## Contents

Note: = family or genus completely covered; $\diamond=$ family or genus only partially covered;
$\sim=$ family or genus only mentioned; numbers in brackets = numbers of species $/$ infraspecific
taxa covered
Introduction ..... 1
What is a Succulent? ..... 1
How to Use This Handbook ..... 1
Scope of Information Presented ..... 1
Crassulaceae $\diamond$ ..... 5
Adromischus ( $28 / 9$ ) ..... 8
Aeonium $(36 / 6)$ ..... 15
Afrovivella ( $1 / 0$ ) ..... 23
Aichryson ( $14 / 0$ ) ..... 24
Cotyledon (10/5) ..... 27
Crassula ( 195 / 88) ..... 32
$\times$ Cremnadia ..... 84
$\times$ Cremneria ( $1 / 0$ ) ..... 84
$\times$ Cremnopetalum ..... 84
Cremnophila ( $2 / 0$ ) ..... 84
Cremnosedum ..... 85
$\times$ Cremsonella ..... 85
$\times$ Dudleveria ..... 85
Dudleya (47/20) ..... 85
Echeveria (139 / 28) ..... 103
$\times$ Grapsonella ..... 128
$\times$ Graptoladia ..... 128
Graptopetalum * (16/2) ..... 128
$\times$ Graptophytum ..... 134
$\times$ Graptosedum ..... 134
$\times$ Graptoveria ..... 134
Hylotelephium ( $27 / 7$ ) ..... 135
Hypagophytum ( $1 / 0$ ) ..... 142
Kalanchoe ( 144 / 11) ..... 143
$\times$ Lenaptopetalum ..... 181
Lenophyllum • (7/0) ..... 181
$\times$ Lenophytum ..... 182
$\times$ Lenoveria ..... 182
Meterostachys ( $1 / 0$ ) ..... 182
Monanthes (9/1) ..... 183
Orostachys (12/4) ..... 186
$\times$ Pachyladia ..... 190
Pachyphytum ( $15 / 0$ ) ..... 190
$\times$ Pachysedum ..... 196
$\times$ Pachyveria ..... 196
Perrierosedum (1/0) ..... 196
Phedimus ( $18 / 0$ ) ..... 196
Pistorinia (3/0) ..... 203
Prometheum $\bullet(8 / 1)$ ..... 204
Pseudosedum (12 / 1) ..... 207
Rhodiola ( 58 / 15) ..... 210
Rosularia * (17 / 9) ..... 227
$\times$ Sedadia ..... 233
Sedella (3/0) ..... 234
$\times$ Sedeveria ..... 235
Sedum (428 / 69) ..... 235
Sempervivum * (63 / 16) ..... 332
Sinocrassula (7/7) ..... 350
Thompsonella * (6/0) ..... 353
$\times$ Thompsophytum $\leqslant$ ..... 354
$\times$ Thompsosedum ..... 354
$\times$ Thompsoveria ..... 354
Tylecodon (46/4) ..... 354
Umbilicus (14/1) ..... 364
Villadia ( $21 / 1$ ) ..... 367
$\times$ Villeveria ..... 374
References ..... 375
Taxonomic Cross-Reference Index ..... 385

## Introduction

## What is a succulent ?

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Other borderline cases included are a number of bulbous and rhizomatous monocotyledons, where examples from several genera are covered, as well as several weakly developed leaf succulents from the Gesneriaceae (e.g. Columnea).

On the other hand, purely halophytic succulents (such as Salicornia) are omitted from these pages since they are as a whole neither adapted to climatically dry conditions nor encountered in collections devoted to succulent plants.
Finally, some families with undoubted claim to (xerophytic) succulence have been excluded from this set of volumes. This notably is the case for the Cactaceae, which will be treated elsewhere. In addition, the families Bromeliaceae and Orchidaceae are also excluded. Both count with a considerable number of mostly leaf succulents, but for both, vast specialist literature and numerous specialist societies are in existence, and this effort does not need to be duplicated here. For all these excluded families, however, a family description is included in the present volumes for the sake of completeness.

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Since all information is presented in strictly alphabetical sequence of families, genera and species (except that monocotyledons and dicotyledons are treated separately, and that the families Aizoaceae, Asclepiadaceae and Crassulaceae occupy their own volumes), it is easy to find the entry for a given species as long as its family placement is known.
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volume. This index contains all the names treated in the volume and for accepted names indicates the page where a treatment can be found, or in the case of synonyms gives the name of the accepted taxon and a page reference as above. For names merely mentioned in the text, the index gives the page reference and the name under which information can be found.

If a completely unknown plant is to be identified, the handbook supplies keys to the genera with succulent representatives for each family. Please note that these keys are designed to work for the succulent taxa treated, and do not necessarily include the total variation encountered in a genus. If the family is not known, the reader is referred to general botanical books that include keys to plant families. Rowley (1980) and Eggli (1994) provided keys for flowering and non-flowering succulents, and Geesink \& al. (1981) produced a well-known book of keys to all flowering plants worldwide.

## Scope of information presented

## Families

The family names adopted are always conforming to the standard form (ending in -aceae); alternative names (such as Compositae for Asteraceae) are not used.

Within each family, the genera are treated in alphabetical sequence, and the same applies to the sequence of species within genera. Some genera of minimal importance or with borderline succulence are only mentioned or at the most described, but no individual species are treated.

The following families are included as a whole, i.e. with all their component species: Agavaceae, Aloaceae and Doryanthaceae in the present volume covering the Monocotyledons, and the Didiereaceae, Fouquieriaceae and Nolanaceae in the Dicotyledons volume. The Aizoaceae and Crassulaceae are covered in their entirety in separate volumes within this series, and the succulent taxa of the Asclepiadaceae likewise occupy a separate volume of the Handbook.

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The family concept adopted more or less follows Mabberley (1987), except for the monocotyledons, where Dahlgren \& al. (1985) is used as a base, with a number of small modifications.

## Genera and species

The entries for genera and species follow the same layout. Names of authors are given in full, with initials added where necessary according to Brummitt \& Powell (1992). The literature reference of the original description or combination is followed by information on typification (where available, see below). In the case of genera, important literature is then cited. This is followed by information on geographical distribution (including notes on ecology where available) and an explanation of the etymology for generic names.

The main part of the entry is made up by the diagnostic description of the taxon, followed by a discussion of its variability, circumscription and/or application where necessary. It should be noted that these descriptions reflect major variability only, but do not include all the reported minor variations.

For larger genera, an outline of the accepted formal or informal classification is also given, with individual taxa or groups numbered in sequence. These sequence numbers are then given at the start of each taxon description to indicate its placement within the genus.

If recent conflicting classifications are available for a given group, this is shortly discussed and the classification adopted is indicated.

Minor spelling variants of epithets are not indicated; instead, the 'corrected' spelling is used throughout for accepted names and synonyms.

## Infraspecific taxa

Infraspecific taxa are given in strict alphabetic order of rank and name (i.e. ranks in the sequence cv., fa., ssp., var.). This is due to the strict alphabetical sorting used when the output for the handbook was generated from a computerized database. It also means that the typical infraspecific taxon (i.e. the one repeating the species name) is not treated first as in many handbooks, but in its appropriate alphabetical sequence.

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with a species are enumerated first, i.e. between the generic entry and the first species. Cultivars associated with a species name are included under that species, either as an entry of their own (and in the same form as subspecies etc.), or, in the case of cultivars of minor importance, in the form of a short mention in the species discussion. Cultivar nomenclature follows the guidelines of the ICBN.

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## Descriptions

The descriptions are as compact, concise and diagnostic as possible. Characters that do not vary for the group concerned are not repeated from the family or genus descriptions. In the case of genera further subdivided, information already presented in the group definitions is also not normally repeated in the descriptions of individual taxa.

## Measurements

All measurements are given in metric units. Measurements without further qualifications always refer to the long axis of the organ described (i.e. length, height etc.); two measurements united with the $\times$-sign stand for length $\times$ width.

## Terminology

Special terms used in descriptions are explained when first used; other botanical terminology is not further explained, and the readers are referred to the numerous botanical glossaries, of which Stearn (1992) is cited by way of a most important and useful example.

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## Crassulaceae

Perennial or rarely annual or hapaxanthic herbs, subshrubs to shrubs (rarely aquatics, or tree-like, or epiphytic, or scandent), usually with succulent $\mathbf{L}$, sometimes with succulent stems or underground caudices; $\mathbf{L}$ opposite and decussate or alternate and spiral, frequently aggregated into Ros, simple, usually entire, or crenate to lobed, glabrous or tomentose; stipules absent; Inf lateral or terminal many-flowered spikes or panicles, rarely few- to 1 flowered and axillary; Fl bisexual or unisexual (then plants $\pm$ dioecious), actinomorphic (except Tylecodon grandiflorus), frequently 5 -merous but varying from 3- to 32 -merous; Sep free or basally united; Pet free or basally united to form a short to long Cl tube; St as many or $2 \times$ as many as Pet, free or fused to them; Ca as many as Pet, superior, free or almost so, basally with a small to conspicuous NSc, gradually tapering into short to long Sty, with few to many ovules; Fr usually dehiscent follicles, capsular; Se smallish, to $1.5-3 \mathrm{~mm}$, elongate, smooth, papillate to longitudinally ridged, mostly brownish.

Distribution: Worldwide but esp. N hemisphere and S Africa.

Literature: Berger (1930); 't Hart (1995); Eggli \& al. (1995).

The family counts $\pm 1400$ species in 33 genera here accepted. It is here treated in its entirety, adopting the consensus classification proposed by Eggli \& al. (1995), but modified to accept the additional genera Afrovivella, Phedimus and Prometheum, and subsuming Bryophyllum under Kalanchoe, and Jovibarba under Sempervivum. The family has no important crop plants, with the exception of numerous taxa of horticultural interest, mainly as hardy perennials for rock gardens, and more recently - for establishing green 'living' roofs. Hylotelephium spectabile is sometimes used in the cut-flower trade. Numerous species from almost all genera are popular in succulent plant collections.
Due to numerous suspected parallel developments, the classification of the family has been difficult, and the identification of species is often problematical because of hybridization (to a limited extent natural, and almost without limits in cultivation, esp. amongst genera in Group F). The traditional circumscription of 6 subfamilies by Berger (1930) was known to be artificial for some time. Recently, a revised classification was proposed by 't Hart (1995), based on molecular and morphological data:

Subfamily Crassuloideae A. Berger 1930: Fl haplostemonous ( $\mathbf{S t}$ as many as $\mathbf{P e t}$ ): Crassula.

Subfamily Sedoideae A. Berger 1930: Fl obdiplostemonous (St $2 \times$ as many as Pet) (with few exceptions):

- Tribe Kalanchoeae 't Hart 1995: L decussate or alternate, flat (rarely terete), crenate or dentate (rarely entire); Fl 4- or 5-merous; Pet united to form a distinct tube; Se costate:

Group A: L alternate: Adromischus, Tylecodon.
Group B: L decussate: Cotyledon, Kalanchoe.

- Tribe Sedeae 't Hart 1995: L mostly alternate, thick, entire (if decussate Pet free and Se costate); Fl (3- to) 5- to 32-merous; Se costate, (multi-) papillate or reticulate:
- Subtribe Telephinae 't Hart 1995: Stems often basally woody, tuberous or sympodial or monopodial rhizomes; $\mathbf{L}$ usually alternate, flat, dentate or crenate (rarely decussate, terete or entire); Fl 5 -merous (if polymerous then $\mathbf{L}$ flat, opposite or whorled); Sep basally connate; Pet usually free (if connate then Se multipapillate); Se costate or multipapillate: Hylotelephium, Hypagophytum, Orostachys, Perrierosedum, Phedimus, Pseudosedum, Rhodiola, Umbilicus.
- Subtribe Sedinae 't Hart 1995: Stems herbaceous, rarely woody or rhizomatous; $\mathbf{L}$ often rosulate or subrosulate, terete or semiterete, or flat and/or dentate-serrate and/or decussate; Fl 4or to 32-merous; Sep basally connate or free; Pet usually free and stellately patent, rarely united; Se reticulate, papillate or costate:
Group C: Plants various; $\mathbf{L}$ in Ros or scattered, glabrous or glandular-hairy; Inf terminal or lateral: Pistorinia, Prometheum, Rosularia, Sedum.
Group D: Plants rosulate, from Europe, W Asia, the Caucasus or Macaronesia, mostly glandular-hairy; Inf mostly terminal; Fl mostly > 5-merous: Aeonium, Aichryson, Monanthes, Sempervivum.
Group E: N American rosulate plants, glabrous but often farinose; Inf lateral; Fl 5-merous: Dudleya.
Group F: American plants, mostly with welldefined Ros, hairy or glabrous; Inf lateral or rarely terminal; Fl mostly 5-merous: Echeveria, Graptopetalum, Lenophyllum, Pachyphytum, Thompsonella, Villadia.


## Key to the genera:

1 Fl with St as many as Pet (haplostemonous): 2

- Fl with St $2 \times$ as many as Pet (obdiplostemonous): 8

2 Fl often (2- to) 4-merous or more rarely 10- to 12-merous (predominantly in Africa; extra-African taxa dwarf minute ephemeral herbs with 2- to 4-merous Fl):

- Fl usually 5-merous (outside Africa): 4 3

3 Perennial herbs with underground tuber or tuberous rhizome; stems deciduous; $\mathbf{L}$ ternate; $\mathbf{F l}$ 10- to 12-merous; Ca 2 -seeded, follicles opening transversally (Ethiopia): Hypagophytum

- Not as above; Ca with > $2 \mathbf{S e}$, follicles opening apically:

Crassula
4 Plants with persistent or monocarpic, dense to lax Ros:

- Plants annual or perennial herbs without obvious Ros:

7
5 Monocarpic Ros-forming herbs (Europe and Asia):

- Perennial shrublets with lax Ros at the stem tips (Mexico): Graptopetalum pentandrum
6 Inf flat-topped (corymbose): Sinocrassula
- Inf thyrsoid-elongate: Orostachys p.p.

7 Annual to perennial herbs; Fr many-seeded follicles opening along the ventral side (Europe and Asia):

Sedum p.p. (e.g. S. rubens)

- Annual minute ephemeral herbs; Fr indehiscent and nutlet-like, each follicle with a single seed (USA: California):

Sedella p.p.
8 Perennial plants, stems perennating but with annually deciduous $\mathbf{L}$, or stems annually deciduous:

- Annual (to biennial) plants, or perennial plants with at least some perennating $\mathbf{L}$ :

14
9 Stems obviously succulent, perennating; L crowded at branch tips (S and SW Africa):

Tylecodon

- Stems not succulent and regularly deciduous and plants perennating with underground root stocks or small caudex (mostly outside of Africa):

10
10 L usually distinctly peltate; Inf terminal racemes or panicles (Asia and E Africa):

Umbilicus p.p.

- L flat, never peltate; Inf usually cymes or corymbs, $\pm$ flat- topped (outside of Africa): 11
11 Plants with tuberous caudex and annually deciduous stems; L alternate; Fl 4- to 6-merous, often unisexual (plants monoecious or dioecious):

Rhodiola

- Plants with or without thickened roots but never with a caudex; $\mathbf{L}$ opposite, alternate or rarely verticillate; Fl various but plants never dioecious:

12
12 L flat:
13

- $\mathbf{L}$ terete-subulate: Villadia p.p.
$13 \mathbf{R}$ thickened, fusiform, and stems annually deciduous; or $\mathbf{R}$ fibrous and stems perennial, woody, forming dwarf shrublets:

Hylotelephium

- $\mathbf{R}$ fibrous; stems annually deciduous: Phedimus

14 Plants with perennial monocarpic Ros: 15

- Plants annual (to biennial), or perennial but then not with monocarpic Ros:21

15 NSc conspicuous, broader and more obvious than the insignificant Pet (Canary and Selvagen Islands): Monanthes p.p.

- NSc inconspicuous, much narrower than the showy Pet:

16
16 Fl 5- (to rarely 6-) merous; Inf corymbose to much elongated and spike-like:

17

- Fl 6- to 32-merous; Inf corymbose to domeshaped, never much elongated: 20
17 Inf flat-topped, corymbose or cymose, fewflowered:

18

- Inf elongate, many-flowered: 19

18 Pet 2.5-4 mm, ascending, white (E Asia):
Meterostachys

- Pet $>4 \mathrm{~mm}$, ascending to spreading, whitish, yellowish, red or pink (E Mediterranean, W Asia):

Prometheum
$\mathbf{1 9} \mathbf{~ B r}$ of the Inf helicoid (Turkey, Iraq, Turkmenistan): Rosularia elymaitica

- Br of the Inf never helicoid (C to E Asia):

Orostachys p.p.
20 Ros sessile, usually $<10 \mathrm{~cm} \varnothing$; Fl 6- to 18-merous, often in shades of pink and purple, rarely white or yellow:

Sempervivum

- Ros sessile or often with a conspicuous and sometimes branched stem, often > $10 \mathrm{~cm} \varnothing$; $\mathbf{F l}$ (6- to) 10- to 32-merous, often in shades of yellow but also whitish, more rarely reddish:

Aeonium
$21 \mathbf{L}$ decussate throughout the whole length of the stems: 23

- $\mathbf{L}$ verticillate or alternate at least in the upper stem parts, or in Ros:

22
22 L verticillate (Africa):
Sedum p.p. (e.g. S. epidendrum)

- $\mathbf{L}$ alternate at least in the upper stem parts, or in Ros:

30
23 Annual to biennial glabrous to glandular-hairy herbs to $15 \mathrm{~cm} ; \mathbf{F l}$ (4- to) 5-merous, white, pink or purplish; Pet 4-5 mm (Mediterranean): $\mathbf{2 4}$

- Perennial herbs (sometimes monocarpic), or shrubs or small trees, or lianas; Fl 4- to 6-merous; Pet $>5 \mathrm{~mm}$, in various colours:

25
24 Annual glabrous herbs; Inf to 5 cm tall:
Phedimus stellatus

- Annual to biennial glandular-hairy herbs; Inf to 60 cm tall: $\quad$ Sedum p.p. (e.g. S. сераеа)
25 Fl 4-merous; herbs (sometimes monocarpic) to shrubs or small trees, or lianas (Africa, Madagascar, Asia, neophytes world-wide):Kalanchoe
- Fl 5- or 6-merous; shrublets or herbs: 26

26 Fl 5-merous, not white (Africa, Caucasus, N America):

28

- Fl (5- to) 6-merous, erect, white: 27

27 Shrublets to 80 cm tall (Madagascar):
Perrierosedum

- Dwarf herbs to 10 cm tall (Europe and N Afri$\mathrm{ca}): \quad$ Sedum p.p. (e.g. S. dasyphyllum)

28 Herbs with creeping stems; $\mathbf{L}$ flat and rather thin-textured; Inf arching; Fl yellow, narrowly urceolate (Caucasus): Umbilicus oppositifolius

- Not with this combination of characters: 29

29 Plants shrubby, often > 50 cm tall; $\mathbf{L}$ not easily detached; Fl conspicuous, campanulate, 2-3 cm long, Pet basally connate, in various shades of orange to red or rarely yellowish (Africa, Arabia):

Cotyledon

- Herbs, 10 - $30(-50) \mathrm{cm}$ tall; $\mathbf{L}$ often easily detached; Fl small, to 1 cm long, yellow or yellowish; Pet free to the base (USA, Mexico):

Lenophyllum
30 Perennial plants with sessile Ros, or shrubby with lax Ros at the stem tips or $\mathbf{L}$ scattered along the length of the stems, or stems short with short internodes and few crowded $\mathbf{L}$ : 31

- Annual (to biennial) plants, or perennial plants, neither with conspicuous Ros nor shrubby: 46
31 NSc conspicuous and more obvious than the insignificant Pet:
- NSc inconspicuous, much smaller than the showy Pet:
32 Fl (5- to) 6- to 9-merous (Canary Islands):
Monanthes p.p.
- Fl 5-merous (Mexico): Sedum longipes

33 Plants shrubby; $\mathbf{L}$ scattered along the length of the stems, never forming well-defined Ros (Americas): 34

- Plants not shrubby, of if shrubby then stems with terminal Ros:
34 Stems slender to wiry and not distinctly succulent:

Villadia p.p.

- Stems distinctly succulent, with $\pm$ flaking papery bark: $\quad$ Sedum p.p. (e.g.S. frutescens)
35 Ros ill-defined, i.e. $L$ crowded and stems with very short inconspicuous Int; Inf terminal spike-like thyrses; Fl 5-merous; Sep very short; Cl tubular (Africa):

Adromischus

- Ros $\pm$ well-defined; Inf lateral; Fl 5-merous (rarely 4- or 6- to 10-merous); Sep usually conspicuous; Cl tubular or stellate: 36
36 Ros to $5 \mathrm{~cm} \varnothing$; $\mathbf{F l}$ white or pale yellowish/reddish (Europe, W and E Asia): 37
- Ros usually > $5 \mathrm{~cm} \varnothing$ ):

37 Fl white (Europe, E Asia):
Meterostachys + Sedum p.p.

- Fl white or pale yellow/reddish (W Asia, E Mediterranean):

Prometheum p.p.
38 Dwarf shrublets with glandular-hairy $\mathbf{L}$ in terminal Ros; Fl yellow, 7- to 8-merous (Canary Islands):

Aichryson p.p.

- Not with this combination of characters: 39

39 Ros stemless, offsetting with brittle runners; $\mathbf{L}$ margins conspicuously ciliate; Fl 5- to 7merous, white tinged reddish (Ethiopia):

Afrovivella

- Not with this combination of characters: 40

40 Ros stemless; Fl 5- to 9 -merous, $\pm$ cup-shaped to $\pm$ urceolate to saucer-shaped, white, whitish, pinkish or pink but never in bright colours, never long-tubular, not very fleshy: 41

- Not with this combination of characters (America):

42
41 Fl 5-merous, white; Pet basally free or almost so (Mexico): $\quad$ Sedum p.p. (S. suaveolens)

- Fl 5- to 9-merous, white to pinkish or pink, Pet basally united (E Mediterranean, Asia Minor to E Asia):

Rosularia p.p.
42 Glabrous shrublets with thickish stems; $\mathbf{L}$ mostly very thick; Inf scape basally $\pm$ L-less, usually unbranched; fertile Bra large, overlapping and $\pm$ hiding the Fl; Fl 5- to 6-merous; Pet with a basal scale on each margin (Mexico):

## Pachyphytum

- Not with this combination of characters; Bra never hiding the $\mathbf{F l}$ :

43
43 Pet free to the base or slightly connate; Fl (4to) 5- (to 10-) merous, long petiolate; Pet usually pale cream with red cross-bands or blotches, or bright pink, stellately spreading (S USA, Mexico): Graptopetalum

- Pet slightly to distinctly connate; Fl 5-merous, coloration not as above: 44
44 Plants never shrubby but old Ros sometimes with short thick stems, sometimes branching dichotomously; Bra semi-amplexicaul, never spurred, not easily detached; Pet hardly to distinctly united, tubular to stellately spreading (W USA and Baja California):

Dudleya

- Plants shrubby or with sessile solitary or offsetting Ros, never dichotomously branching; Bra not semi-amplexicaul, spurred or not: $\mathbf{4 5}$
45 Inf narrow thyrses or spicate, erect, with 10-70 1- to 12-flowered cincinni; Sep subequal in size; Pet shortly connate, thin-textured, upper $1 / 2$ stellately spreading (Mexico): Thompsonella
- Inf racemose, cymose-paniculate or rarely spicate; Sep often strongly unequal in size; Pet basally distinctly connate, usually distinctly fleshy, often bright pink to red (S USA to Argentina):

Echeveria
46 (from 30) Minute annual herbs; Fl 6- to 7-merous, dirty white; NSc conspicuously broader than the small Pet (Canary Islands):

Monanthes icterica

- Annual to perennial herbs; Fl 5- to 12-merous; NSc inconspicuous and never broader than the Pet:

47
47 Annual herbs; Fl 5- to 12-merous: 48

- Annual or perenial herbs; Fl 5- to 6-merous; Pet free to distinctly united, in various colours: $\mathbf{5 0}$
48 Fl 6- to 12-merous; Pet completely free, yellow (Canary Islands):

Aichryson p.p.

- Fl 5- to 9-merous; Pet hardly to distinctly connate, not yellow:

49



Sedum compressum

c Sedum craigii

e Sedum cymatopetalum

g Sedum hirsutum ssp. hirsutum

b Sedum corynephyllum

d Sedum cupressoides

f Sedum dasyphyllum var. dasyphyllum

h Sedum jaccardianum

