

DIVERSITY WITHIN MEDITERRANEAN CRASSULACEAE

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Abstract

The cosmopolitan Crassulaceae comprises about 177 species in the Mediterranean region which, with respect to species richness, is the third centre of diversity within the family. Except for *Hylotelephium telephium* and *Rhodiola rosea*, the Mediterranean Crassulaceae are endemic to the region or Eurasia. The Crassulaceae originated in Africa, but attained its greatest diversity in tribus Sedae after arrival on the Northern Hemisphere. Most successful is subtribus Sedinae which comprises the large, polyphyletic genus *Sedum* and its derivatives. Subtribus Sedinae comprises two lineages, the *Acre*-lineage and *Leucosedum*-lineage, which differ in morphological and molecular characters, but have similar distribution patterns. In Eurasia the *Leucosedum*-lineage was the most successful, comprising about 75% of all Mediterranean species of Crassulaceae. In addition to some 69 *Sedum* species it gave rise to the segregate genera *Aeonium*, *Aichryson*, *Monanthes*, *Prometheum*, *Rosularia*, *Pistorinia*, and *Sempervivum* (*Jovibarba*). Although the centres of speciation of these segregate genera as well as the infrageneric taxa of *Sedum* are located in different parts of the Mediterranean region there is a distinct parallelism in several evolutionary trends within these taxa, e.g. development of the rosulate habit, the polymerous and/or sympetalous flower, and the glandular and often fragrant indumentum.

Introduction

The Crassulaceae is a medium-sized family of leaf succulents with 1300-1500 species and with an almost cosmopolitan distribution. Crassulaceae occur predominantly in the temperate and subtropical zones of the northern hemisphere and Africa where they are most frequent in (semi-)arid and rocky (mountainous) habitats, often at high altitudes. Although most species are outstandingly adapted to withstand drought and survive in habitats with a variable water supply through a series of morphological (succulence) and physiological specializations (crassulacean acid metabolism), the family is notably absent from the true deserts. The Crassulaceae comprises four conspicuous centres of diversity, i.e. Mexico and the south-western US with some 300 species, Southern Africa with some 250 species, the Mediterranean region and Macaronesia with more than 200 species, and south-eastern Asia with about 200 species.

In the Mediterranean region Crassulaceae is represented with some 177 species in 12 genera (Greuter & al., 1986). In Table 1 the genera and species are arranged according to the infrafamilial classification designed by Berger (1930). According to this arrangement Mediterranean Crassulaceae comprises five out of six subfamilies, except for the strictly American Echeverioideae. At the genus level the large, northern hemisphere, hold-all taxon *Sedum* dominates with 66% of the species. Following the delimitation of the Mediterranean region proposed in Med-checklist none of Berger's subfamilies and only the small genera, *Mucizonia*, *Pistorinia*, and *Telmisa*, are endemic

Subfamilies ¹⁾	Genera ²⁾	Species ²⁾
Crassuloideae	<i>Crassula</i> L.	3
Kalanchoideae	<i>Kalanchoe</i> Adan.	1
Cotyledoideae	<i>Mucizonia</i> (DC.) Batt. & Trabut	2
	<i>Pistorinia</i> DC.	4
	<i>Umbilicus</i> DC.	12
Sempervivoideae	<i>Aeonium</i> Webb & Berth.	1
	<i>Jovibarba</i> (DC.) Opiz	4
	<i>Sempervivum</i> L.	33
Sedoideae	<i>Rhodiola</i> L.	1
	<i>Rosularia</i> (DC.) Stapf	18
	<i>Sedum</i> L.	97
	<i>Telmisssa</i> Fenzl	1
5	12	177

Table 1. Subfamilies, genera, and number of species of Crassulaceae in the Mediterranean region. 1) BERGER (1930); 2) GREUTER & al. (1986).

to the region, but at the species level the amount of endemism is very high (about 60%). Only two species, i.e. *Hylotelephium telephium* (= *Sedum telephium*) and *Rhodiola rosea*, are not restricted to Mediterranean centre of diversity which also encompasses Macaronesia and the most of Eurasia (Europe, North Africa, and the Near East).

Evolution and infrafamilial classification of the Crassulaceae

The 6 subfamilies of BERGER'S (1930) classification of the Crassulaceae are primarily taxonomic units and defy evolutionary interpretation, except for the suggestion of a sudden appearance of the whole family including all higher taxa in their fullest complexity (at the infrafamilial and generic levels). In contrast, the infrafamilial classification of the Crassulaceae which is summarized in Table 2 ('T HART, 1995) shows a gradual evolution of the major taxa and also gives a logical explanation of distribution patterns of the higher taxonomic categories. This classification is based on morphology in combination with the results of a phylogenetic analyses of chloroplast DNA variation (VAN HAM, 1994; 'T HART 1995). It is strongly supported by embryological (MAURITZON, 1933), pollen morphological (HIDEUX, 1981), micromorphological ('T HART & BERENDSEN, 1980; KNAPP, 1994), and phytochemical characters (STEVENS, 1995a,b; STEVENS & al., 1995).

Most probably the Crassulaceae originated in Africa, as the two most basal branches of the phylogeny contain the predominantly southern African taxa (VAN HAM, 1994; 'T HART, 1995). The basal split in the Crassulaceae is between subfamily Crassuloideae and the rest of the family, which is united in the subfamily Sedoideae, and separates

Taxon	Species	Genera	Origin
subfamily Crassuloideae	c.250	2	S Africa
subfamily Sedoideae			
tribus Kalanchoeae	c.250	5	S Africa
tribus Sedeae			
subtribus Telephiinae	c.150	8	Asia
subtribus Sedinae	c.700	18	N Hemisphere

Table 2. Numbers of species and genera, and distribution of the infrafamilial taxa of the Crassulaceae (after 'T HART, 1995).

the haplostemonous taxa with opposite leaves from taxa which never have this unique combination of characters. Subfamily Sedoideae is divided into two tribes, the African Kalanchoeae and the Sedeae which is confined to the Northern hemisphere. Tribus Kalanchoeae comprises BERGER'S (1930) subfamily Kalanchoideae and the southern African members of Berger's subfamily Cotyledonoideae and are characterized by the unique combination of 4- or 5-merous flowers with connate petals, costate seeds, and usually flat, crenate or dentate, often petiolate and decussate leaves.

After arrival on the northern hemisphere Crassulaceae attained its greatest diversity in tribus Sedae. Tribus Sedae is divided into two subtribes, the predominantly Asian Telephiinae and the Sedinae which occur on all three (sub)continents of the Northern hemisphere. A link with the African Kalanchoeae can still be observed in the basal branch of the Sedae, subtribus Telephiinae, of which many species also have flat and often crenate or dentate leaves. Subtribus Telephiinae is further characterized by predominantly 5-merous, obdiplostemonous flowers with free petals. The occurrence of tubers, tuberous roots, or woody or thickened rhizomes (monopodial or sympodial) are also very characteristic for this group. Many taxa of subtribus Telephiinae have previously been attributed to *Sedum*, either as subgenus, section, or series (OHBA, 1978) and they have collectively also been referred to as the "flat-leaved, Asian sedums" ('T HART, 1984, 1991).

Subtribus Sedinae comprises about one half of the species and genera of the Crassulaceae. It contains the very large genus *Sedum* s.s. which appears to be strongly paraphyletic (VAN HAM, 1994; 'T HART, 1995) and gave rise to several genera which in BERGER'S (1930) classification belong to the subfamilies Echeverioideae, Sempervivoideae, and Cotyledonoideae as well as Sedoideae. VAN HAM (1994) distinguished four clades within the well-defined lineage comprising subtribus Sedinae, the *Acre*-, *Aeonium*-, *Leucosedum*-, and *Sempervivum*-clade. Molecular support for the *Acre*-clade is very strong and monophyly of this clade is further indicated by several phytochemical as well as morphological characters such as the unique occurrence of alkaloids (STEVENS, 1995a & b; STEVENS & al., 1995), the reticulate testa ('T HART & BERENDSEN, 1980; KNAPP, 1994), and absence of glandular trichomes (JENSEN, 1966; 'T HART, 1991). The other three clades are less distinct and may even be combined in a monophyletic lineage, the *Leucosedum*-clade, as sistergroup to the *Acre*-clade (VAN HAM, 1994).

To distinguish between the two lineages within paraphyletic *Sedum* the genus has been divided into two subgenera ('T HART, 1995). *Sedum* species belonging to the *Acre*-clade are classified in *Sedum* subgenus *Sedum* and the species belonging to the *Leucosedum*-clade (including the *Aeonium*- and *Sempervivum*-clades) are provisionally united in *Sedum* subgenus *Gormaniana* (Table 3). The two subgenera, however, are still paraphyletic as they both contributed to the evolution of segregate genera within subtribus Sedinae ('T HART, 1982, 1995; VAN HAM 1994). Both subgenera occur on all three continents of the northern hemisphere, but they differ distinctly with respect to their respective centres of diversity. The *Acre*-clade (*S.* subgenus *Sedum*) is most diverse in Mexico and, in addition to *Sedum*, gave rise to *Echeveria*, *Graptopetalum*, *Pachyphytum*, and *Villadia*. The combined *Leucosedum*-clade (*S.* subgenus *Gormaniana*), on the other hand, has its major centre of diversity in Eurasia and a secondary centre in Northern America. In addition to *Sedum* it comprises Eurasian genera like *Aeonium*, *Aichryson*, *Monanthes*, and *Sempervivum* as well as the American genus *Dudleya*.

Infrafamilial Taxa ¹⁾	Genera ¹⁾	Species ²⁾
Crassuloideae	<i>Tillaea</i> L.	3
Sedoideae		
tribus Kalanchoae	<i>Kalanchoe</i> Adan.	1
tribus Sedae		
subtribus Telephiinae	<i>Hylotelephium</i> H. Ohba	2
	<i>Rhodiola</i> L.	1
	<i>Phedimus</i> Rafin.	
	subgen. <i>Phedimus</i>	4
	<i>Umbilicus</i> DC.	12
subtribus Sedinae		
<i>Acre</i> -clade	<i>Sedum</i> L.	
	subgen. <i>Sedum</i>	22
<i>Leucosedum</i> -clade	<i>Sedum</i> L.	
	subgen. <i>Gormaniana</i> Clausen (= <i>Mucizonia</i> , = <i>Telmisa</i>)	69
	<i>Aeonium</i> Webb & Berth.	1
	<i>Jovibarba</i> (DC.) Opiz	4
	<i>Prometheum</i> (Berger) H. Ohba	7
	<i>Rosularia</i> (DC.) Stapf	14
	<i>Pistorinia</i> DC.	4
	<i>Sempervivum</i> L.	33
	13	177

Table 3. Infrafamilial taxa, genera, and number of species of Crassulaceae in the Mediterranean region. 1) 'T HART (1995); 2) GREUTER & al. (1986).

Systematics and distribution of the Mediterranean Crassulaceae

About 87% of the Mediterranean Crassulaceae species belong to subtribus Sedinae (Table 3). The other species either belong to the semi-aquatic, cosmopolitan *Tillaea*, or are widely distributed representatives of taxa otherwise restricted to southern Africa, e.g. *Kalanchoe laciniata*, or Asia, e.g. *Hylotelephium telephium* (= *Sedum telephium*), and *Rhodiola rosea*, except for the endemics *Hylotelephium anacampseros* (= *Sedum anacampseros*), *Phedimus* subgenus *Phedimus*, and *Umbilicus*. Furthermore, except for *Tillaea* and *Umbilicus*, these taxa have only a limited distribution in the Mediterranean region (Greuter & al., 1986).

The *Acre*-lineage of subtribus Sedinae is represented with 22 *Sedum* species in the Mediterranean region. In contrast to the exuberant evolution of this taxon in Mexico, where diversification resulted in a species complex (comparium) with over 200 species (Uhl, 1992) it plays only a minor role in Crassulaceae diversity in the Mediterranean region and Eurasia. In Eurasia the *Acre*-lineage contains only small or monotypic groups (comparia or series), except for the relatively young *Sedum* series *Alpestris* which comprises 13 species ('T HART, 1991).

Crassulaceae diversity in the Mediterranean region is mainly due to extensive speciation and differentiation of the *Leucosedum*-lineage of subtribus Sedinae which comprises about 75% of all Mediterranean Crassulaceae species. In addition to some 69 *Sedum* species (GREUTER & al., 1986), which are classified in 25 or more series (comparia) of *S.* subgenus *Gormanina*, the *Leucosedum*-lineage gave rise to at least 7 segregate genera, i.e. *Aeonium*, *Aichryson*, *Monanthes*, *Prometheum*, *Rosularia*, *Pistorinia*, and *Sempervivum* (*Jovibarba*) which in all comprises about another 120 species.

Centres of speciation of the infrageneric taxa of *Sedum* and of the segregate genera are apparently randomly distributed over the Mediterranean region, though much of the variation is concentrated in three regions ('T HART, 1991, 1994) which apparently acted as primary centres of diversity of the present flora. These centres are located in the Ibero-Moroccan, the Aegean, and the Irano-Turanian region. Secondary centres of diversity are the Western Alps and Northern Africa (Cyrenaica and Tunisia). From these centres of diversity the species spread freely in all directions, though a majority of the migration routes appears to be East-West orientated ('T HART, 1994). Some taxa spread successfully over most of the Mediterranean region. Successful distribution is primarily related to life-form, the annual species are more widely distributed, though it is tempting to assume that old groups have spread further than young ones. Local, regional and single country endemics are either neo-endemics or paleo-endemics. Whereas neo-endemics may be recognizable by high basic chromosome numbers, either through dysploidy or (allo)polyploidy, e.g. *Sedum alsinefolium* ($x=13$) from the Western Alps and *S. multiceps* ($x=29$) and *S. tuberosum* ($x=23$) from Northern Africa, paleo-endemics such as *Prometheum tymphaeum* ($x=7$) and *Sedum creticum* ($x=11$) show a tendency toward cytological conservatism as the other species of *Prometheum* and *Sedum* series *Cepaea* have $x=7$ and $x=11$, respectively.

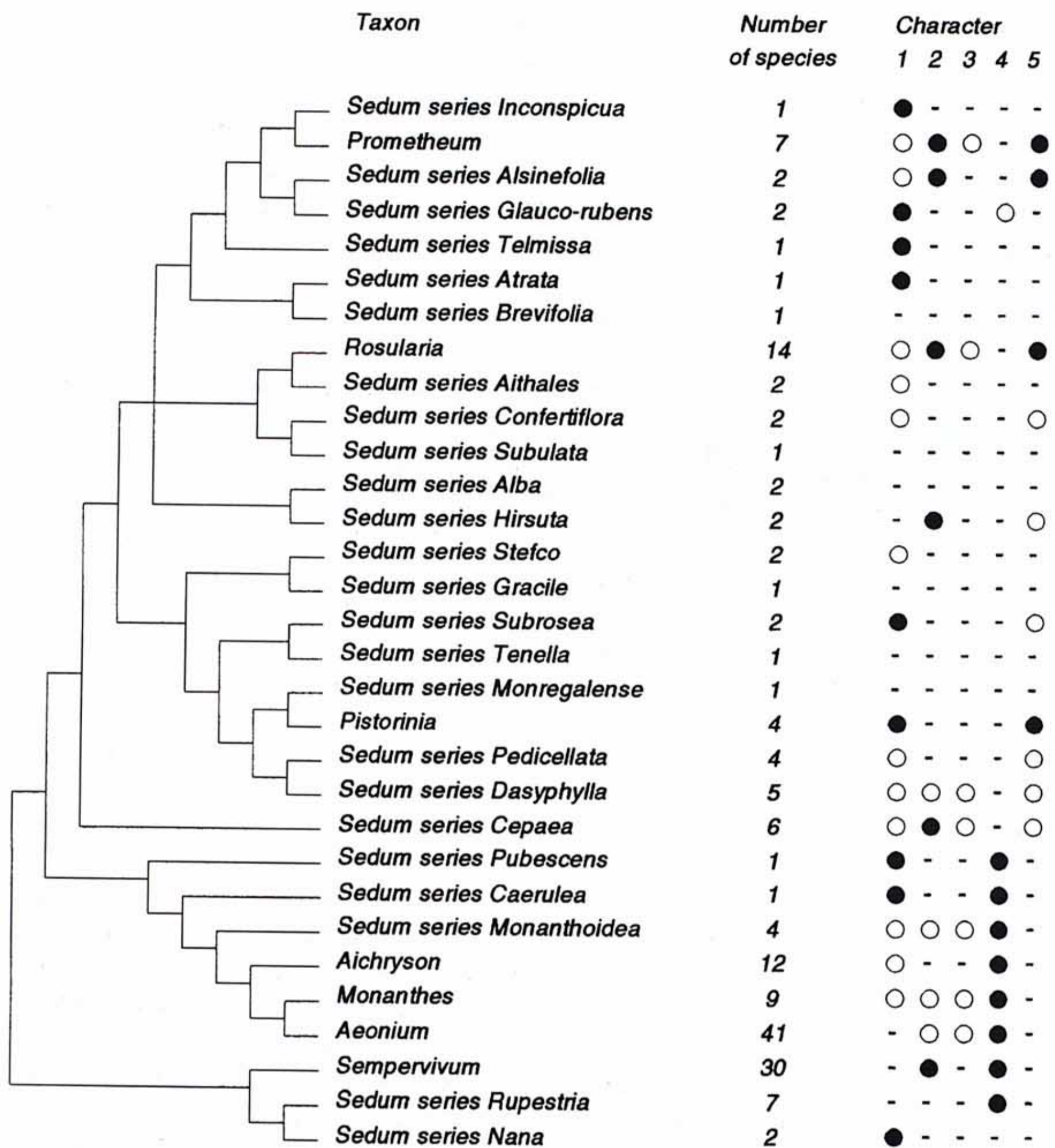


Fig. 1. Distribution of 5 morphological features characteristic for Mediterranean Sedinae of the *Leucosedum*-lineage plotted against the summarized phylogeny based on chloroplast DNA restriction site analysis of this taxon (VAN HAM, 1994). The characters are numbered: 1 annual habit; 2 rosettes; 3 monopodial stem; 4 polymeric flowers; 5 sympetalous. ● indicates presence of the character in all species; ○ presence of the character in some species; - absence of the character.

Evolutionary patterns in Mediterranean Crassulaceae

Although the Mediterranean species of the combined *Leucosedum*-lineage of subtribus Sedinae evolved from three or more different centres of diversity there is a series of morphological adaptations which is unique for this group and this region. The

glandular idumentum is characteristic for the whole *Leucosedum*-lineage, but this feature is evidently most prominent in Mediterranean taxa. Furthermore, to my knowledge, distinctly fragrant Crassulaceae plants occur only in the Mediterranean region. The leaves of *S. alsinefolium* and *S. fragrans* have a pleasant flowery smell ('T HART, 1983) and so do the leaves of *S. jaccardianum* (and *Aeonium balsamiferum*). The densely glandular pubescent inflorescences and upper cauline leaves of several taxa have a distinctly resinous smell, for example species of *Rosularia* (EGGLI, 1988), *Prometheum*, *Sedum* series *Aithales*, *S.* series *Cepaea*, *S.* series *Dasyphylla*, *S.* series *Glaucorubens*, and *S.* series *Hirsuta*. The inflorescences and flowers *S. caeruleum* emit a cocoa-like scent.

In figure 1 the distribution of 5 morphological features, which are characteristic for Mediterranean Sedinae of the *Leucosedum*-lineage, is plotted against the summarized phylogeny of these genera and infrageneric taxa based on chloroplast DNA restriction site analysis (VAN HAM, 1994). The distribution of the character states of these features over the tree indicates the multiple origin of each character within this lineage. The annual, rosulate, and monopodial habit evolved independently in widely different groups and the origin of these traits is not correlated with the three main centres of diversity of Mediterranean Crassulaceae. The same holds true for floral characters such as the number of floral parts and sympetaly which are widely scattered over the genera and infrageneric taxa.

Conclusions

Diversity within Mediterranean Crassulaceae is mainly due to extensive speciation and differentiation within the *Leucosedum*-lineage of subtribus Sedinae which comprises about 75% of all Mediterranean species. In the Mediterranean region and the adjacent Macaronesian archipelago the *Leucosedum*-lineage gave rise to some 69 *Sedum* species and more than half of the Crassulaceae genera of the region. Parallel and convergent evolution led to a high incidence of homoplasy among genera and infrageneric *Sedum* taxa throughout the whole region and irrespective to the origin of the group. Although this homoplasy complicates classification considerably the recurrence of these unique, though homoplasious, morphological features renders the Mediterranean Crassulaceae flora its distinctive character.

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