect, with age usually decumbent to pendent, not or few-branched; leaves obovate, spatulate, elliptic-oblong or lanceolate, usually very thick, usually conspicuously glaucous-farinose; inflorescences almost always simple cincinni, first drooping, later \pm erect; floral bracts 5–9 mm in sect. *Diotostemon* or usually 13–30 mm in sect. *Pachyphytum*; sepals erect, appressed, almost equal (sect. *Diotostemon*) or (often strongly) unequal (sect. *Pachyphytum*); petals erect (sect. *Diotostemon*) or spreading to divaricate

(sect. *Pachyphytum*), \pm oblong to oblanceolate, white to pink, rarely orange to red(dish), inner face in upper part often with red blotch in sect. *Pachyphytum*, laterally near base with appendages which form two free, 1–2 mm large scales beneath filaments; antepetalous filaments connate with corolla, antesepalous ones (almost) free; nectary scales oblong, \pm yellowish(-white); carpels erect at anthesis, \pm free; stylodia inconspicuously offset to abruptly narrowing; fruits usually divergent follicles; seeds fairly smooth. $n = 31-33, 62, 64, 66, 96, 99, \pm 124, \pm 128, \pm 160, \pm 186$. Fifteen species, in eastern central Mexico, (600–)1,200–2,500 m.

Divided into sections *Diotostemon* and *Pachyphytum* (Thiede in Eggli 2003). The morphology of the petal scales was studied by Leinfellner (1954); similar scales also occur in some *Echeveria* species. *Pachyphytum* may be nested within *Echeveria* and closest to its sect. *Urceolatae* (Thiede in Eggli 2003).

II. SUBFAM. KALANCHOIDEAE A. Berger (1930).

Shoots \pm woody*; tissues (always?) with crystal sand*; petals connate to strongly developed corolla tube*; anthers with terminal, \pm spherical connective appendage*; seeds with few (4–6) costae* in side view, coronate*. $x = 9^*$.

Genera 29–32.

Note that Kalanchoideae are morphologically highly derived, although cladistically they are the second clade branching off from the remainder of the family.

29. *Adromischus* Lem.

Adromischus Lem., Jard. Fleur. misc. 2:58–59 (1852); Pilbeam et al., *Adromischus* (1998), synopsis.

Shrublets to ± 20 cm; stems fleshy-woody; leaves flat to almost terete, glabrous or glandular-hairy, often with thick wax bloom; inflorescences erect spike-like thyrsoids or spikes without terminal flower, to 55 cm, with few to numerous, 1–5-flowered dichasia; flowers usually erect, rarely pendulous (*A. phillipsiae* (Marloth) Poelln.); corolla usually long and narrow; petals white to pink to red, rarely bright orange, lobes at sinuses joined by thin membrane; filaments slightly exerted or included, papillate where connate with corolla tube; carpels elongate; fruits follicles, (always?) dehiscent completely along ventral

suture. $n = 9$. About 28 species, Namibia, South Africa (especially Succulent and Little Karoo).

30. *Kalanchoe* Adans.

Fig. 28

Kalanchoe Adans., Fam. Pl. 2:248 (1763); Hamet, Bull. Herb. Boiss. II, 7:870–900 (1907) & 8:17–48 (1908); Hamet & Lapostolle, Genre *Kalanchoe* au Jardin Botanique “Les Cèdres” (1964); Raadts, Willdenowia 8:101–157 (1977), rev. E. Afr.; Fernandes, Bol. Soc. Brot. II, 53:325–442 (1980), African taxa; Boiteau & Allorge-Boiteau, *Kalanchoe* de Madagascar (1995); Gehrig et al., Pl. Sci. 160:827–835 (2001), mol. phylog.

Bryophyllum Salisbury (1805).

Kitchingia Baker (1881).

Shrublets to shrubs, rarely rosulate or small trees, or biennial to annual; leaves usually decussate, rarely alternate, verticillate or subrosulate, \pm flat, rarely terete, sometimes \pm incised or 3- to 5-foliate, margins usually crenate, serrate or dentate, partly with bulbils (usually in sect. *Bryophyllum*), rarely entire; inflorescences rarely axillary, corymbose or paniculate thyrsoids, partial inflorescences dichasial, rarely inflorescences few- to 1-flowered; flowers 4-merous, \pm erect (usually in sect. *Kalanchoe*) or pendent (usually in sects. *Kitchingia* and *Bryophyllum*); sepals free, connate or forming long, sometimes \pm inflated tube (usually in sect. *Bryophyllum*); petals usually brightly coloured, lobes shorter than corolla tube, erect, spreading or reflexed; filaments exerted or included, connate to corolla tube at base (sect. *Bryophyllum*) or at or above middle (sects. *Kalanchoe* and *Kitchingia*); carpels free to somewhat connate at base, erect or somewhat spreading (sect. *Kitchingia*); fruits erect follicles. $n =$ usually 17, also 18, 20, 34, 35, 36, 51, 85. About 144 species, mainly Madagascar, eastern and southern Africa, to tropical Africa, Arabia and tropical and Southeast Asia; some taxa (especially *K. pinnata* (Lam.) Pers.) are neophytic invaders throughout the tropics.

Divided into three sections: the widespread sect. *Kalanchoe*, and the Malagasy sects. *Kitchingia* and *Bryophyllum*.

31. *Tylecodon* Toelken

Tylecodon Toelken, Bothalia 12:378 (1978); van Jaarsveld & Koutnik, *Tylecodon* & *Cotyledon* (2004), rev.

Shrublets or dwarf geophytes to pachycaul dwarf trees to 2.5 m; stems succulent, rarely woody, usually with flaking bark; leaves usually crowded at stem tips, soft-herbaceous, with elongate

epidermal cells with sinuate anticlinal walls, often (always?) with bladder-cells idioblasts, usually completely drought-deciduous; inflorescences thyrsoids with one to several dichasia; petals white, greenish, yellowish or mauve, rarely reddish; filaments usually exerted, hairy where connate with corolla tube; fruits follicles, dehiscent apically only; seeds with irregular costae. Forty-six species, winter-rainfall regions of Namibia and South Africa, mainly Succulent Karoo. Growing season autumn to early summer; flowering \pm in summer.

Sister to *Cotyledon*, according to molecular data (Mort et al. 2001). The two genera have in common basally hairy filaments.

32. *Cotyledon* L.

Cotyledon L., Sp. Pl.: 429 (1753); van Jaarsveld & Koutnik, *Tylecodon* & *Cotyledon* (2004), rev.; Mort et al., Amer. J. Bot. 92:1170–1176 (2005), mol. phylog.

Procumbent to erect shrublets to shrubs, rarely climbers; stems usually becoming woody; leaves decussate, flat or terete, rarely lobed or orbicular, glabrous or (glandular) hairy; inflorescences thyrsoids with several dichasia, ending in monochasia with one to many pendent flowers; corolla tube hairy or glabrous; dried calyx/corolla complex circumscissile along basal groove; filaments exerted, hairy where connate with corolla tube; carpels tapering into erect stylopodia; nectary scales \pm cuplike. $n = 9$. Eleven species, southern and eastern tropical Africa, south-western Arabian Peninsula.

According to molecular data (Levsen et al., l.c.), the variable *Cotyledon orbiculata* L. is polyphyletic. The circumscissile calyx/corolla complex present in all *Cotyledon* is found also in at least some *Tylecodon* and *Kalanchoe* spp. (Moran 2000), and may represent a synapomorphy for these three genera.

III. SUBFAM. CRASSULOIDEAE Burnett (1835).

Leaves decussate*, rarely ternate or whorled; flowers haplostemonous*; anthers slightly introrse*, nucellus tenuinucellate*; fruits opening \pm completely along whole suture, but releasing seeds through apical pore*; seeds sinuate-unipapillate*. Genera 33 + 34.

Note that Crassuloideae are morphologically highly derived, although cladistically they are the first clade branching off from the remainder of the family.

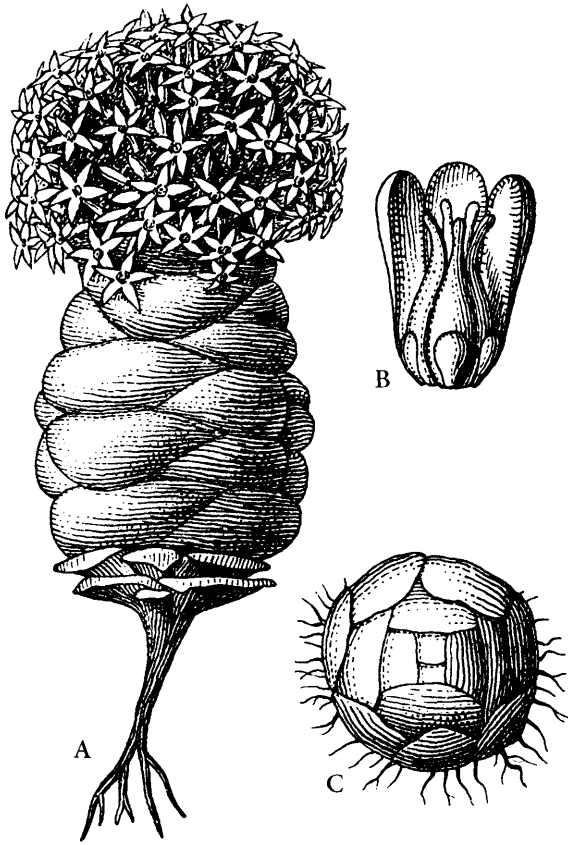


Fig. 31. Crassulaceae. *Crassula columnaris*. A Flowering plant. B Flower, opened out. C Young plant seen from above. (Berger 1930)

33. *Crassula* L.

Fig. 31

Crassula L., Sp. Pl.: 282 (1753); Toelken, Contr. Bolus Herb. 8 (1977), rev. southern African taxa; Tölken, J. Adelaide Bot. Gard. 3:57–90 (1981), rev. Austral. taxa; Bywater & Wickens, Kew Bull. 39:699–728 (1984), rev. New World taxa; Mort et. al., IOS Bull. 12:35–36 (2004), mol. phylog. (abstract).

Tillaea L. (1753).

Rochea DC. (1802).

Perennial or rarely annual herbs to (sub)shrubs, rarely tuberous geophytes; glabrous, papillate or hairy; leaves decussate or rarely in whorls of 4, partly with bladder-cell idioblasts and leaf bases connate within a pair (usually in subg. *Crassula*); inflorescences thyrsoids with 1 to many dichasia, sometimes partial inflorescences glomerate, monochasia or reduced to solitary flowers; corolla urn-shaped to tubular or stellate; flowers (2–)5(–12)-merous, usually small; sepals shortly connate at base; petals shortly connate

at base, partly with apex papillate on outer face and with distinct appendage (usually in subg. *Crassula*) often \pm whitish; filaments shortly adnate to petals at base and alternate with these; carpels usually free; fruits rarely nutlike and indehiscent. $n = 8, 7$ and polyploids. About 195 species; mainly southern Africa, a few species in sub-Saharan Africa and south-western Arabia, some ephemeral herbs ('*Tillaea*') distributed worldwide, and the only genus of the family in Australia.

Divided into the paraphyletic subg. *Disporocarpa* with nine sections (hydathodes of type I, rarely type II; $n = 8$, rarely 7) and subg. *Crassula* with eleven sections (hydathodes of type II; $n = 7$ with two satellites; Friedrich 1973; Toelken 1977 l.c.; Martin and von Willert 2000). The ephemeral herbs of sects. *Helophytum* and *Glomeratae*, often segregated as genus *Tillaea*, are nested within *Crassula*, according to molecular data ('t Hart unpubl. data).

34. *Hypagophytum* A. Berger

Hypagophytum A. Berger in Engler & Prantl, Nat. Pflanzenfam., ed. 2, 18a:467–468 (1930); Gilbert, Opera Bot. 121:47–50 (1993).

Tuberous geophytes; stems one to few, drought-deciduous; leaves ternate, sessile or with petiole-like base, somewhat spurred at base, flat; inflorescences usually with 3 monochasia below terminal flower; flowers 10–12-merous, stellate; sepals free; petals white or with faint pink tinge; carpels free, laterally compressed, constricted into two segments, upper part spiny-papillate, with long filiform stylodia; fruits 2-seeded, breaking transversely at the constriction, upper seed dispersed within the upper part of the carpel, lower seed released separately. Only 1 species, *H. abyssinicum* (Hochst. ex A. Rich.) A. Berger in north-western Ethiopian highlands.

Characterised by a unique combination of specialised features, which all occur in *Crassula* (tubers with annual shoots, whorled leaves, hydathodes along leaf margins, haplostemonous and polymorous flowers, and the peculiar fruits). The seed surface structure was given as costate by Gilbert (1989 and l.c.) and Knapp (1994), which prompted 't Hart (1995: 169) to place the genus in his 'Sedoideae'. However, according to Knapp (1997), the seed surface structure in fact corresponds to the sinuate-papillate (*Crassula*-) type, clearly favouring the placement in Crassuloideae. *Hypagophytum* may be nested within *Crassula* and closest to

its sect. *Petrogeton*, which shares the tuberous habit and exhibits in some species leaves with short petiole and in whorls of 4, monochasial inflorescences with stellate and polymerous flowers, and long filiform styloids. The same peculiar fruit type is found in sect. *Glomeratae* p.p. (cf. Stopp 1957).

Selected Bibliography

- Akiyama, S., Ohba, H., Wu, S.-K. 2001. A new variety of *Sinocrassula paoshingensis* (S.H. Fu) H. Ohba et al. (Crassulaceae). *J. Jap. Bot.* 76:222–226.
- Alm, T. 2004. Ethnobotany of *Rhodiola rosea* (Crassulaceae) in Norway. *Sida* 21, 1:321–344.
- Bahadur, B., Ramaswamy, N., Srikanth, R. 1986. Studies on the floral biology and nectar secretion in some *Kalanchoe* species (Crassulaceae). In: Kapil, R.P. (ed.) *Pollination biology – an analysis*. New Delhi: Inter-India Publications, pp. 251–259.
- Baskin, J.M., Baskin, C.C. 1972. Germination characteristics of *Diamorpha cymosa* seeds and an ecological interpretation. *Oecologia* (Berlin) 10:17–28.
- Baskin, J.M., Baskin, C.C. 1977. Germination ecology of *Sedum pulchellum* Michx. (Crassulaceae). *Amer. J. Bot.* 64:1242–1247.
- Behnke, H.-D. 1991. Distribution and evolution of forms and types of sieve-element plastids in the dicotyledons. *Aliso* 13:167–182.
- Berger, A. 1930. Crassulaceae. In: Engler, A., Prantl, K., *Die natürlichen Pflanzenfamilien*, ed. 2, 18a. Leipzig: W. Engelmann, pp. 352–483.
- Bland, K.P. 1995. *Phytomyza rhodiolae* Griffiths, 1976 (Diptera: Agromyzidae), a leaf-miner in roseroot, *Sedum rosea* (Crassulaceae), new to Britain. *Entomol. Gaz.* 46:267–269.
- Boiteau, P., Allorge-Boiteau, L. 1995. *Kalanchoe* (Crassulacées) de Madagascar. *Systématique, écophysologie et phytochimie*. Paris: Karthala.
- Böttcher, W., Jäger, E.J. 1984. Zur Interpretation der Verbreitung der Gattung *Sedum* L. s.l. (Crassulaceae) und ihrer Wuchsformtypen. *Wissensch. Z. Univ. Halle* 33:127–141.
- Bowman, R.N. 1983. Intraspecific variability of leaf cuticle alkanes in *Sedum lanceolatum* along an elevational gradient. *Biochem. Syst. Ecol.* 11:195–198.
- Braun, U. 1987. A monograph of the Erysiphales (powdery mildews). *Nova Hedwigia*, Beih. 89:1–700.
- Braun-Blanquet, J., Sutter, R. 1982. Zur Kenntnis der Crassulaceen-Pioniergesellschaften in den Bündner Alpen. *Jahresber. Naturf. Gesell. Graubünden* 99:75–83.
- Burchard, O. 1929. Beiträge zur Ökologie und Biologie der Kanarenpflanzen. *Bibl. Bot.* 98:1–262, pls. 1–78.
- Byalt, V.V. 1997. *Meterostachys sikokianus* (Crassulaceae), a new species and genus for the flora of China (in Russian with English summary). *Bot. Zhurn. (Moscow & Leningrad)* 82:128–130.
- Byalt, V.V. 1998. *Orostachys paradoxa*, a rare species from the Russian far East. *Cact. Succ. J. (U.S.)* 70:262–263.
- Bywater, M. 1980. Observations on seeds of *Crassula* sect. *Rosulares*. *Kew Bull.* 35:401–402.
- Bywater, M., Wickens, G.E. 1983. New world species of the genus *Crassula*. *Kew Bull.* 39:699–728.
- Caballero, A., Jiménez, M.S. 1977. Contribución al estudio anatómico foliar de las crassuláceas canarias. *Vieraea* 7:115–132.
- Calie, P.J. 1981. Systematic studies in *Sedum* section *Ternata* (Crassulaceae). *Brittonia* 33:498–507.
- Candolle, A.P. de 1828. *Mémoire sur la famille des Crassulacées*. Paris: Treuttel & Würtz.
- Clausen, R.T. 1959. *Sedum* of the Trans-Mexican Volcanic Belt: an exposition of taxonomic methods. Ithaca: Comstock.
- Clausen, R.T. 1975. *Sedum* of North America north of the Mexican Plateau. Ithaca: Cornell University Press.
- Clausen, R.T. 1977. Biennial species of *Sedum* of the Sierra Madre Occidental and the Mexican Plateau. *Bull. Torrey Bot. Club* 104:209–217.
- Cronquist, A. 1968. *The evolution and classification of flowering plants*. Boston: Houghton Mifflin.
- Cullen, J. 1995. Crassulaceae. In: Cullen, J., Alexander, J.C.M., Brady, A., Brickell, C.D., Green, P.S., Heywood, V.H., Jorgensen, P.-M., Jury, S.L., Knees, S.G., Leslie, A.C., Matthews, V.A., Robson, N.K.B., Walters, S.M., *The European Garden Flora, IV. Dicotyledons, part II. Dilleniaceae to Krameriaceae*. Cambridge: Cambridge University Press, pp. 170–244.
- Davis, G.L. 1966. See general references.
- Deil, U. 1991. Rock communities in tropical Arabia. In: Engel, T., Frey, W., Kürschner, H. (eds) *Contribuciones selectae ad floram et vegetationem orientis*. Berlin: Flora et Vegetatio Mundi, pp. 175–187.
- Denton, M.F. 1979. Cytological and reproductive differentiation in *Sedum* section *Gormaniana* (Crassulaceae). *Brittonia* 31:197–211.
- Denton, M.F. 1982. Revision of *Sedum* section *Gormaniana* (Crassulaceae). *Brittonia* 34:48–77.
- Denton, M.F., Kerwin, J.L. 1980. Survey of vegetative flavonoids of *Sedum* section *Gormaniana* (Crassulaceae). *Canad. J. Bot.* 58:902–905.
- Ebel, F., Hagen, A., Kümmel, F. 1991a. Beobachtungen zur Wuchsrhythmik von *Orostachys spinosus* (L.) Sweet (Crassulaceae). *Wissensch. Z. Univ. Halle* 40:47–68.
- Ebel, F., Hagen, A., Kümmel, F. 1991b. Beobachtungen zur Wuchsrhythmik und “Knospbildung” einiger *Greenovia*- und *Aeonium*-Arten (Crassulaceae). *Flora* 85:187–200.
- Eckert, G. 1966. *Entwicklungsgeschichtliche und blütenanatomische Untersuchungen zum Problem der Obdiplostemonie*. *Bot. Jahrb. Syst.* 85:523–604.
- Eggl, U. 1988. A monographic study of the genus *Rosularia* (Crassulaceae-Sedoideae). *Bradleya* suppl. 6:1–119.
- Eggl, U. (ed.) 2003. *Illustrated Handbook of Succulent Plants, VI. Crassulaceae*. Berlin Heidelberg New York: Springer.
- Eglington, G., Gonzalez, A.G., Hamilton, R.J., Raphael, R.A. 1962. Hydrocarbon constituents of the wax coatings of plant leaves: a taxonomic survey. *Phytochemistry* 1:89–102.
- Ellenberg, H. 1996. *Vegetation Mitteleuropas mit den Alpen*. 5. Auflage. Stuttgart: Ulmer.
- Endress, P.K., Stumpf, S. 1991. The diversity of stamen structures in ‘lower’ Rosidae (Rosales, Fabales, Proteales, Sapindales). *Bot. J. Linn. Soc.* 107:217–293.

- Engelmann W. 1960. Endogene Rhythmik und photoperiodische Blühinduktion bei *Kalanchoe*. *Planta* 55:496–511.
- Erdtman, G. 1952. See general references.
- Fehrenbach, S., Barthlott, W. 1988. Mikromorphologie der Epicuticular-Wachse der Rosales s.l. und deren systematische Bedeutung. *Bot. Jahrb. Syst.* 109:407–428.
- Fernandes, F.M. 1997. Restoration programme for Madeira's endangered plants. *Plant Talk* no. 10:19
- Fétre, J., Lebègue, A. 1964. Embryogénie des Crassulacées. *C. R. Acad. Sci. Paris* 258:5035–5038.
- Fishbein, M. et al. 2001. See general references.
- Friedrich, H.-C. 1973. Zur Cytotaxonomie der Gattung *Crassula*. *Garcia de Orta, Sér. Bot.* 1:49–66.
- Fröderström, H. 1930–1935. The genus *Sedum*. A systematic essay. I–IV. *Acta Horti Gothoburgensis* 5:1–75, 6:1–111, 7:1–126, 10:1–262.
- Gess, S., Gess, F., Gess, R. 1998. Birds, wasps and *Tylecodon*. Pollination strategies of two members of the genus *Tylecodon* in Namaqualand. *Veld Flora* 84:56–57.
- Gilbert, M.G. 1985. The genus *Sedum* in Ethiopia. *Bradleya* 3:48–52.
- Gilbert, M.G. 1989. Crassulaceae. In: Hedberg, I., Edwards, S. (eds) *Flora of Ethiopia, III. Pittosporaceae to Araliaceae*. Addis Ababa: Ethiopian National Herbarium, pp. 5–26.
- Golding, J. (ed.) 2002. *Southern African Plant Red Data List*. Pretoria: SABONET.
- Gontcharova, S.B. 1999. Ornamentation of the testa of some Eastern Asian Sedoideae (Crassulaceae). *Bull. Natl Sci. Mus., Tokyo, ser. B* 25:131–141.
- Gregory, M. 1998. Crassulaceae. In: Cutler, D.F., Gregory, M. (eds) *Anatomy of the Dicotyledons, 2nd edn. IV. Saxifragales (sensu Armen Takhajan 1983)*. Oxford: Clarendon Press, pp. 201–220.
- Günthart, A. 1902. Beiträge zur Blütenbiologie der Cruciferen, Crassulaceen und der Gattung *Saxifraga*. *Bibl. Bot.* 58:1–97.
- Ham, R.C.H.J. van 1994. Phylogenetic implications of chloroplast DNA variation in the Crassulaceae. Thesis, University of Utrecht.
- Ham, R.C.H.J. van, Hart, H. 't 1998. Phylogenetic relationships in the Crassulaceae inferred from chloroplast DNA restriction-site variation. *Amer. J. Bot.* 85:123–134.
- Hart, H. 't 1975. The pollen morphology of 24 European species of the genus *Sedum* L. *Pollen Spores* 16:373–387.
- Hart, H. 't 1982. The systematic position of *Sedum tuberosum* Coss. & Let. (Crassulaceae). *Proc. Koninkl. Nederl. Akad. Wetensch., ser. C* 85:497–508.
- Hart, H. 't 1985a. Chromosome numbers in *Sedum* (Crassulaceae) from Greece. *Willdenowia* 15:115–135.
- Hart, H. 't 1985b. Sexual reproduction and hybridisation in *Sedum telephium* (Crassulaceae). *Acta Bot. Neerl.* 34:1–4.
- Hart, H. 't 1985c. The vascular pattern of the flowers of *Sedum anacampseros* (Crassulaceae). *Acta Bot. Neerl.* 34:119–121.
- Hart, H. 't 1990. Variation in the structure of the flowers of *Sedum*. *Sedum Soc. Newslett.* 13:11–17.
- Hart, H. 't 1991. Evolution and classification of the European *Sedum* species (Crassulaceae). *Flora Mediterranea* 1:31–61. Madrid: OPTIMA.
- Hart, H. 't 1994a. The evolution of life-forms, growth-forms secondary growth in Eurasian Sedoideae (Crassulaceae). *Bradleya* 12:37–56.
- Hart, H. 't 1994b. The unilacunar two-trace nodal structure of the caudex of *Rhodiola rosea* L. (Crassulaceae). *Bot. J. Linn. Soc.* 116:235–241.
- Hart, H. 't 1995. Intrafamilial and generic classification of the Crassulaceae. In: Hart, H. 't, Eggli, U. (eds) *Evolution and systematics of the Crassulaceae*. Leiden: Backhuys, pp. 159–172.
- Hart, H. 't 1997a. Crassulaceae. In: Oldfield, S., tom. cit., pp. 20–23.
- Hart, H. 't 1997b. Diversity within Mediterranean Crassulaceae. *Lagascalia* 19:93–100.
- Hart, H. 't, Alpinar, K. 1999. *Sedum ince* (Crassulaceae), a new species from southern Anatolia. *Edinburgh J. Bot.* 56:181–194.
- Hart, H. 't, Arkel, J. van 1985. Quantitative aspects of the influence of day-length and temperature on *Sedum telephium* (Crassulaceae). *Acta Bot. Neerl.* 34:115–118.
- Hart, H. 't, Berendsen, W. 1980. Ornamentation of the testa in *Sedum* (Crassulaceae). *Pl. Syst. Evol.* 135:107–117.
- Hart, H. 't, Bleij, B. 1999. Nieuwe namen in *Sempervivum* Sect. *Jovibarba* (Crassulaceae). *Succulenta (NL)* 78:35–42.
- Hart, H. 't, Bleij, B. 2003. *Phedimus*. In: Eggli, U. (ed.) *Illustrated Handbook of Succulent Plants, VI. Crassulaceae*. Berlin Heidelberg New York: Springer, pp. 196–203.
- Hart, H. 't, Eggli, U. 1995. Introduction: evolution of Crassulaceae systematics. In: Hart, H. 't, Eggli, U. (eds) *Evolution and systematics of the Crassulaceae*. Leiden: Backhuys, pp. 7–15.
- Hart, H. 't, Eggli, U. 1998. Cytotaxonomic studies in *Rosularia* (Crassulaceae). *Bot. Helvetica* 98:223–234.
- Hart, H. 't, Koek-Noorman, J. 1989. The origin of the woody Sedoideae (Crassulaceae). *Taxon* 38:535–544.
- Hart, H. 't, Sandbrink, J.M., Csikos, I., Ooyen, A. van, Brederode, J. van 1993. The allopolyploid origin of *Sedum rupestre* subsp. *rupestre* (Crassulaceae). Natural hybrids in *Sedum* (Crassulaceae) 4. *Pl. Syst. Evol.* 184:195–206.
- Hart, H. 't, van Ham, R.C.H.J., Stevens, J.F., Elema, E.T., Klis, H. van, Gadella, T.W.J. 1999. Biosystematic, molecular and phytochemical evidence for the multiple origin of sympetaly in Eurasian Sedoideae (Crassulaceae). *Biochem. Syst. Ecol.* 27:407–426.
- Hegnauer, R. 1964. *Chemotaxonomie der Pflanzen*. Band 3. Dicotyledoneae: Acanthaceae–Cyrillaceae. Basel: Birkhäuser, pp. 572–584.
- Hegnauer, R. 1989. *Chemotaxonomie der Pflanzen*, Band 8. Nachträge zu Band 3 und Band 4 (Acanthaceae bis Lythraceae). Crassulaceae: pp. 342–350, 710. Basel: Birkhäuser.
- Hideux, M.J. 1981. Le pollen. Données nouvelles de la microscopie électronique et de l'informatique: structure du sporoderme de Rosidae-Saxifragales, étude comparative et dynamique. Paris: Agence de Coopération Culturelle et Technique.
- Huber, H. 1961. Crassulaceae. In: Hegi, G. (ed.) *Illustrierte Flora von Mittel-Europa*. 2. Auflage. Band IV/2. Teil. Teilband A. München: Carl Hanser, pp. 62–125.
- Hutchinson, J. 1973. *The families of flowering plants*, ed. 3. Oxford: Clarendon Press.

- Huxley, A., Griffiths, M., Levy, M. (eds) 1997. The New RHS Dictionary of Gardening. 4 vols. London: MacMillan.
- Jaarsveld, E.J. van 1994. The distribution of *Tylecodon* and *Cotyledon* (Crassulaceae) in South Africa and Namibia. In: Seyani, J.H., Chikuni, A.C. (eds) Proc. XIII Plenary Meeting AETFAT, Malawi, pp. 1157–1163.
- Jacob, F.H. 1964. A new species of *Thuleaphis* from Wales, Scotland, and Iceland (*Thuleaphis sedi* n. sp. on *Sedum rosea*). Proc. Roy. Entomol. Soc., London, ser. B, Taxonomy 33:111–116.
- Jäger-Zürn, I. 1989. Zur Kenntnis von *Crassula pageae* Tölken (syn. *Pagella archeri*). Trop.-subtrop. Pflanzenwelt 70:1–71. Mainz: F. Steiner.
- Jalas, J., Suominen, J., Lampinen, R., Kurtto, A. 1999. Atlas Florae Europaeae. Distribution of vascular plants in Europe, 12. Helsinki: Committee for Mapping the Flora of Europe & Societas Biologica Fennica Vanamo.
- Jay, M. 1971. Quelques problèmes taxonomiques et phylogénétiques des Saxifragacées vus à la lumière de la biochimie flavonique. Bull. Mus. Natl. Hist. Nat. II, 42:754–775.
- Jensen, L.C.W. 1966. Comparative anatomical studies in three subfamilies of the Crassulaceae. Ph.D. Thesis, University of Minnesota.
- Jiménez C., G., Soberón M., J. 1989. Laboratory rearing of *Sandia xami xami* (Lycaenidae, Eumaeini). J. Res. Lepidoptera 27:268–271.
- Johnson, S.D., Ellis, A., Carrick, P., Swift, P., Horner, N., Janse van Rensburg, S., Bond, W.J. 1993. Moth pollination and rhythms of advertisement and reward in *Crassula fascicularis* (Crassulaceae). S. African J. Bot. 59:511–513.
- Johri, B.M. et al. 1992. See general references.
- Jorgensen, T.H., Olesen, J.M. 2000. Growth rules based on the modularity of the Canarian *Aeonium* (Crassulaceae) and their phylogenetic value. Bot. J. Linn. Soc. 132:223–240.
- Jorgensen, T.H., Olesen, J.M. 2001. Adaptive radiation of island plants: Evidence from *Aeonium* (Crassulaceae) of the Canary Islands. Perspec. Pl. Ecol. Evol. Syst. 4:29–42.
- Jürgens, N. 1995. Contributions to the phytogeography of *Crassula*. In: Hart, H. 't, Eggli, U. (eds) Evolution and systematics of the Crassulaceae. Leiden: Backhuys, pp. 136–150.
- Keeley, J.E. 1998. CAM photosynthesis in submerged aquatic plants. Bot. Rev. 64:121–175.
- Kim, J.-H. 1994. Pollen morphology of genus *Sedum* in Korea. J. Pl. Biol. 37, 2:245–252.
- Kluge, M., Brulfert, J. 1996. Crassulacean acid metabolism in the genus *Kalanchoe*: ecological, physiological and biological approaches. In: Winter, K., Smith, A.P., Smith, J.A.C. (eds) Crassulacean acid metabolism. Biochemistry, ecophysiology and evolution. Berlin Heidelberg New York: Springer, pp. 324–335.
- Knapp, R. 1973. Die Vegetation von Afrika. Stuttgart: G. Fischer.
- Knapp, U. 1994. Skulptur der Samenschale und Gliederung der Crassulaceae. Bot. Jahrb. Syst. 116:157–187.
- Knapp, U. 1997. Samenoberfläche und Systematik der Saxifragaceae und Crassulaceae. Ph.D. Thesis, University of Kaiserslautern, pp. 1–234.
- Krach, J.E. 1976. Samen Anatomie der Rosifloren. 1. Die Samen der Saxifragaceae. Bot. Jahrb. Syst. 97:1–60.
- Kurkin, V.A., Zapesochnaya, G.G. 1986. The chemical composition and pharmacological properties of *Rhodiola* plants (in Russian). Khim.-farm. Zhurn. 20:1231–1244.
- Leinfellner, W. 1954. Beiträge zur Kronblattmorphologie. III. Die Kronblätter der Gattung *Pachyphytum*. Oesterr. Bot. Z. 101:586–591.
- Levin, G.A., Mulroy, T.W. 1985. Floral morphology, nectar production, and breeding systems in *Dudleya* subgenus *Dudleya* (Crassulaceae). Trans. San Diego Soc. Nat. Hist. 21:57–70.
- Lippert, W. 1995. Familie Crassulaceae. Dickblattgewächse. In: Weber, H.E. (ed.) Gustav Hegi, Illustrierte Flora von Mitteleuropa, Band IV, Teil 2A: Spermatophyta: Angiospermae, Dicotyledones 2(2), 3. Auflage. Berlin: Blackwell, pp. 69–129.
- Lösch, R. 1990. Funktionelle Voraussetzung der adaptiven Nischenbesetzung in der Evolution der makaronesischen Semperviven. Diss. Bot. 146:1–482.
- Manheim, B.S. Jr, Mulroy, T.W., Hogness, D.K., Kerwin, J.L. 1979. Interspecific variation in leaf wax of *Dudleya*. Biochem. Syst. Ecol. 7:17–19.
- Marchant, T.A., Alarcon, R., Simonsen, J.A., Koopowitz, H. 1998. Population ecology of *Dudleya multicaulis* (Crassulaceae): a rare narrow endemic. Madroño 45:215–220.
- Martin, C.E., Willert, D.J. von 2000. Leaf epidermal hydathodes and the ecophysiological consequences of foliar water uptake in species of *Crassula* from the Namib desert in Southern Africa. Pl. Biol. 2:229–242.
- Mauritzon, J. 1930. Beitrag zur Embryologie der Crassulaceen. Bot. Notiser 1930:233–250.
- Mauritzon, J. 1933. Studien über die Embryologie der Familien Crassulaceae und Saxifragaceae. Lund: Hakan Ohlssons.
- Mayuzumi, S., Ohba, H. 2004. The phylogenetic position of Eastern Asian Sedoideae (Crassulaceae) inferred from chloroplast and nuclear DNA sequences. Syst. Bot. 29:587–598.
- Merxmüller, H., Friedrich, H.-C., Grau, J. 1971. Cytotaxonomische Untersuchungen zur Gattungsstruktur von *Crassula*. Ann. Naturhist. Mus. Wien 75:111–119.
- Mes, T.H.M. 1995. Phylogenetic and systematic implications of chloroplast and nuclear spacer sequence variation in the Macaronesian Sempervivoideae and related Sedoideae. In: Hart, H. 't, Eggli, U. (eds) Evolution and systematics of the Crassulaceae. Leiden: Backhuys, pp. 30–44.
- Mes, T.H.M. 1996. Origin and evolution of the Macaronesian Sempervivoideae (Crassulaceae). Ph.D. Thesis, University of Utrecht.
- Mes, T.H.M., Hart, H. 't 1994. *Sedum surculosum* and *S. jaccardianum* (Crassulaceae) share a unique 70 bp deletion in the chloroplast DNA *trnL* (UAA)–*trnF* (GAA) intergenic spacer. Pl. Syst. Evol. 193:213–221.
- Mes, T.H.M., Hart, H. 't 1996. The evolution of growth-forms in the Macaronesian genus *Aeonium* (Crassulaceae) inferred from chloroplast RFLPs and morphology. Mol. Ecol. 5:351–363.
- Mes, T.H.M., Brederode, J. van, Hart, H. 't 1996. Origin of the woody Macaronesian Sempervivoideae and the phylogenetic position of the East African species of *Aeonium*. Bot. Acta 109:477–491.
- Mes, T.H.M., Wijers, G.J., Hart, H. 't 1997. Phylogenetic relationships in *Monanthes* (Crassulaceae) based on mor-

- phological, chloroplast and nuclear DNA variation. *J. Evol. Biol.* 10:193–216.
- Meusel, H., Jäger, E., Weinert, E. 1965. Vergleichende Chorologie der zentralen europäischen Flora. Band 1. Crassulaceae. Jena: G. Fischer.
- Moran, R. 1949. *Graptopetalum bartramii* in Chihuahua. *Desert Pl. Life* 21:53–56.
- Moran, R. 1996. *Altamiranoa* into *Sedum* (Crassulaceae). *Haseltonia* 4:46.
- Moran, R. 2000. Circumscission in *Cotyledon*: with thoughts on what is *Cotyledon*, and on how A.P. de Candolle was right all along and they should have listened. *Cact. Succ. J. (U.S.)* 72:306–308.
- Moran, R., Meyrán, J. 1974. *Tacitus bellus*, un nuevo género y especie de Crassulaceae de Chihuahua, México. *Cact. Soc. Mex.* 19:75–84.
- Morgan, D.R., Soltis, D.E. 1993. Phylogenetic relationships among members of Saxifragaceae sensu lato based on *rbcl* sequence data. *Ann. Missouri Bot. Gard.* 80:631–660.
- Mort, M.E., Soltis, D.E., Soltis, P.S., Francisco-Ortega, J., Santos-Guerra, A. 2001. Phylogenetic relationships and evolution of Crassulaceae inferred from *matK* sequence data. *Amer. J. Bot.* 88:76–91.
- Mort, M.E., Soltis, D.E., Soltis, P.S., Francisco-Ortega, J., Santos-Guerra, A. 2002. Phylogenetics and evolution of the Macaronesian clade of Crassulaceae inferred from nuclear and chloroplast sequence data. *Syst. Bot.* 27:271–288.
- Moteeteetee, A., Nagendran, C.R. 1997. Comparative anatomical studies in five southern African species of *Crassula*. I. Structure of the stem and the root. *S. African J. Bot.* 63:90–94.
- Nakanishi, H. 2002. Splash seed dispersal by raindrops. *Ecol. Res. (Tokyo)* 17:663–671.
- Newton, D.J., Chan, J. 1998. South Africa's trade in southern African succulent plants. Johannesburg: TRAFFIC East/Southern Africa.
- Nyffeler, R. 1992. A taxonomic revision of the genus *Monanthes* Haworth (Crassulaceae). *Bradleya* 10:49–82.
- Ohba, H. 1978. Generic and infrageneric classification of the Old World Sedoideae (Crassulaceae). *J. Fac. Sci., Univ. Tokyo III, Bot.* 12:139–198.
- Ohba, H. 1989. Biogeography of the genus *Rhodiola* (Crassulaceae), with special reference to the floristic interaction between the Himalaya and the Arctic Region. In: Ohba, H., Hayami, I., Mochizuki, K. (eds) Current aspects of biogeography in West Pacific and East Asian regions. University of Tokyo, pp. 115–133.
- Oldfield, S. (ed.) 1997. Cactus and Succulent Plants – Status Survey and Conservation Action Plan. Gland and Cambridge: IUCN/SSC Cactus and Succulent Specialist Group.
- Olfelt, J.P., Furnier, G.P., Luby, J.L. 1998. Reproduction and development of the endangered *Sedum integrifolium* ssp. *leedyi* (Crassulaceae). *Amer. J. Bot.* 85:346–351.
- Olfelt, J.P., Furnier, G.P., Luby, J.L. 2001. What data determine whether a plant's taxon is distinct enough to merit legal protection? A case study of *Sedum integrifolium* (Crassulaceae). *Amer. J. Bot.* 88:401–410.
- Parnell, J. 1991. Pollen morphology of *Jovibarba* Opiz and *Sempervivum* L. (Crassulaceae). *Kew Bull.* 46:733–738.
- Parra, V., Vargas, C.F., Eguiarte, L.E. 1993. Reproductive biology, pollen and seed dispersal, and neighborhood size in the hummingbird-pollinated *Echeveria gibbiflora* (Crassulaceae). *Amer. J. Bot.* 80:153–159.
- Parra, V., Vargas, C.F., Eguiarte, L.E. 1998. Is *Echeveria gibbiflora* (Crassulaceae) fecundity limited by pollen availability? An experimental study. *Funct. Ecol.* 12:591–595.
- Pérez de Paz, P.L. 1980. Contribución al atlas palinológico de endemismos Canario-Macaronésicos. Part III. *Bot. Macar.* 7:77–112. Gran Canaria: Jardín Botánico.
- Pilon-Smits, E.A.H. 1992. Variation and evolution of Crassulacean Acid Metabolism in *Sedum* and *Aeonium* (Crassulaceae). Ph.D. Thesis, University of Utrecht.
- Quimby, M.W. 1971. The floral morphology of the Crassulaceae. Ph.D. Thesis, Cornell University, Ithaca.
- Raads, E. 1979. Rasterelektronenmikroskopische und anatomische Untersuchungen an Konnektivdrüsen von *Kalanchoe* (Crassulaceae). *Willdenowia* 9:169–175.
- Riefner, R.E. Jr, Bowler, P.A., Mulroy, T.W., Wishner, C. 2003. Lichens on rock and biological crusts enhance recruitment success of rare *Dudleya* species (Crossulaceae) in Southern California. *Crossosoma* 29:1–36.
- Rivas-Martínez, S., Wildpret de la Torre, W., del Arco, M., Rodríguez, O., Pérez de Paz, P.L., García-Gallo, A., Acebes, J.R., Fernández-González, F. 1993. Las comunidades vegetales de la Isla de Tenerife (Islas Canarias). *Itinera Geobot.* 7:169–374.
- Rocén, T. 1928. Beitrag zur Embryologie der Crassulaceen. *Svensk Bot. Tidsskr.* 22:368–376.
- Rocher, E.J. de, Harkins, K.R., Galbraith, D.W., Bohnert, H.J. 1990. Developmentally regulated systemic endopolyploidy in succulents with small genomes. *Science* 250:99–101.
- Rünger, W., Wehr, B. 1969. Über den Einfluss der Tageslänge und der Temperatur auf die Blütenbildung einiger *Echeveria*-Arten. *Gartenbauwissenschaft* 34:111–143.
- Said, C. 1982. Les nectaires floraux des Crassulacées. Étude morphologique, histologique et anatomique. *Bull. Soc. Bot. France Lett. Bot.* 129:231–240.
- Savolainen, V., Chase, M.W. et al. 2000. See general references.
- Savolainen, V., Fay, M.F. et al. 2000. See general references.
- Schönland, S. 1894. Crassulaceae. In: Engler, A., Prantl, K., Die natürlichen Pflanzenfamilien, ed. 1, 3, 2a. Leipzig: W. Engelmann, pp. 23–38.
- Sharma, A.K., Gosh, S. 1967. Cytotaxonomy of Crassulaceae. *Biol. Zentralbl. suppl.* 86:313–336.
- Sin, J.-H., Yoo, Y.-G., Park, K.-R. 2002. A palynotaxonomic study of the Korean Crassulaceae. *Korean J. Electron Microscopy* 32:345–360.
- Soltis, D.E., Soltis, P.E. 1997. Phylogenetic relationships in Saxifragaceae sensu lato: a comparison of topologies based on 18S rDNA and *rbcl* sequences. *Amer. J. Bot.* 84:504–522.
- Soltis, D.E. et al. 2000. See general references.
- Soltis, D.E., Fishbein, M., Kuzoff, R.K. 2003. Re-evaluating the evolution of epigyny: data from phylogenetics and floral ontogeny. *Intl J. Pl. Sci.* 164:S251–S264.
- Souèges, R. 1936. Les relations embryogéniques des Crassulacées, Saxifragacées et Hypéricacées. *Bull. Soc. Bot. France* 83:317–329.
- Stevens, J.F. 1995a. Chemotaxonomy of the Eurasian Sedoideae and Sempervivoideae. In: Hart, H. 't, Eggli, U. (eds) Evolution and systematics of the Crassulaceae. Leiden: Backhuys, pp. 30–44.

- Stevens, J.F. 1995b. The systematic and evolutionary significance of phytochemical variation in the Eurasian Sedoideae and Sempervivoideae (Crassulaceae). Groningen: Rijks University.
- Stevens, J.F., Hart, H. 't, Hendriks, H., Malingré, T.M. 1992. Alkaloids of some European and Macaronesian Sedoideae and Sempervivoideae (Crassulaceae). *Phytochemistry* 31:3917–3924.
- Stevens, J.F., Hart, H. 't, Hendricks, H., Malingré, T.M. 1993. Alkaloids of the *Sedum acre*-group (Crassulaceae). *Pl. Syst. Evol.* 185:207–217.
- Stevens, J.F., Hart, H. 't, Bolck, A., Zwaving, J.H., Malingré, T.M. 1994. Epicuticular wax composition of some European *Sedum* species. *Phytochemistry* 35:389–399.
- Stevens, J.F., Hart, H. 't, van Ham, R.C.H.J., Elema, E.T., van den Ent, M.M.V.X., Wildeboer, M., Zwaving, J.H. 1995. Distribution of alkaloids and tannins in the Crassulaceae. *Biochem. Syst. Ecol.* 23:157–165.
- Stevens, J.F., Hart, H. 't, Elema, E.T., Bolck, A. 1996. Flavonoid variation in Eurasian *Sedum* and *Sempervivum*. *Phytochemistry* 41:503–512.
- Stevens, P.F. 2005. See general references.
- Stopp, K. 1957. Aberrante Dehiscenzformen bei Früchten einiger *Crassula*-Arten. *Beitr. Biol. Pflanzen* 34:165–175.
- Supratman, U., Fujita, T., Akiyama, K., Hayashi, H. 2001. Insecticidal compounds from *Kalanchoe daigremontiana* x *tubiflora*. *Phytochemistry* 58:311–314.
- Takhtajan, A.L. 1969. Flowering plants, origin and dispersal. Washington, DC: Smithsonian Institution Press, pp. 1–310.
- Teeri, J.A., Overton, J. 1981. Chloroplast ultrastructure in two Crassulacean species and an F₁ hybrid with differing biomass delta ¹³C values. *Pl. Cell Environ.* 4:427–431.
- Teeri, J.A., Stowe, L.G., Murawski, D.A. 1978. The climatology of two succulent plant families: Cactaceae and Crassulaceae. *Canad. J. Bot.* 56:1750–1758.
- Thiede, J. 1995. Quantitative phytogeography, species richness, and evolution of American Crassulaceae. In: Hart, H. 't, Egli, U. (eds) *Evolution and systematics of the Crassulaceae*. Leiden: Backhuys, pp. 89–123.
- Thiede, J. 2004. The genus *Dudleya* Britton & Rose (Crassulaceae): its systematics and biology. *Cact. Succ. J. (U.S.)* 76:4–11.
- Thiede, J., Hart, H. 't 1999. Transfer of four Peruvian *Altamiranoa* species to *Sedum* (Crassulaceae). *Novon* 9:124–125.
- Thorne, R.F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. *Aliso* 6:57–66.
- Thorne, R.F. 1983. Proposed new realignments in the angiosperms. *Nordic J. Bot.* 3:75–117.
- Thorne, R.F. 1992. An updated phylogenetic classification of the flowering plants. *Aliso* 13:365–389.
- Tillson, A.H. 1940. The floral anatomy of the Kalanchoideae. *Amer. J. Bot.* 27:595–600.
- Toelken, H.R. 1977. A revision of the genus *Crassula* in southern Africa. Parts 1 & 2. *Contr. Bolus Herb.* 1–331, 332–595.
- Toelken, H.R. 1986. Crassulaceae. In: Jessop, J.P., Toelken, H.R. (eds) *Flora of South Australia*. Part I. Adelaide: Government Printing Office, pp. 418–428.
- Torrey, J., Gray, A. 1838. A flora of North America, I. New York: Wiley & Putnam.
- Troll, W. 1964. Die Infloreszenzen. Erster Band. Stuttgart: G. Fischer.
- Troll, W. 1969. Die Infloreszenzen. Zweiter Band, 1. Teil. Stuttgart: G. Fischer.
- Troll, W., Weberling, F. 1989. Infloreszenzuntersuchungen an monotelen Familien. Stuttgart: G. Fischer.
- Uhl, C.H. 1948. Cytotaxonomic studies in the subfamilies Crassuloideae, Kalanchoideae, and Cotyledonoideae of the Crassulaceae. *Amer. J. Bot.* 35:695–706.
- Uhl, C.H. 1961. The chromosomes of the Sempervivoideae (Crassulaceae). *Amer. J. Bot.* 48:114–123.
- Uhl, C.H. 1970. Chromosomes of *Graptopetalum* and *Thompsonella* (Crassulaceae). *Amer. J. Bot.* 57:1115–1121.
- Uhl, C.H. 1976–1992. Chromosomes of Mexican *Sedum*. I–VI. *Rhodora* 79:629–640, 80:491–512, 82:377–402, 85:243–252, 87:381–423, 94:362–370.
- Uhl, C.H. 1992. Polyploidy, dysploidy, and chromosome pairing in *Echeveria* (Crassulaceae) and its hybrids. *Amer. J. Bot.* 79:556–566.
- Uhl, C.H. 1993–1995. Intergeneric hybrids in the Mexican Crassulaceae. I–V. *Cact. Succ. J. (U.S.)* 65:271–273, 66:74–80, 175–179, 214–217, 67:144–147.
- Uhl, C.H. 1994–2005. Chromosomes and hybrids of *Echeveria* (Crassulaceae). I–IX. *Haseltonia* 2:79–80, 3:25–33, 3:34–48, 4:66–88, 5:21–36, 6:63–90, 8:71–82, 9:121–145, 11:138–149.
- Uhl, C.H. 1996. Chromosomes and polyploidy in *Lenophyllum* (Crassulaceae). *Amer. J. Bot.* 83:216–220.
- Uhl, C.H., Moran, R. 1972. Chromosomes of Crassulaceae from Japan and South Korea. *Cytologia* 37:59–81.
- Uhl, C.H., Moran, R. 1973. The chromosomes of *Pachyphytum* (Crassulaceae). *Amer. J. Bot.* 60:648–656.
- Uhl, C.H., Moran, R. 1999. Chromosomes of *Villadia* and *Altamiranoa* (Crassulaceae). *Amer. J. Bot.* 86:387–397.
- U.S. Fish and Wildlife Service 2004. Threatened and Endangered Species System (TESS). <http://endangered.fws.gov/wildlife.html>
- Visser, J. 1981. South African parasitic flowering plants. Cape Town: Juta.
- Vogel, S. 1954. Blütenbiologische Studien als Elemente der Sipplgliederung, dargestellt an der Flora Südafrikas. *Bot. Stud.* 1:1–338.
- Wakabayashi, M., Ohba, H. 1999. Chromosome numbers of seven species of *Sedum* and *Sinocrassula indica* (Crassulaceae) in East Himalaya. *J. Jap. Bot.* 74:228–235.
- Wassmer, A. 1955. Vergleichend-morphologische Untersuchungen an den Blüten der Crassulaceen. Winterthur: P.G. Keller.
- Wickens, G.E., Bywater, M. 1980. Seed studies in *Crassula* subgen. *Disporocarpa*. *Kew Bull.* 34:629–637.
- Wikström, N., Savolainen, V., Chase, M.W. 2001. Evolution of the angiosperms: calibrating the family tree. *Proc. Roy. Soc. London, ser. B* 268:2211–2219.
- Wyatt, R., Stoneburger, A. 1981. Patterns of ant-mediated pollen dispersal in *Diamorpha smallii* (Crassulaceae). *Syst. Bot.* 6:1–7.
- Xu, J.F., Liu, C.B., Han, A.M., Feng, P.S., Su, Z.G. 1998. Strategies for the improvement of salidroside production in cell suspension cultures of *Rhodiola sachalinensis*. *Pl. Cell Rep.* 17:288–293.

Yamagishi, T., Haruna, M., Yan, X.-Z., Chang, J.-J., Lee, K.-H. 1989. Antitumor agents, 110. 1,2 bryophyllin B, a novel potent cytotoxic bufadienolide from *Bryophyllum pinnatum*. J. Nat. Prod. 52:1071–1079.

Yoshikawa, M., Shimada, H., Shimoda, H., Murakami, N., Yamahara, J., Matsuda, H. 1996. Bioactive constituents

of Chinese natural medicines. II. Rhodiolae Radix (1): chemical structures and antiallergic activity of rhodiocyanosides A and B from the underground part of *Rhodiola sachalinensis* (Pall.) Fisch. et Mey. (Crasulaceae). Chem. Pharmaceut. Bull. (Tokyo) 44:2086–2091.

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Professor Dr. KLAUS KUBITZKI
Universität Hamburg
Biozentrum Klein-Flottbek und Botanischer Garten
Ohnhorststraße 18
22609 Hamburg
Germany

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