Floral morphology, micro-morphology and palinology of selected *Sedum s.l.* species (Crassulaceae)

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Abstract

Sedum L. (Crassulaceae) is a large and taxonomically difficult genus whose delimitation and classification are under debate. Due to the controversial results of previous cytological, morphological, and molecular studies, further investigations are needed in order to gain a shared taxonomy of the current recognized species clades.

In the present paper, morphological and micro-morphological features of 23 selected Mediterranean species of *Sedum s.l.* - collected from *exsiccata* or fresh specimens throughout Italy - were investigated, in order to provide additional data toward their classification above species level. In particular, the study focused on flower structure and morphology, floral epidermal surfaces and pollen morphology.

The distribution pattern of the examined micro-characters across the species revealed a wide range of variation and different combinations of the single characters. NMDS analysis allowed individuating discrete groups that showed a general consistency with the current systematic delimitation of species groups.

Our study also evidenced for the first time the wide morphological variability of nectaries and of the glandular *indumentum*, not previously investigated in detail. In addition, we proposed the combined use of floral diagrams and floral formulae as valuable tools in studying the variability of flower structure at genus level.

Keywords: *Sedum, Hylotelephium, Phedimus*, systematics, Mediterranean, floral diagrams, floral formulae, scanning electron microscope.

1. Introduction

Sedum L. (subfamily Sempervivoideae) is the largest genus in the Crassulaceae family, with a worldwide distribution; in Europe it predominantly occurs in the Mediterranean region (Webb, 1964; Webb et al., 1993; Thiede and Eggli, 2007). Its generic delimitation has long been debated (Mort et al., 2001, 2010). On the basis of anatomical, morphological and cytological characters, several authors (Praeger, 1921; Fröderström, 1930, 1931, 1932, 1936; Clausen, 1975; 't Hart, 1982) retained *Sedum* as a hold-all taxon with only a few additional genera within the subfamily, whereas others (Borissova, 1969; Ohba, 1977, 1978; Grulich, 1984) segregated *Sedum* into controversial genera (Van Ham and 't Hart, 1998; Mort et al., 2001), among which only the Eastern Asian *Hylotelephium* Ohba*, Phedimus* Rafin., *Rhodiola* L.*,* and *Umbilicus* DC. received wide formal taxonomic recognition (Mauyzumi and Ohba, 2004).

Molecular investigations in the subfamily Sempervivoideae (Van Ham, 1995; 't Hart, 1995; Van Ham and 't Hart, 1998; Mort et al., 2001; Mayuzumi and Ohba, 2004; Gontcharova et al., 2006; Carrillo-Reyes et al., 2009) supported the institution of six major clades (Thiede and Eggli, 2007): *Hyloelephium, Rodhiola, Acre, Aeonium, Leucosedum*, and *Sempervivum*, the last four including *Sedum s.s*., with *Acre* and *Leucosedum* being the bulk of the genus. Because the molecular data at this lower level is unreliable, the monophyly inside the clades is only supported by morphological and phytochemical characters ('t Hart, 1991; Stevens et al., 1994, 1996),.

Inside *Sedum s.l.*, habit, life-form, leaf arrangement and floral morphology are considered valuable features, even if affected by extensive homoplasy (Mort et al., 2001). For the European species, 't Hart and Koek-Normann (1989) and 't Hart (1991) attributed systematic value to micro-morphological characters such as testa ornamentation, shape of the micropylar region, presence/absence of glandular trichomes. Based on these characters and on extensive hybridization programs, 't Hart (1991) classified the European *Sedum* species in 27 series (*sensu* Berger, 1930), corresponding to a "*comparium*" *sensu* Danser (1929).

Literature considers *Sedum* highly paraphyletic ('t Hart, 1995; Van Ham and 't Hart 1998; Mort et al. 2001; Carrillo-Reyes et al., 2009; Gontcharova and Gontcharova, 2009; Mort et al. 2010), recognizing two distinct subgenera: *Gormania,* including *Aeonium, Sempervivum*, and *Leucosedum* clades, and *Sedum*, corresponding to the *Acre* clade *pro parte*. Thiede and Eggli (2007) assigned these clades at the tribal rank.

In the Mediterranean region, *Sedum* diversity is mainly due to the extensive differentiation of *Leucosedum* clade ('t Hart, 1991; 't Hart, 1997). *Acre* clade contains small or monothypic groups, except for *Sedum* series *Alpestria* Berger (1930). The *Sempervivum* clade is represented by *Sedum* series *Rupestria* Berger (1930), a natural and well-delimited Euro-Mediterranean taxon, raised to the genus level (*Petrosedum*) by Grulich (1984), and not yet recognised formally. The other clades include genera which are well represented in Asia: *Hylotelephium* (except for the endemic *H. anacampseros*) for the *Hylotelephium* clade, and *Phedimus, Rodhiola* (except for the endemic *R. rosea*)*,* and *Umbelicus* for the *Rodhiola* clade.

Considering the controversial results of the different analyses, further investigations are necessary in order to gain a shared taxonomy of the group, especially with reference to the European *Sedum* species (Carrillo-Reyes et al, 2009).

In the present paper, morphological and micro-morphological features of selected Mediterranean species of *Sedum s.l.* are investigated (Table 1; Fig. 1) to provide additional data toward their systematic delimitation

above species level. In particular, the study focuses on the floral structure, and epidermal and pollen micro-morphology. The consistency of the new data with the current systematic delimitation of species groups has been taken into consideration.

2. Materials and methods

Sedum s.l. species with wide Mediterranean distribution (Table 1) were selected, based on their availability and distribution in Italy, in order to examine the following: flower structure and morphology; floral epidermal surfaces; pollen morphology.

Plant sampling. A total of 56 specimens referred to 23 taxa were investigated; they were collected at the blooming period in the wild, or sampled from *exsiccata* stored in the Herbarium Centrale Italicum of Florence (S1). Identification followed Pignatti (1982) and Webb et al. (1993); nomenclature is after Euro+Med (2006-), with the exception of the genus *Hylotelephium* (Conti et al. 2005).

Flower structure. Observations were performed on a minimum of ten flowers per species, operating under a dissecting microscope. The flower structure was described by the combined use of floral diagrams and floral formulae (de Craene 2010), with slight modifications. The general morphology of nectaries was also described.

Flower epidermal micromorphology. Fully-open mature flower elements (floral pedicel, sepals, petals, androecium, gynoecium and seeds) were observed, with special focus on the presence/absence of a glandular *indumentum* and on the epidermal cell types of the abaxial and adaxial surfaces of sepals and petals. Samples from *exsiccata* were also examined to confirm the observations on fresh specimens. For SEM investigation, fresh samples were fixed in FAA, dehydrated with acetone, critical point dried and gold-coated.

The distribution of the epidermal patterns of sepals and petals was recorded following three axes: abaxial-adaxial axis, proximo-distal axis and medio-lateral axis. Epidermis was classified based on cell-shape traits (the primary sculpture) and on the fine relief of the cell wall (or secondary sculpture, see Barthlott, 1990); terminology is according to Kay et al. (1981). Terminology of seed coat anatomy and sculpturing were after ‘t Hart and Berendsen (1980).

Pollen morphology. For LM analysis, pollen grains were acetolyzed (Erdtman, 1969) and stored in a 50% water/glycerol solution v/v. For SEM analysis, acetolyzed pollen grains were washed in acetone, dried and gold-coated. LM measurements were taken from at least 30 pollen grains per sample: a) length of polar axis (P) and equatorial axis (E) and their ratio (P/E); b) length of colpi; c) width of colpi; d) length of mesocolpia; e) length of the side of the polar triangle; f) wall thickness in the middle of the mesocolpium. Terminology is after Punt et al. (2007).

Data analysis. Statistical data processing was performed on 70 different floral characters, among which the features traditionally used in the taxonomic treatment of *Sedum s.l.* (S2). Non Metric Multidimensional Scaling (NMDS) analysis, using the Jaccard Index as measure of similarity, was used to display the distribution of the examined *taxa* in relation to their attribution to five of the clades established by Thiede and Eggli (2007) in a two-dimensional space. All these procedures were performed using PAST 3.0 (Hammer and Harper, 2006).

3. Results

The distribution pattern of the different micro-characters investigated in the examined species are summarized in Table 2.

Flower structure. *Sedum* presents complete flowers provided with small nectaries. Two basic flower types were recognized on the basis of the position of the ovary; several sub-types separated depending on the degree of connation of sepals and petals, the features of androecium and the presence/absence of bracts in the distal part of the inflorescence (Table 2; Fig. 2, a-l):

F1. Hypogynous flower. Flower (6), 5, (4)-merous, sometimes with different number of elements per whorl. The ovary is superior, apocarpic, formed by a variable number of one-loculed carpels with free styles. Three different subgroups were recognized:

F1.1. *Dialysepalous calyx* and *dialypetalous corolla*. Flowers 5-merous, subtended by bracts, white or white-pinkish in color. Androecium obdiplostemonous, composed of 5 outer antepetalous stamens, adnate to the corolla, and 5 inner antesepalous free elements (Fig. 2, a).

F1.2. *Gamosepalous calyx* and *dialypetalous corolla*. Flower (6), 5, (4)-merous. On the basis of the characteristics of the androecium, two subgroups were recognized:

F1.2.1. *Obdiplostemonous androecium with free stamens*. Flowers 6-merous, yellow. Androecium composed of 6 outer free stamens opposite the petal, and 5 longer antesepalous stamens. This pattern occurs in species: **A.** with flower subtended by a bract (Fig. 2, b); **B.** with flowers devoid of bracts (Fig. 2, c).

F1.2.2. *Obdiplostemonous androecium with outer stamens adnate to petals*. Flowers 5-merous, white, white-pinkish, pink or yellow. Androecium composed of 5 outer stamens opposite the petal and adnate to the corolla, and 5 longer antesepalous, free stamens. This pattern occurs in species: **A**. with flowers subtended by bracts (Fig. 2, d) - *S. hispanicum* (Fig. 2, e) displays the same features, but presents esamerous flowers -; **B**. with flowers devoid of bracts (Fig. 2, f); **C.** with flowers devoid of bracts and provided with imbricate petals (Fig. 2, g).

F1.2.3. *Haplostemonous androecium*. Androecium formed by one single whorl of antesepalous free stamens. This pattern occurs in species with corollas white-pinkish in color: **A**. with 5-merous flowers subtended by bracts (Fig. 2, h); **B.** 5-merous flowers without bracts (Fig. 2, i); **C**. 4-merous flowers with bracts (Fig. 2, j).

F1.3. *Gamosepalous calyx* and *gamopetalous corolla*. Flowers 5-merous, white or white-pinkish, without bracts. Androecium obdiplostemonous, composed of 10 stamens adnate to the corolla (Fig. 2, k).

F2. **Perigynous flowers**. Flowers 5-merous, white-pinkish or pink, with gamosepalous calyx and dialypetalous corolla. Androecium obdiplostemonous with 5 antepetalous stamens, adnate to the corolla, and 5 antesepalous elements (Fig. 2, l). The gynoecium is formed by five one-loculated carpels, free for most of their length, close and sunken in the cup-shaped receptacle.

Nectary morphology. The nectaries are basal scale-like appendages opposite the petals, adnate to carpels, highly variable in size, morphology and color. They are generally very small (0.25-0.50 x 0.25-0.50 cm), but larger (0.75-1.00 x 0.80-1.00 cm) in *S. atratum* subsp. *atratum* and *S. hispanicum*. They are colorless (*S.*

alpestre) or white-greenish (*S. album, S. andegavense*) up to yellow (*Sedum* series *Rupestria*) and dark orange (*S. atratum* subsp. *atratum*).

Based on the overall morphology, two main types were distinguished (Table 2; Fig. 3):

- **N1.** stipitate nectaries, further distinguished on the basis of the distal margin features: **N1.1.** entire; **N1.2.** lobate; **N1.3.** toothed.
- **N2.** sessile nectaries, with distal margin: **N2.1.** entire; **N2.2.** lobate; **N2.3.** toothed.

Flower epidermal micromorphology. Two main epidermis types were observed: papillose and tabular. Further subdivisions were based on cell outline and sculpturing of the periclinal walls. Presence/absence of a glandular *indumentum,* trichome distribution and morphology were also considered.

Glandular trichomes. Glandular trichomes occur on the whole floral surface (pedicels, bracts, abaxial surface of sepals and petals, ovary) in *S. cepaea, S. dasyphyllum, S. hispanicum, S. monregalense, S. rubens* and *S. villosum* subsp. *villosum*. Sporadic glandular hairs were observed at least on one floral whorl in *S. ochroleucum, S. rupestre* and *S. sexangulare*. All of the trichomes present stalk and heads formed by biserially arranged cells (Fig. 4).

Five basic types of glandular trichomes were distinguished (Tables 2-3; Fig. 4, a-i):

T1. Sessile, bicellular glands (Fig. 4a).

T2. Short-stalked trichomes with 2-celled thin stalk and four-celled globose head (Fig. 4, b).

T3. Short-stalked trichomes with 2-celled stalk and four-celled clavate head (Fig. 4, c).

T4. Erect trichomes, 30-80 µm long, with a long-stalk (two cells in two rows), two evident neck cells and a nearly globose or club-shaped head of four secretory cells (Fig. 4, d-f).

T5. Suberect, benting trichomes, up to 150 µm long, with a long-stalked (six or eight cells in two rows), two neck cells and a globose or club-shaped head of two-four secretory cells (Fig. 4, g-i).

Flower pedicel. The epidermis consists of longitudinally oblong smooth cells with straight or slightly undulate outline.

Sepals. Three main epidermal types were observed (Table 2; Fig. 5, a-c). No difference occurred between adaxial and abaxial surface.

S1. Isodiametric to slightly oblong smooth cells (50-70 µm) with deeply wavy anticlinal cell walls and scattered stomata (Fig. 5, a).

S2. Oblong smooth cells, roughly rectangular to polygonal (40-50 x 80-100 µm) in outline with linear or faintly wavy anticlinal walls and scattered stomata (Fig. 5, b).

S3. Longitudinally long cells and transversely short cells, smooth and roughly rectangular in outline with undulate anticlinal walls and numerous regularly arranged stomata (Fig. 5, c).

Petals. Three main epidermal types were distinguished on the adaxial side of the medio-proximal region of the petal (Table 2; Fig. 6):

Pad1. Papillose-conical striate cells with striae radiating outwards from the top of the cone (Fig. 6, a).

Pad2. Tabular elongated cells with straight or faintly undulate anticlinal walls and smooth (**Pad2.A**,

Fig. 6, b) or striate surface (**Pad2.B**, Fig. 6, c).

Pad3. Tabular striate cells with deeply undulate anticlinal walls (Fig. 6, d).

The petal abaxial side is characterized by longitudinally oblong cells with deeply undulate anticlinal walls. Three epidermal patterns were distinguished:

Pab1. Striate cells with prominent and regularly-spaced striae (Fig. 6, e).

Pab2. Rugulate cells (Fig. 6, f).

Pab3. Oblong smooth cells with wavy anticlinal walls (Fig. 6, g-h).

Stamens. In all of the examined taxa, a single epidermal type was observed on filaments: cells longitudinally oblong, with straight anticlinal walls (Table 2; Fig. 7, a). The cuticular surface is smooth at the proximal portion, characterized by very faint longitudinal striae at the distal region. The filaments are generally hairless, with the exception of *S. rupestre* and *S. sediforme* which display unicellular papillae on the adaxial side of the base (Fig. 7, b).

The anthers, highly variable in shape (Fig. 7, c-e) from globose (**A1**) and subglobose (**A2**) to oblong (**A3**), exhibit rugose or striate cells with a deeply sinuous profile up to acquiring a jigsaw-puzzle shape in *S. acre* (Fig. 7, f).

Carpels and seeds. Carpel and seed data are according to 't Hart (1991) and summarized in Table 2. These data were integrated with new observations on *H. anacampseros* and *H. maximum* seeds which display a costate testa and an acute apex (Table 2).

Pollen morphology. Pollen grains are prolate-spheroidal to prolate, the first ones prevailing in *Sedum*, the latter in *Hylotelephium* and *Phedimus* (Table 4). The polar axis (P) ranges from 12.80 µm to 29.40 µm, the equatorial axis (E) from 10.90 µm to 24.80 µm. The grains are tricolporate, occasionally tetracolporate in *S. rubens*, with colpi ranging from 11.3 up to 22.5 µm in length and from 0.5 up to 4.5 µm in width at the equatorial region (Table 4). Colpus ends are elongated and can be united at the poles, forming a parasyncolpus in *S. sexangulare* and *S. thartii*. In the other species, the polar triangle has a side measuring from 2.3 to 4.5 µm. The colpus margins may be distinct and prominent (*S. acre, S. andegavense, S. atratum* subsp. *atratum, S. cepaea* and *S. dasyphyllum*), faintly prominent (*Sedum* series *Rupestria*, *S. album*, *S. alpestre, S. caespitosum, S. hispanicum* and *S. sexangulare*), or indistinct, as it occurs in the remaining species. Exine is 1.10-1.40 µm in thickness, with the exception of *S. andegavense*, where it reaches 2.13 µm (Table 4). The surface displays rugulate patterns (Fig. 8 a-h). The differences in the pollen ornamentation mainly refer to the density, orientation and length of the ridges (lirae). Two main types were distinguished (Table 2):

PG1. Rugulate-granulate exine, psilate at the colpus margins. The lirae are irregularly arranged and randomly anastomosed. The space among the lirae may be granular (Fig. 8, c-d), characterized by thick and solid muri or perforate.

PG2. Rugulate-striate pollen grain. The lirae are closely spaced and are distinctly evident at the colpus margins: they form a random anastomosing pattern arranged on quite different layers (Fig. 8, e-f). A more

regular pattern with packed striae was observed in *S. andegavense* (Fig. 8, g-h).

Data analysis

NMDS analysis (Fig. 9; S3) highlighted that all of the clades are discrete groups. This segregation resulted particularly evident for *Sempervivum* clade that is well-separated from *Acre*, *Leucosedum* and *Telephium* clades, but not well-separated from *Rhodiola*. *Acre* is clearly separated with respect to *Leucosedum*.

Discussion

While morphology and micro-morphology of the reproductive structures of the selected *Sedum* species revealed a wide range of variation and different combinations of the single characters, NMDS analysis allowed individuating discrete groups.

The species of the *Sempervivum* clade (*Sedum* ser. *Rupestria*) essentially display homogeneity in the flower structure and morphology – *e.g.* gamosepalous calyx and dialypetalous corolla, obdiplostemonous androecium with free stamens, sessile nectaries with entire margin – and micro-morphology – *e.g.* papillose-conical cells on the petal adaxial side, and rugulate-granulate pollen grains. Therefore, the analysis of these characters not previously considered further support the recognition of *Sedum* ser. *Rupestria* as a well-defined taxonomic unit.

The species of the *Acre* clade present the same basic flower structure with regard to calyx, corolla and androecium, but the outer stamens are adnate to petals; the pollen grains are rugulate-striate. The only exception is *S. acre* which presents totally-free sepals and petals, free elements of the androecium and rugulate-granulate pollen grains. The clade also displays variability in the morphology of the nectaries. Therefore, the flower features support the position of 't Hart (1991), who segregated *S. acre* within the series *Acria,* including the other species within the series *Alpestria*.

High variability of the examined characters is present in the *Leucosedum* clade, which includes the species belonging to the informal group "white-flowered *Sedum* species" ('t Hart, 1982). All of the species display elongated cell with smooth or faintly striate surface on the corolla's adaxial side. The androecium is obdiplostemonous except for *S. andegavense, S. caespitosum* and *S. rubens* that exhibit an aplostemonous androecium. Within this clade, the floral structure, the morphology of nectaries and pollen appear highly variable making the separation of discrete subgroups difficult. Only the presence of a glandular *indumentum* constituted by stalked trichomes allows grouping *S. album, S. cepaea*, *S. dasyphyllum*, *S. hispanicum*, *S. monregalense*, *S. rubens* and *S. villosum* subsp. *villosum*; the pubescence involves all or most of the floral whorls, with the exception of *S. album* that shows glandular hairs only on carpels.

In our results, the species belonging to *Hylotelephium* (*Telephium* clade) are well-separated from the representatives of *Sedum s.s.* and *Phedimus*, supporting their segregation from *Sedum s.s.* They shared most of the examined microcharacters with the exception of nectaries.

P. stellatus, belonging to the *Rodhiola* clade, also appears isolated from all of the other examined species on the basis of the presence of a peryginous flower and on the equal length of sepals and petals. In addition, this species displays an exclusive epidermal type on the sepal surfaces (S3).

The investigation on the flower epidermal micromorphology indicated a noteworthy correlation between the colour of the petals and the main epidermal patterns observed on the adaxial surfaces. Indeed, the white, white-pinkish or pink colours are invariably associated to papillose-conical striate cells (Pad1), with the exception of the species belonging to the genera *Hylotelephium* and *Phedimus*, characterized by elongated cells. The colour yellow is associated with elongated smooth or faintly striate cells (Pad2). The occurrence of papillose-conical cells has been associated with several roles in pollinator attraction, brightness enhancement, and tactile clues (Ojeda et al., 2009). The different petal cell patterning between the papillose-conical-celled white flowers and the elongated-celled yellow flowers was only detected in the European *Sedum* species.

Based on ontogenetic studies, previous authors established which is the most advanced character-state for some of the investigated features ('t Hart and Berendsen, 1980; 't Hart and Koek-Noorman 1989; 't Hart, 1991): basally fused sepals *versus* free sepals, presence of glandular hairs *versus* hairless condition, costate testa of the seeds *versus* reticolate testa. 't Hart (1991) recognized that species sharing the same degree of evolution for all of the above-mentioned micro-characters can be easily hybridized, thus proving that they are genetically more closely related. In this work the toothed nectary (states N1.3 and N2.3) was invariably found in species displaying the most advanced state for all the above-mentioned characters. Therefore, we may infer that the toothed margin represents a more specialized state in comparison to the entire margin.

Conclusions

Despite the high number of the examined micro-characters, it is noteworthy that the flower structure alone resulted very diverse within *Sedum s.l.* In this regard, the use of floral formulae, the reading of which is facilitated by the graphical representation of floral diagrams – providing additional indications about the presence/absence of bracts – was found to be a powerful and effective way to describe the floral diversity. Therefore, the integration of data deriving from the combined use of these complementary techniques is here recommended as a highly valuable and insightful tool in studying variability at genus level.

The accurate analysis of the flower structure also allowed individuating for the first time the occurrence of glandular trichomes in *S. ochroleucum* and *S. rupestre*, and of a costate testa in the seeds of the representatives of *Hylotelephium* genus.

Our study also evidenced the wide morphological variability of the nectaries - whose structure deserves to be further investigated, also in relation to the reproductive strategies of the species - and of the glandular *indumentum,* not previously investigated in detail.

In conclusion, the distribution pattern of the examined micro-characters within and across the species groups submitted to NMDS analysis proved that the five clades are discrete groups. In particular, the *Sempervivum* clade was confirmed to correspond to a well-separated taxonomic unit that should be recognized at the genus rank (*i.e. Petrosedum*) as proposed by Grulich (1984).

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Captions to Figures

Figure 1. Current infrageneric delimitation of the examined *Sedum s.l.* species. [1)] 't Hart (1991); [2)] Thiede and Eggli (2007).

Figure 2 a-l. Floral diagrams and floral formulae (de Craine 2010) of the investigated species. **a**. *S. acre*, *S. dasyphyllum*. **b**. *S. ochroleucum* and *S. rupestre*. **c**. *S. sediforme, S. montanum* and *S. thartii*. **d**. *S. alpestre*, *S. annuum*, *S. atratum* subsp. *atratum*, *S. brevifolium* and *S. sexangulare*. **e.** *S. hispanicum*. **f**. *Hylotelephium anacampseros* and *S. villosum* subsp. *villosum*. **g**. *Hylotelephium maximum*, *S. cepaea*, and *S. monregalense*. **h**. *S. rubens*. **i**. *S. caespitosum*. **j**. *S. andegavense*. **k**. *S. album*. **l**. *Phedimus stellatus.*

Symbols used in floral diagrams: floral axis, a black dot on the top of the diagram; main subtending bract, a black crescent-shaped line, with a small tip on its abaxial side, located in the lower part of the diagram; sepal, a black crescent-shaped line if the sepals are free, or a circumference with black prominent crescent-shaped lines if the sepals are connate; petal, the same in white; stamen, a pair of small white circles, representing the cross-sections of the anthers, without a line through the centre if they are free, or with a line through the centre if they are adnate to the corolla; carpels, white circles inscribed within a larger black circle, representing the cross-section of the ovary at the level of the attachment of the ovules. When the ovary is semi-inferior, this is shown by small grey triangles inserted on the periphery of the ovary.

Symbols used in floral formulae: Floral simmetry: ∗, actinomorphous flower. Floral whorls: K, calyx; C, corolla; A, androecium; G, gynoecium: G̲, superior ovary; G̃, semi-inferior ovary. Numbers of parts: number following the floral whorl symbols indicate the number of the elements in each whorl; + more than one whorl can be distinguished. Fusion of floral parts: (...), fusion within a whorl or between the same organs; [...], fusion between whorls of different organs.

Figure 3. Nectary morphology in the examined *Sedum s.l.* species.

Figure 4. SEM micrographs showing the different types of glandular trichomes in the examined *Sedum s.l.* species: a) T1 sessile trichomes, petal abaxial surface of *S. sexangulare*; b) T2 short-stalked trichome, sepal abaxial surface of *S. dasyphyllum*; c) T3 short-stalked trichomes, petal adaxial side of *S. ochroleucum*; d, e, f) T4 long-stalked trichomes, petal abaxial sides of *S. monregalense*; g, h, i) T5 long-stalked trichomes, floral pedicel of *S. hispanicum*.

Scale bars = 50 μm (a, h); 20 μm (b-d, g); 500 μm (e); 200 μm (f, i).

Figure 5. SEM micrographs showing the different types of epidermal patterns observed on the sepals of the examined *Sedum s.l.* species: a) S1, *S. acre*; b) S2, *H. anacampseros*; c) S3, *P. stellatus*.

Scale bars = 50 μm (a); 100 μm (b); 200 μm (c).

Figure 6. a-d. SEM micrographs showing the different types of epidermal patterns observed on the petal adaxial side of the examined *Sedum s.l.* species: a) Pad1, papillose-conical striate cells, *S. rubens*; b) Pad2A, smooth tabular elongated cells, *H. maximum*; c) Pad2B, striate tabular elongated cells*, S. sediformei*; d) Pad3, striate tabular cells with a deeply wave-like profile, *S. rupestre*. e-h. SEM micrographs showing the different types of epidermal patterns observed on the petal abaxial side: e) Pab4, striate cells with a wave-like profile, *S. montanum*; f) Pab5, rugulate cells with a wave-like profile, *S. brevifolium*; g) Pab6, oblong smooth cells with a wave-like profile, *S. villosum* subsp. *villosum*; h) Pab6, ribbon-like cells with a wavy profile, *S. cepaea.*

Scale bars = 20 μm (a-e); 50 μm (f-h).

Figure 7. SEM micrographs showing the stamens of the examined *Sedum s.l.* species: a) filament, *S. annuum*; b) unicellular papillae at the base of the filament in *S. rupestre*; c) A1 globose anther, *S. album;* d) A2 subglose anther, *S. sexangulare*; e) A3 elongated anther, *S. sediforme*; f) particular of the anther surface in *S. acre*.

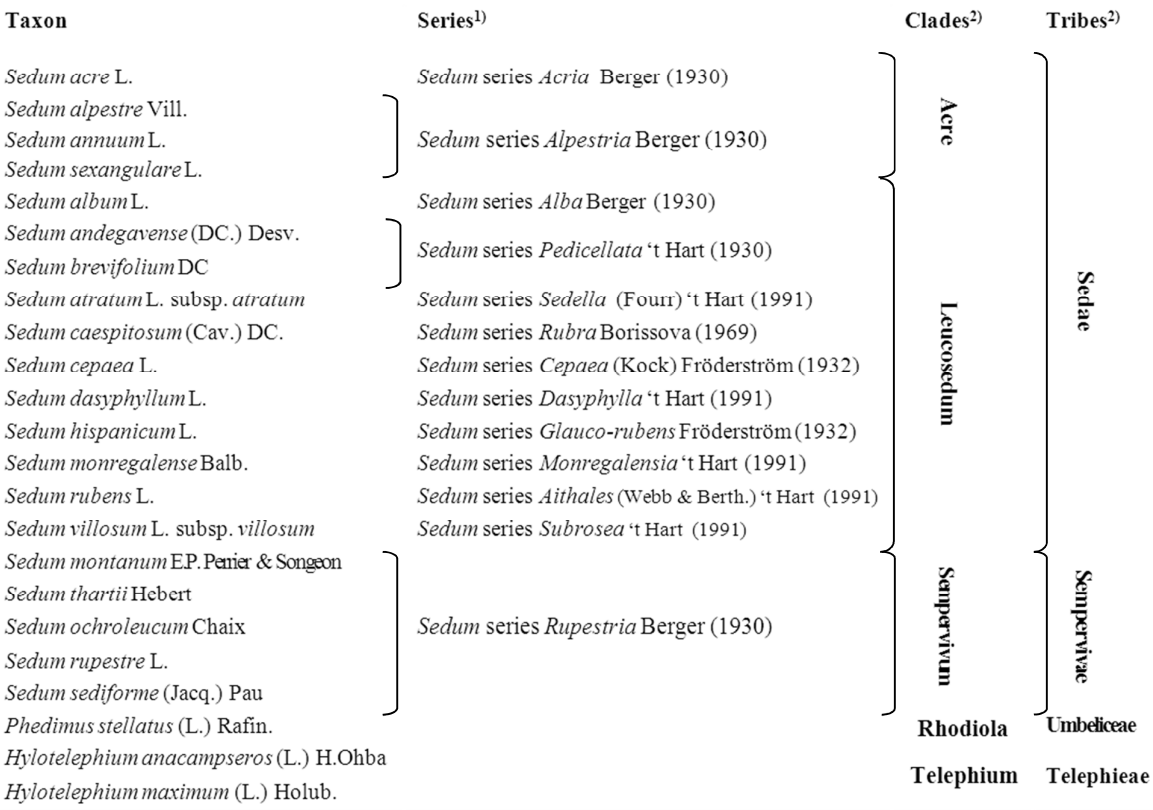
Scale bars = 100 μm (a, b, f); 200 μm (c, d); 500 μm (e); 50 μm (f-h).

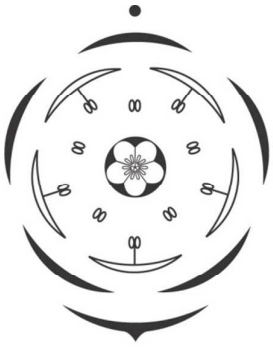
Figure 8. SEM micrographs showing the pollen grains of the examined *Sedum s.l.* species: a) rugulate exine (*S. brevifolium*; b) pollen grain with distinct and prominent colpus margins (*S. cepaea*) ; c, d) PG1 rugulate-granulate pollen grain of *S. montanum*; e, f) PG2 rugulate-striate pollen grain of *S. alpestre*; g, h) PG2 rugulate-striate pollen grain of *S. andegavense.*

Scale bars = 5 μm (a, b, c, e, g); 2 μm (d, f. h).

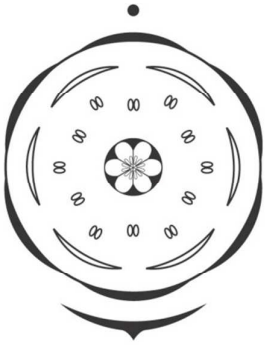
Figure 9. NMDS ordination showing the distribution of the examined species in relation to their attribution to five of the clades established by Thiede and Eggli (2007): O = *Rhodiola* clade, □ = *Acre* clade, × = *Leucosedum* clade, • = *Telephium* clade, + = *Sempervivum* clade.

Figure 1





* K5 [C5 A5]+5 G5



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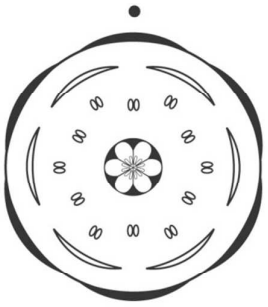

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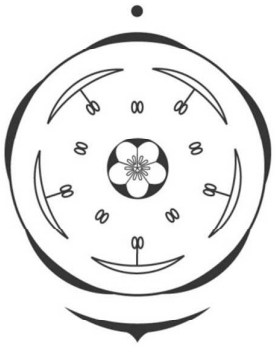

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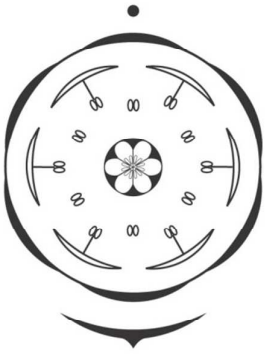
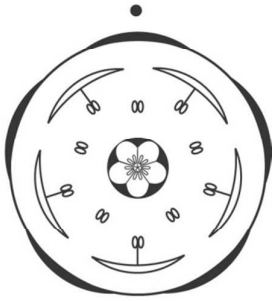


* K(6-7) [C6-7 A6-7]+6-7 G6-7



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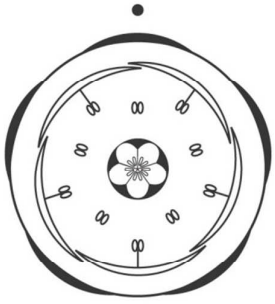

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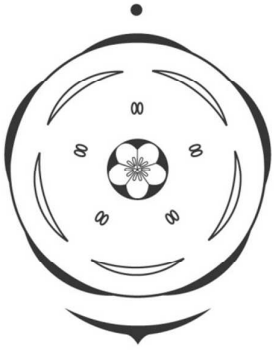

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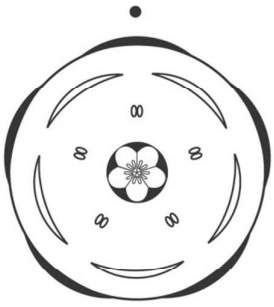

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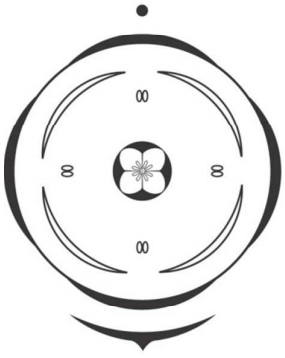

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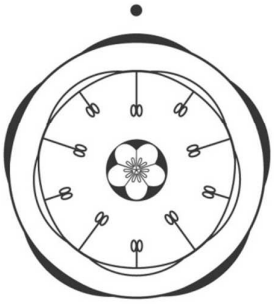
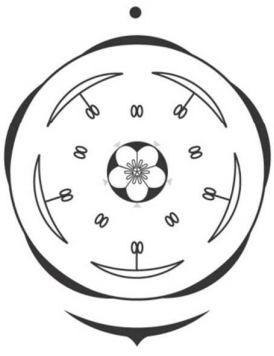
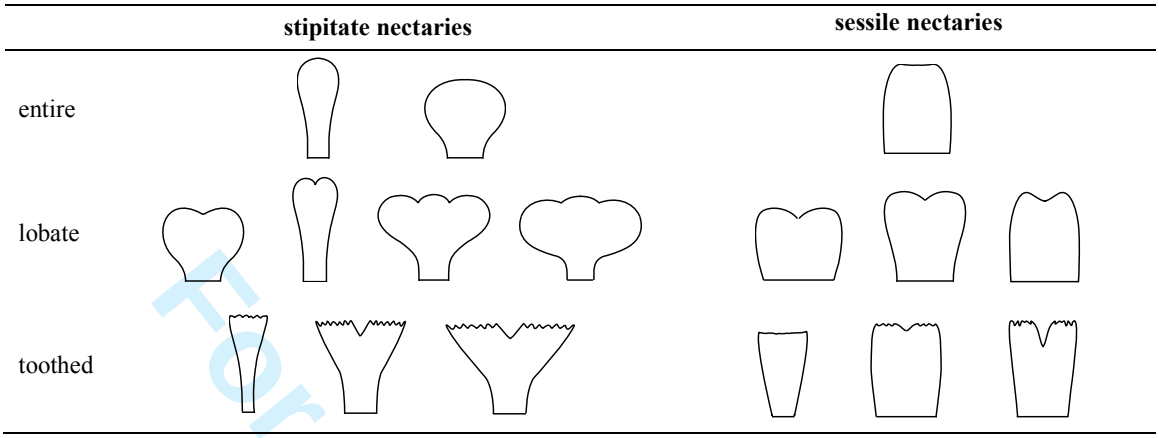


* K(5) [C(5) A5]+5 G5



* K(5) [C5 A5]+5 G̃5

Figure 3



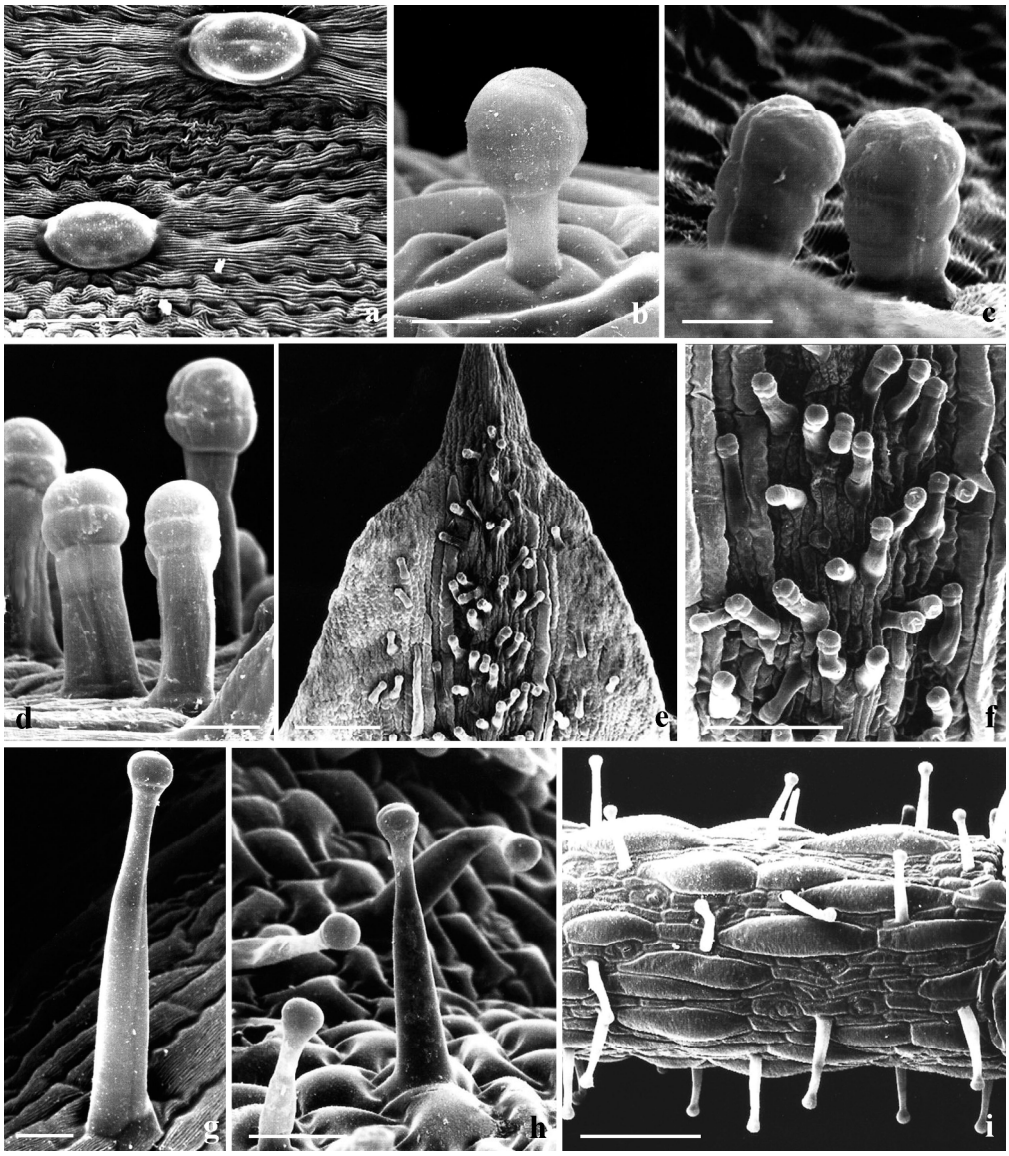
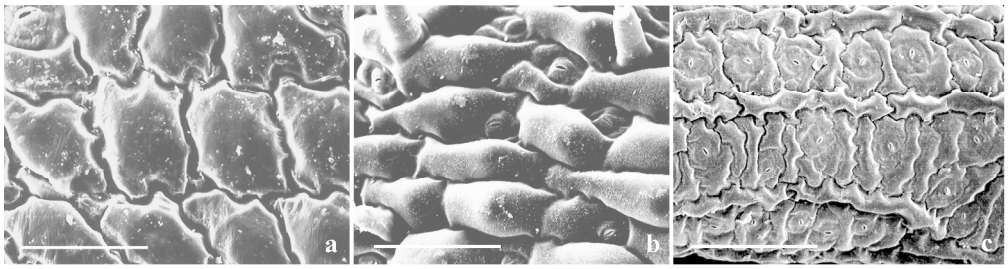


Figure 4. SEM micrographs showing the different types of glandular trichomes in the examined *Sedum s.l.* species: a) T1 sessile trichomes, petal abaxial surface of *S. sexangulare*; b) T2 short-stalked trichome, sepal abaxial surface of *S. dasyphyllum*; c) T3 short-stalked trichomes, petal adaxial side of *S. ochroleucum*; d, e, f) T4 long-stalked trichomes, petal abaxial sides of *S. monregalense*; g, h, i) T5 long-stalked trichomes, floral pedicel of *S. hispanicum*.
Scale bars = 50 μm (a, h); 20 μm (b-d, g); 500 μm (e); 200 μm (f, i).



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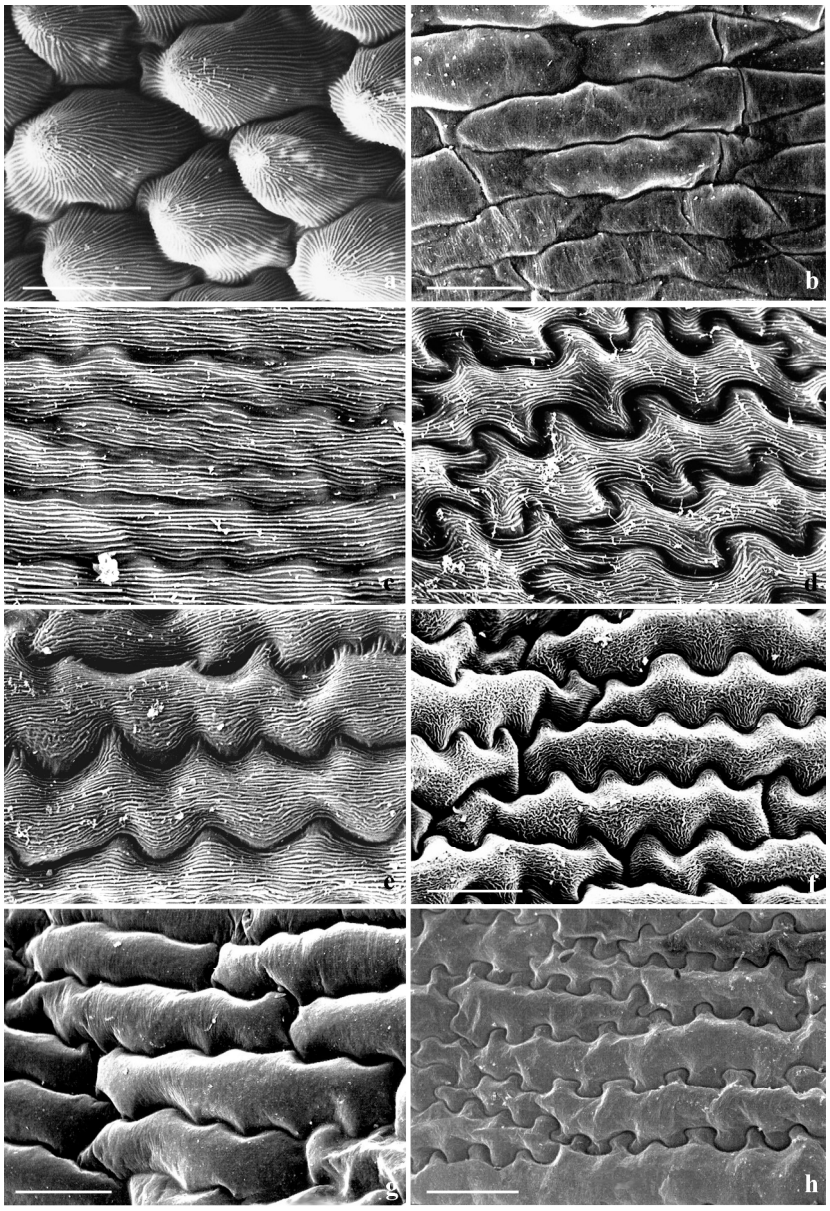
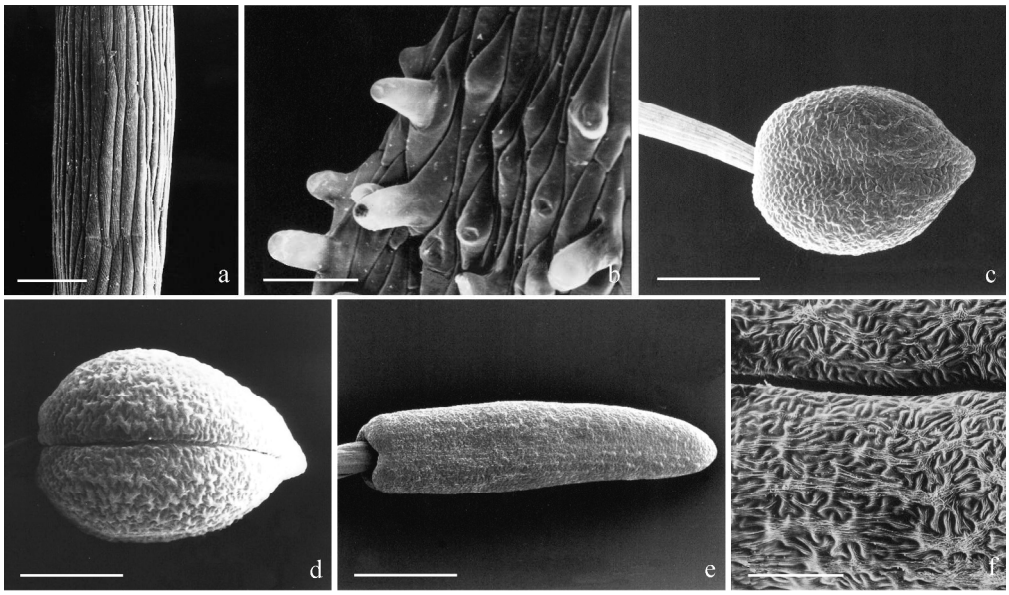


Figure 6. a-d. SEM micrographs showing the different types of epidermal patterns observed on the petal adaxial side of the examined *Sedum s.l.* species: a) Pad1, papillose-conical striate cells, *S. rubens*; b) Pad2A, smooth tabular elongated cells, *H. maximum*; c) Pad2B, striate tabular elongated cells, *S. sediforme*; d) Pad3, striate tabular cells with a deeply wave-like profile, S. rupestre. e-h. SEM micrographs showing the different types of epidermal patterns observed on the petal abaxial side: e) Pab4, striate cells with a wave-like profile, *S. montanum*; f) Pab5, rugulate cells with a wave-like profile, *S. brevifolium*; g) Pab6, oblong smooth cells with a wave-like profile, *S. villosum* subsp. *villosum*; h) Pab6, ribbon-like cells with a wavy profile, *S. cepaea*.
Scale bars = 20 μm (a-e); 50 μm (f-h).



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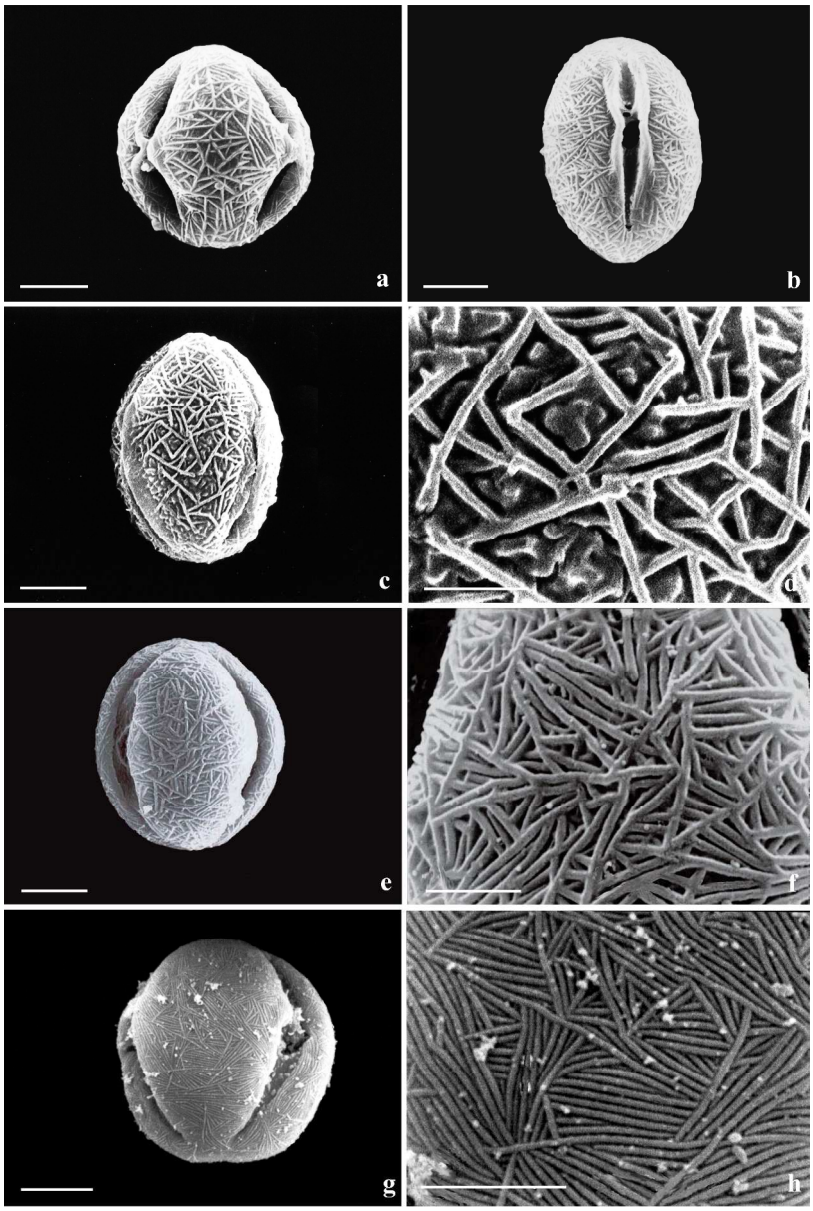
Scale bars = 100 μm (a, b, f); 200 μm (c, d); 500 μm (e); 50 μm (f-h).



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Scale bars = 5 μm (a, b, c, e, g); 2 μm (d, f. h).

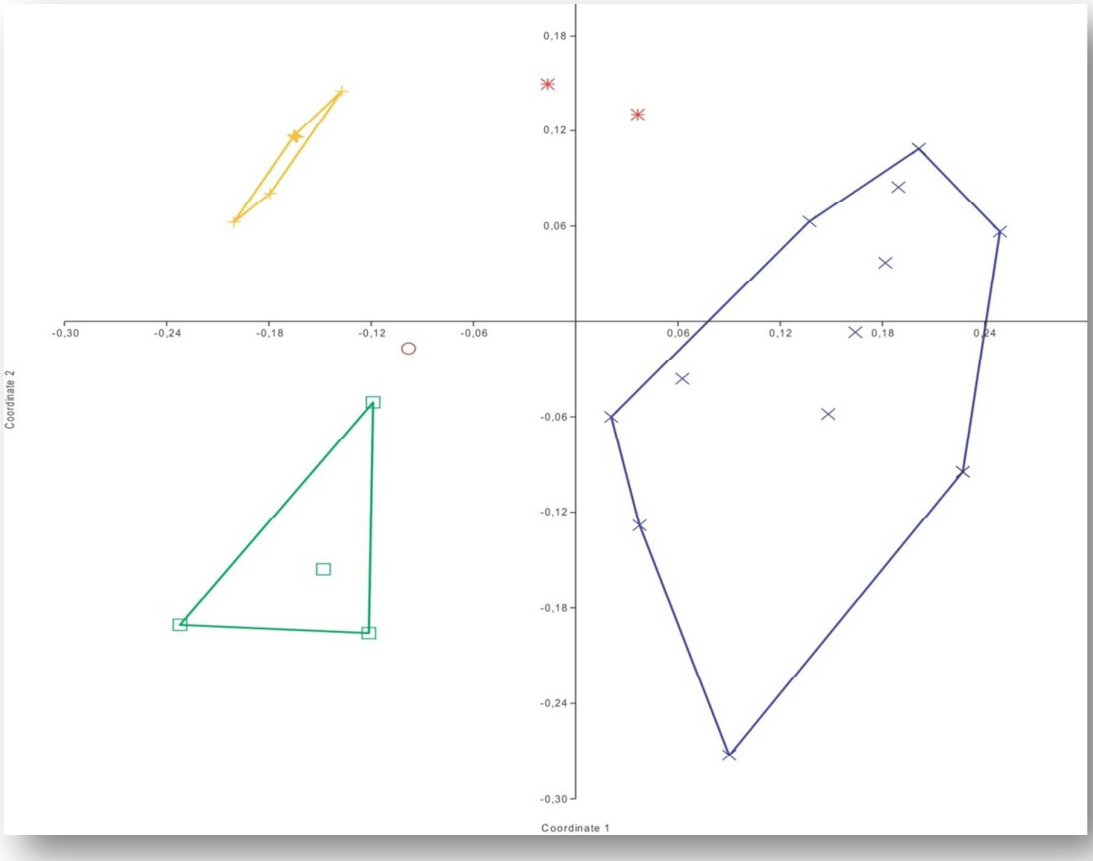

Table 1. Distribution of the examined Mediterranean *Sedum s.l. taxa* in Southern Europe (Euro+Med, 2006). The occurrences have also been checked in recent local floras or revisions (Tison et al., 2014; Misfud et al., 2015).

		Albania	Balearic Islands	Bosnia-Ercegovina	Corse	Crete	Croatia	Cyprus	East Aegean Islands	France	Greece	Italy	Makedonija	Malta	Montenegro	Portugal	Sardinia	Serbia and Kosovo	Sicily	Slovenia	Spain
***Acre* clade**	*S. acre*	+	-	+	+	+	+	-	+	+	+	+	+	-	+	+	+	+	+	+	+
	S. alpestre	+	-	+	+	-	+	-	-	+	+	+	+	-	-	-	+	+	-	+	+
	S. annuum	+	-	-	+	-	+	-	+	+	+	+	+	-	+	-	-	+	-	+	+
	S. sexangulare	+	-	+	-	-	+	-	-	+	+	+	+	-	+	-	-	+	-	+	-
***Leucosedum* clade**	*S. album*	+	+	+	+	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+
	S. andegavense	-	-	-	+	-	-	-	-	+	-	+	-	-	-	+	+	-	-	-	+
	S. atratum subsp. *atratum*	+	-	+	-	-	+	-	-	+	+	+	+	-	-	-	-	+	-	+	+
	S. brevifolium	-	-	-	+	-	-	-	-	+	-	+	-	-	-	+	+	-	-	-	+
	S. caespitosum	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+
	S. cepaea	+	-	+	+	+	+	-	+	+	+	+	+	-	+	-	+	+	+	-	+
	S. dasyphyllum	+	+	+	+	-	+	-	-	+	+	+	+	-	+	-	+	+	+	+	+
	S. hispanicum	+	-	+	-	+	+	-	+	-	+	+	+	-	+	-	-	+	+	+	-
	S. monregalense	-	-	-	+	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	-
	S. rubens	+	+	-	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	-	+
	S. villosum subsp. *villosum*	-	-	-	+	-	+	-	-	+	-	+	-	-	+	-	-	+	-	+	+
***Sempervivum* clade**	*S. montanum*	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	+	+
	S. thartii	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	+	-
	S. ochroleucum	+	-	+	-	-	+	-	+	+	+	+	+	-	+	-	-	+	+	+	+
	S. rupestre	+	-	+	+	-	+	-	-	+	+	+	+	-	-	-	+	+	+	+	+
	S. sediforme	+	+	-	+	+	+	+	+	+	+	+	-	+	-	+	+	-	+	-	+
***Rhodiola* clade**	*P. stellatus*	+	+	+	+	-	+	-	-	+	+	+	-	+	-	-	+	-	+	-	-
***Telephium* clade**	*H. anacampseros*	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	-	+
	H. maximum	+	-	+	+	-	+	-	-	+	+	+	-	-	+	+	+	+	-	+	+

Table 2. Distribution pattern of the morphological and micro-morphological features examined in the selected *Sedum s.l.* species.

Clade	Species	Flower structure	Nectary morphology	Glandular trichomes	Sepals	Petals		Anthers	Pollen grain	Stylus	Testa ornament	Seed apex
Acre	*S. acre*	F1.1	N1.1/N1.2	-	S1	Pad2.B	Pab2	A2	PG1	bent	reticulate	acute
	S. alpestre	F1.2.2.A	N1.3	-	S1	Pad2.B	Pab1	A1	PG2	bent	reticulate	acute
	S. annuum	F1.2.2.A	N2.3	-	S1	Pad2.B	Pab1	A1	PG2	bent	reticulate	acute
	S. sexangulare	F1.2.2.A	N2.1	T1	S1	Pad2.B	Pab2	A2	PG2	erect	reticulate	acute
Leucosedum	*S. album*	F1.3	N1.2	T5	S1	Pad1	Pab2	A1	PG1	erect	costate	acute
	S. andegavense	F1.2.3	N1.2	-	S1	Pad1	Pab2	A1	PG3	erect	costate	acute
	S. atratum subsp. *atratum*	F1.2.2.A	N2.3	-	S1	Pad1	Pab2	A1	PG1	erect	costate	acute
	S. brevifolium	F1.2.2.A	N1.2	-	S1	Pad1	Pab2	A1	PG2	bent	costate	acute
	S. caespitosum	F1.2.3	N1.1	-	S1	Pad1	Pab2	A1	PG1	erect	costate	acute
	S. cepaea	F1.2.2.C	N2,3	T5	S2	Pad1	Pab3	A1	PG1	suberect	costate	coronate
	S. dasyphyllum	F1.1	N1.1/N1.2	T2	S1	Pad1	Pab3	A1	PG2	erect	costate	acute
	S. hispanicum	F1.2.2.A	N1.3	T5	S2	Pad1	Pab3	A2	PG1	erect	costate	acute
	S. monregalense	F1.2.2.C	N1.3	T4	S2	Pad1	Pab1	A1	PG1	erect	costate	acute
	S. rubens	F1.2.3	N1.3	T5	S2	Pad1	Pab3	A1	PG2	erect	costate	acute
	S. villosum subsp. *villosum*	F1.2.2.B	N1.1	T5	S2	Pad1	Pab3	A2	PG1	erect	costate	coronate
Sempervivum	*S. montanum*	F1.2.1.B	N2.1	-	S1	Pad2.B	Pab1	A3	PG1	erect	costate	acute
	S. tahrtii	F1.2.1.B	N2.1	-	S1	Pad2.B	Pab1	A3	PG1	erect	costate	acute
	S. ochroleucum	F1.2.1.A	N2.1	T3	S1	Pad3	Pab2	A3	PG1	erect	costate	acute
	S. rupestre subsp. *rupestre*	F1.2.1.A	N2.1	T3	S1	Pad3	Pab1	A3	PG1	erect	costate	acute
	S. sediforme	F1.2.1.B	N2.1	-	S1	Pad2.B	Pab1	A3	PG1	erect	costate	acute
Rodhiola	*P. stellatus*	F2	N2.2	-	S3	Pad2.B	Pab1	A3	PG2	erect	costate	acute
Telephium	*H. anacampseros*	F1.2.2.B	N1.2	-	S2	Pad2.B	Pab3	A2	PG1	erect	costate	acute
	H. maximum	F1.2.2.C	N2.2	-	S2	Pad2.A	Pab3	A2	PG1	erect	costate	acute

Table 3. Distribution pattern of the different types of glandular trichome observed in *S. sexangulare, S. dasyphyllum, S. ochroleucum, S. rupestre, S. monregalense, S. album, S. cepaea, S. hispanicum, S. rubens, S. villosum* subsp. *villosum*.

	pedicel	**bract**	**sepal**	**petal** abaxial	**petal** adaxial	**carpel**
S. sexangulare				**T1**		
S. dasyphyllum	**T2**	**T2**	**T2**	**T2**		**T2**
S. ochroleucum *S. rupestre*					**T3**	
S. monregalense	**T4**	**T4**	**T4**	**T4**		**T4**
S. album						**T5**
S. cepaea *S. hispanicum* *S. rubens* *S. villosum* subsp. *villosum*	**T5**	**T5**	**T5**	**T5**		**T5**

Table 4. Morphometric features examined in the pollen grains of the selected *Sedum s.l.* species. P: polar axis; E: equatorial diameter.

Clade	Species	P	E	P/E	shape	exine thickness	colpus		polar triangle side	mesocolpium length
							width	length		
Acre	*S. acre*	(18.0-) 18.8 ± 0.6 (-19.2)	(15.8-) 16.5 ± 0.6 (-18.0)	1.14	Subprolate	1.20	15.1	2.59	2.74	9.50
	S. alpestre	(18.0-) 19.2 ± 1.0 (-20.3)	(15.8-) 18.1 ± 0.7 (-20.3)	1.06	Prolate-spheroidal	1.44	15.6	2.67	2.94	11.00
	S. annuum	(20.3-) 22.9 ± 1.5 (-27.0)	(16.9-) 19.0 ± 1.2 (-21.4)	1.20	Subprolate	1.20	17.8	2.08	3.13	12.60
	S. sexangulare	(21.4-) 22.0 ± 0.6 (-22.5)	(19.2-) 20.1 ± 0.4 (-20.3)	1.10	Prolate-spheroidal	1.36	20.6	4.28	0	11.40
Leucosedum	*S. album*	(20.3-) 20.7 ± 0.7 (-22.5)	(16.9-) 18.6 ± 1.0 (-20.3)	1.12	Prolate-spheroidal	1.20	17.6	2.52	2.60	11.10
	S. andegavense	(22.5-) 24.7 ± 1.1 (-27.0)	(19.2-) 21.0 ± 1.0 (-22.5)	1.17	Subprolate	2.13	17.3	2.67	3.77	11.90
	S. atratum subsp. *atratum*	(19.2-) 21.1 ± 1.2 (-24.8)	(18.0-) 20.2 ± 1.3 (-22.5)	1.04	Prolate-spheroidal	1.42	15.1	2.52	3.40	12.20
	S. brevifolium	(12.8-) 17.5 ± 2.3 (-21.3)	(10.9-) 14.2 ± 2.6 (-17.4)	1.20	Subprolate	1.16	12.9	2.21	2.52	9.60
	S. caespitosum	(20.3-) 22.6 ± 1.1 (-24.8)	(15.8-) 17.5 ± 1.1 (-19.2)	1.30	Subprolate	1.20	17.5	2.59	4.13	10.50
	S. cepaea	(19.2-) 20.0 ± 0.6 (-21.4)	(18.0-) 18.4 ± 0.6 (-19.2)	1.09	Prolate-spheroidal	1.24	17.1	2.00	4.50	12.90
	S. dasyphyllum	(18.0-) 19.3 ± 0.6 (-20.3)	(16.9-) 17.8 ± 0.4 (-18.0)	1.41	Prolate	1.20	13.5	2.52	2.40	12.40
	S. hispanicum	(20.3-) 21.2 ± 0.8 (-22.5)	(18.0-) 18.7 ± 0.9 (-20.3)	1.10	Prolate-spheroidal	1.90	17.1	3.33	3.90	11.30
	S. monregalense	(21.4-) 21.7 ± 0.5 (-22.5)	(18.0-) 18.7± 0.7 (-20.3)	1.16	Subprolate	1.20	18.5	2.67	2.67	11.30
	S. rubens	(23.7-) 25.5 ± 1.7 (-29.)	(22.5-) 24.2 ± 0.8 (-24.8)	1.06	Prolate-spheroidal	1.20	18.5	4.21	4.06	14.05
	S. villosum subsp. *villosum*	(16.2-) 18.2 ± 2.6 (-25.3)	(15.9-) 17.3 ± 1.5 (-20.7)	1.05	Prolate-spheroidal	1.84	15.1	2.65	2.66	10.60
Sempervivum	*S. montanum*	(21.4-) 23.9 ± 1.6 (-26.8)	(16.1-) 18.3 ± 0.8 (-19.9)	1.30	Subprolate	1.08	18.3	2.83	4.04	14.00
	S. thartii	(18.5-) 20.6 ± 1.6 (-23.6)	(15.2-) 18.6 ± 1.5 (-21.8)	1.10	Prolate-spheroidal	1.00	18.4	3.56	0	13.70
	S. ochroleucum	(18.0-) 18.5 ± 0.7 (-20.3)	(15.8-) 16.0 ± 0.4 (-16.9)	1.15	Subprolate	1.20	16.1	3.62	2.45	9.20
	S. rupestre subsp. *rupestre*	(21.4-) 22.5 ± 1.2 (-24.8)	(16.9-) 18.7 ± 1.0 (-20.3)	1.20	Subprolate	1.20	18.5	2.45	4.23	11.30
	S. sediforme	(19.2-) 19.9 ± 0.5 (-20.3)	(18.0-) 18.8 ± 0.9 (-20.3)	1.06	Prolate-spheroidal	1.20	15.8	3.11	3.57	11.15
Rhodhiola	*P. stellatus*	(20.3-) 22.2 ± 1.1 (-24.8)	(15.8-) 17.0 ± 1.1 (-18.0)	1.30	Subprolate	1.20	17.1	0.56	2.67	10.90
Telephium	*H.anacampseros*	(23.7) 26.2 ± 1.4 (-29.3)	(19.2-) 20.2 ± 0.6 (-21.4)	1.30	Subprolate	1.20	19.5	2.23	2.30	13.20
	H. maximum	(15.8-) 18.7 ± 1.2 (-20.3)	(11.3-) 13.7 ± 0.9 (-15.8)	1.37	Prolate	1.11	13.1	1.20	2.50	9.40

S1. Examined specimens of the selected *Sedum s.l.* species. Specimens collected in the wild are in roman; specimens sampled from *exsiccata* stored in the Herbarium Centrale Italicum (FI) are in bold.

Sedum acre L.	Monte Morello (Fi), 20.05.01, Pignotti Appennino Tosco-Emiliano: Traversa (Fi), 01.06.01, Giuliani Montepoli (Fi), 13.06.02, Giuliani
Sedum album L.	Alpi Apuane: P.sso del Vestito, 22.05.01, Giuliani Appennino Tosco-Emiliano: P.sso Raticosa, 18.07.02, Giuliani Appennino Tosco-Emiliano: Sasso di San Zanobi, 18.07.02, Giuliani
Sedum alpestre Vill.	Appennino Pistoiese: cima M.te Fortezza, 09.07.02, Giuliani Appennino Pistoiese: Foce al Campolino, 09.07.02, Giuliani
Sedum andegavense (DC.) Desv.	**Capraia: cima Monte Castello, 20.05.1898, *sine collector*** **Montecristo: lungo il sentiero La Villa – rovine del Convento, 06.05.1957, CHIARUGI, BAVAZZANO** **Montecristo: Il Belvedere, 23-27.04.1974, PAOLI, BAVAZZANO**
Sedum annum L.	**Alpi di Barga (Ms), 19.07.1857, *sine collector*** **App. Lucchese: rupi sotto al Lago Baccio, 24.07.1881, *sine collector***
Sedum atratum L.subsp. *atratum*	**Alpi Apuane: Pania della Croce, 18.06.1891, *sine collector*** **Alpi Apuane: da Campo Cecina alla vetta del M.te Sagro, 18.06.1969, MOGGI, ARRIGONI, NARDI, BAVAZZANO**
S. brevifolium DC.	**Isola d'Elba: La Tavola, M.te di Cote (Marciana), 09.06.1999, MANNOCCI**
Sedum caespitosum (Cav.) DC.	**Isola d'Elba: M.te Perone (sopra Marciana), 05.05.1900, *sine collector*** **Poggio S. Romolo (Fi), 21.04.1928, CHIARUGI**
Sedum cepaea L.	Alpi Apuane: S. Carlo, 22.05.01, Giuliani Monte Morello (Fi), 20.05.01, Giuliani Montepoli (Fi), 15.06.02, Giuliani Galliano di Mugello (Fi), 01.07.02, Giuliani
Sedum dasyphyllum L.	Tra Fiesole e Vincigliata (Fi), 19.05.01, Giuliani Alpi Apuane: S. Carlo, 22.05.01, Giuliani S. Jacopo (Fi), 28.05.02, Giuliani Montepoli (Fi), 13.06.02, Giuliani
Sedum hispanicum L.	Firenze, 20.05.01, Giuliani
Sedum monregalense Balbis	Alpi Apuane: Arni, 22.05.01, Giuliani Appennino Tosco-Emiliano: Sasso di San Zanobi, 19.06.02, Giuliani Appennino Tosco-Emiliano: Sasso di San Zanobi, 18.07.02, Giuliani
Sedum montanum E.P. Pierre & Songeons.	**Anti-Appennino Toscano: Cornate di Gerfalco, 22.07.1965, DE DOMINICIS** **Alpi Apuane: Foce del Pollaro del Sangro, 21.07.1995, *sine collector***
Sedum ochroleucum Chiax	Tra S. Jacopo e Caldine (Fi), 26.05.01, Giuliani
Sedum rubens L.	Alpi Apuane: P.sso del Vestito, 22.05.01, Giuliani Galliano di Mugello (Fi) 05.06.01, Giuliani
Sedum rupestre L.	Monteloro (Fi), 26.05.01, Giuliani Diacceto (Fi), 26.05.01, Mariotti Lippi Isola d'Elba: Rio nell'Elba, 07.05.02, Giuliani Isola d'Elba: pendici M.te Strega, 07.05.02, Giuliani
Sedum sediforme (Jacq.) Pau	**M.te Argentario (Gr): Isolotto di Porto Ercole, 10.06.1990, BALDINI** M.te Argentario (Gr): lungo la Panoramica, 06-06-2011, Giuliani **Isola di Giannutri (Gr): Monte Mario, versante di Cala Maestra, 07.07.1996, DA SILVA, BALDINI** **Isola di Giannutri (Gr): Pian di Fagiano, 15.06.1999, BALDINI**
Sedum sexangulare L.	S. Jacopo (Fi), 26.05.01, Giuliani Castel di S. Niccolò (Ar) loc. Rifiglio, 26.05.01, Mariotti Lippi Paterno, Vaglia (Fi), 07.06.02, Giuliani
Sedum thartii Hebert	**Liguria: Alpes Maritimes, Environs de St. Martin - Lantosque, 08.07.1865, THURET**
Sedum villosum L. subsp. *villosum*	**Montalbano, Carmignano: Villa di Artimino (Po), 09.05.2010, CARTA, GESTRI, PERUZZI**
Hylotelephium anacampseros (L.) H.Ohba	**Emilia: versante NE Sprone di M.te Prado (Reggio Emilia), 15.08.1983, TOMASELLI** **Emilia: Lizzano in Belvedere, M.te Corno alle Scale, 06.08.1987, FOGGI** Appennino Pistoiese: Alpe Tre Potenze, 15.07.03, Foggi
Hylotelephium maximum (L.) Suter	Alpi Apuane: Fornovolasco, 27.07.01, Giuliani Orto Botanico di Firenze, 08-19.09.02, Giuliani, Mariotti Lippi
Phedimus stellatus (L.) Rafin	Cantagallo (Po), 29.05.01, Pignotti Isola d'Elba: pendici M.te Strega, 07.05.02, Giuliani Isola D'Elba: Eremo di Santa Caterina, 07.05.02, Giuliani

S2. List of the floral characters and character states used in the statistical data processing.

Character	Code	Character state (yes/no)	Character	Code	Character state (yes/no)
Flower arrangement	01	cyme	Androecium type	37	obdiplostemonous
	02	corymb		38	haplostemonous
	03	panicle	Anther colour	39	red
	04	bracteate		40	yellow
	05	pedicellate	Anther shape	41	globose
Trichome type	06	sessile		42	subglobose
	07	stalked		43	elongated
Trichome distribution	08	presence on pedicel	Stamen arrangement	44	antepetalous and free
	09	presence on calyx		45	antepetalous and adnate
	10	presence on corolla		46	antesepalous and free
	11	presence on carpels		47	antesepalous and adnate
	12	on staminal filaments	Ovary type	48	superior
Floral symmetry	13	4-merous		49	inferior
	14	5-merous	Stylus type	50	erect
	15	6-merous		51	suberect
Calyx type	16	dialysepalous		52	bent
	17	gamosepalous	Nectary type	53	stipitate
Sepal apex	18	acute		54	sessile
	19	obtuse	Nectary margin	55	entire
Sepal length	20	equal		56	lobate
	21	non equal		57	toothed
Sepal epidermal pattern	22	S1	Pollen shape	58	spheroidal
	23	S2		59	subprolate-prolate
	24	S3	Pollen sculpturing	60	PG1
Corolla type	25	dialypetalous		61	PG2
	26	gamopetalous	Colpus margin	62	prominent
Aestivation	27	imbricate vs non imbricate	Polar axis length	63	</= 20 µm.
Corolla colour	28	white		64	> 20 µm.
	29	pink	Side of the polar triangle	65	< 3 µm.
	30	yellow		66	> 3 µm.
Epidermal pattern of petal adaxial side	31	Pad1	Seed testa ornamentation	67	reticulate
	32	Pad2		68	costate
	33	Pad3	Seed micropylar region type	69	acute
Epidermal pattern of petal abaxial side	34	Pab1		70	coronate
	35	Pab2			
	36	Pab3			

S3. General data matrix used in the NMDS analysis.

	S. ochroleucum	*S. rupestre*	*S. sediforme*	*S. montanum*	*S. thartii*	*S. acre*	*S. alpestre*	*S. annuum*	*S. sexangulare*	*S. villosum* subsp. *villosum*	*S. album*	*S. andegavense*	*S. brevifolium*	*S. atratum* subsp. *atratum*	*S. caespitosum*	*S. cepaea*	*S. dasyphyllum*	*S. hispanicum*	*S. monregalense*	*S. rubens*	*P. stellatus*	*H. anacampseros*	*H. maximum*
1	0	0	0	0	0	1	1	1	1	0	1	1	1	0	1	0	1	1	0	1	1	0	1
2	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0
4	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	0	1	1	0	0	1	0	0
5	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	1
6	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
7	1	1	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	0	1	0
8	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	0	0	0	0
9	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	1	1	0	0	0
10	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	1	1	0	0	0
11	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	1	1	1	0	0	0
12	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
14	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1
15	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
16	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
17	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
18	1	1	1	1	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1
19	0	0	0	0	0	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0	0
20	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1
21	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
22	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	0	0	0	0	0	0
23	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	1	1	1	0	1	1
24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
25	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
26	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1
28	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	0	0	1
29	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0
30	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
31	0	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	0
32	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
33	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	0	1	1	0
34	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0
35	1	0	0	0	0	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	1	0	1	1
37	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
38	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	1	1	1	1	0	1	1	1
39	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
40	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0
41	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
42	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	1	0	1	1	0	0	0
43	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	1
44	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
45	1	1	1	1	1	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0
46	0	0	0	0	0	1	1	1	1	1	1	0	0	1	0	1	1	1	1	0	1	1	1
47	1	1	1	1	1	1	1	1	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1
48	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
49	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1
50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
51	1	1	1	1	1	0	0	0	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1
52	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0
53	0	0	0	0	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0
55	1	1	1	1	1	1	0	1	1	0	0	1	1	1	0	1	1	0	0	0	1	0	1
56	1	1	1	1	1	1	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	1	1
58	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	1	1	1	0	0	0
59	1	0	1	0	0	1	1	0	1	1	1	0	0	1	0	1	1	1	0	1	0	0	0
60	0	1	0	1	1	0	0	1	0	0	0	1	1	0	1	0	0	0	1	0	1	1	1
61	1	1	1	1	1	1	0	0	0	1	1	0	0	1	1	1	0	1	1	0	0	1	1
62	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0	0	1	1	0	0
63	0	0	0	0	0	1	0	0	0	1	0	1	1	1	0	1	1	0	0	0	0	0	0
64	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1
65	0	1	1	1	1	0	1	1	1	0	1	1	1	1	1	1	0	1	1	1	1	1	0
66	1	0	0	0	1	1	0	0	1	0	1	0	1	0	0	0	1	0	1	0	1	1	1
67	0	1	1	1	0	0	1	1	0	1	0	1	0	1	1	1	0	1	0	1	0	0	0
68	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0

69	1	1	1	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
70	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1
71	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0