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Evolution and classification of the European *Sedum* species (*Crassulaceae*)

Abstract

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The results of extensive cytological and morphological studies, and of an extensive hybridization programme involving 53 of the 54 European *Sedum* species plus 8 additional species from N Africa and Anatolia, are summarized. Species are defined biologically so that all interspecific hybrids are completely sterile. Nevertheless, 27 comparia could be defined within which the species can be crossed whereas crosses between species of different comparia are unsuccessful. It is possible to define these comparia morphologically, too, so that they are recognized as monophyletic units and given formal taxonomic recognition at the rank of series. The 27 series thus defined within *Sedum* sect. *Sedum*, 10 of which are described as new and 3, newly named, are all characterized and keyed out. Their centres of origin and evolution are identified, and a new hypothesis of the evolutionary history of the genus *Sedum* — a paraphyletic taxon that is best kept in its present circumscription in the interest of taxonomic and nomenclatural stability — is presented. [Editors' abstract]

1. Introduction

Sedum L. comprises about 500 species which are almost exclusively confined to the subtropical and temperate regions of the northern hemisphere. In Europe *Sedum* occurs predominantly in the Mediterranean region. Of the 54 species of *Sedum* native to Europe roughly two thirds are confined to southern Europe and the countries bordering the Mediterranean Sea. About one third of the species has successfully colonized western, central and eastern Europe, but only seven of them have reached northern Europe (Webb 1964).

Sedum is generally considered to contain the most primitive and ancient *Crassulaceae*. This view was first put forward by Schönland (1891) who regarded *Sedum* as the core genus of the *Crassulaceae* and derived all other genera from this central one. Furthermore, *Sedum* can not be defined by synapomomorphies and most probably it is paraphyletic (the taxon is derived from a common ancestor, but it does not include all possible descendants of this ancestor). In recent studies of relationships between genera of *Crassulaceae* it has been demonstrated that several advanced groups, such as for instance *Echeveria* DC., *Aeonium* Webb & Berth., *Kalanchoe* Adanson, *Monanthes* Haw., *Sempervivum* L., are indeed closely related to different, and in an evolutionary sense, distinct, parts of *Sedum* (Clausen 1975, Uhl 1976, Hideux 1981, Hart 1982b).

The classification of paraphyletic taxa is notoriously difficult and usually there is no simple solution to the problem (Funk 1985). In this respect *Sedum* is no exception and the nomenclature of many species still bears the marks left by contrasting views about their systematic position (see chapter 10). In practice paraphyletic taxa are generally dealt with in either of the following ways: they are lumped or split. In *Sedum*, however, neither method leads consistently to well-defined genera (Berger 1930).

Taxonomists adhering to the broad generic view usuallly arrange the species of large genera into numerous infrageneric taxa. For *Sedum* the first formal infrageneric classifications were proposed by Koch (1843) and Boissier (1872). They were mainly based on habit. The reverberations of these classifications can still be traced in recent treatments of *Sedum* (Berger 1930, Webb 1964, Maire 1977), though its principles have long since been invalidated (Hamet 1929, Fröderström 1930). Subsequent infrageneric classifications of the Old World species of *Sedum* by Maximowicz (1884), Praeger (1921), Huber (1929), Berger (1930), Fröderström (1930, 1932), Borissova (1939, 1969), and Maire (1977) disagree to a large extent, except for a few comparatively distinct taxa such as for example the *S. rupestre* group and the *S. spurium* (= *S. involucratum*) group, and they therefore never became widely accepted.

Berger (1930) preferred a comparatively narrow genus concept and tentatively proposed to split the large genera of the *Crassulaceae* into more easily recognizable, smaller taxa. A rigorous application of this principle to *Sedum* has recently been advocated and put into practice by Ohba (1977, 1978), and Grulich (1984), and was led *ad absurdum* by Löve & Löve (1985a, b). Although the above-mentioned authors claimed that their urge to break down the large and heterogeneous genus *Sedum* was solely based on the necessity to get "smaller, independent, and natural genera", the net result of their actions is merely a massive change of names, whereas the number of paraphyletic taxa has remained the same or has been increased.

In this study a classification of the European *Sedum* species is proposed based on evolutionary relationships. The article consists of two parts. The first part (chapters 2-8) contains a discussion of the results of combined studies of the morphological and cytological variation, the hybridization patterns, and the distribution of the taxa. It is concluded with a summary of the evolution of *Sedum* in the Europe. In the second part (chapters 9 and 10) the infrageneric taxa are formally described, and a key to the series is presented.

2. Cytology

Cytologically the *Crassulaceae* are the most diverse group of angiosperms (Uhl 1963). The 54 European species of *Sedum* fit well into this general pattern. They comprise about 140 different cytotypes (Table 1). There is a continuous series of basic chromosome numbers ranging from $x = 5$ to $x = 18$, and additionally the numbers $x = 20, 22, 24, 25$, and 37 have been observed.

The most prominent feature of the cytological variation in *Sedum* is the number of polyploids which is significantly higher than the average for angiosperms (Grant 1971, Stebbins 1971). Of the 140 cytotypes of *Sedum* in Europe about 64% are (auto) polyploids which belong to intraspecific polyploid series. In addition, 40% of the diploid cytotypes have a basic number of $x = 14$ or higher, and these taxa can also be regarded as polyploids (Stebbins 1950, 1971, Grant 1971). This brings the total number of polyploids in *Sedum* up to approximately 80%.

Most probably a majority of the higher (secondary) basic numbers result from allopolyploidy. The allopolyploid origin of *S. montanum* subsp. *orientale* ($2n = 2x =$ c. 98) and *S. rupestre* subsp. *rupestre* ($2n = 2x = 112$) has been demonstrated experimentally by means of resynthesis of these taxa from their putative parent species (Hart 1978, Hart & al. 1990). An allopolyploid origin seems also quite likely for many other species with secondary basic numbers, but this has still to be demonstrated.

In addition to polyploidy much cytological variation is due to dysploid changes at the diploid as well as at the polyploid level (Table 1). Most probably, dysploid changes of the basic chromosome number in *Sedum* are due to chromosome fusion or fission rather than to aneuploidy (Ehrendorfer 1963). In *Sedum* dysploid changes due to Robertsonian translocations are rather frequent (Table 1; arrows indicate the direction of the dysploid changes), though in general this type of chromosomal rearrangement is less common in plants than in animals (White 1978). The evolutionary significance of Robertsonian translocations is obviously the reduction of the recombination rate for genes expressing adaptively favourable and interacting characters (Dobzhansky & al. 1977, White 1978, Hart & al. in prep.). Dysploid changes have been analysed in a few *Sedum* species, but the selective advantages of the chromosomal rearrangements, if any, are still unknown. An example is provided by the karyotypes of the two diploid cytotypes of *S. cepaea* with the chromosome numbers $2n = 20$ and $2n = 22$, respectively. The total length of the chromosomes of the karyotype is the same in the two cytotypes (Table 2). The fusion of two pairs of small chromosomes of the cytotype with $2n = 22$ chromosomes accounts for the differences between the two karyotypes (Fig.1a, b). The presence of a tetraploid cytotype with the chromosome number $2n = 44$, the much wider distribution of the $2n = 22$ cytotype, and the occurrence of the basic number $x = 11$ in the genetically closely related *S. creticum*, *S. cyprium*, and *S. tristriatum*, all indicate that the dysploid change in *S. cepaea* was due to chromosome fusion (descending dysploidy) rather than to chromosome fission.

The chromosomes of all European *Sedum* species are small, generally less than 2 µm long, and in many species less than 1 µm. Notwithstanding the small size of the chromosomes, considerable variation in length can be observed between species (Fig. 1a-e). Perennial species and species with low basic numbers usually have relatively long chromosomes (1-2 µm), whereas species with high, secondary basic numbers and annual species most often have very small chromosomes (less than 1 µm). Within a polyploid series the diploid cytotypes always have larger chromosomes than the polyploid cytotypes. In some taxa the chromosomes of high polyploids are only about half the size of the chromosomes of related diploid cytotypes.

The karyotypes of most European *Sedum* species are rather symmetrical. Some species and cytotypes, however, have a very asymmetrical karyotype (Fig. 1b, e). The differences in the size of the chromosomes of a single karyotype can be due to chromosomal rearrangements such as Robertsonian translocations, as for instance in *S. cepaea* (Fig. 1b), or they may result from hybridization or alloploidy. Examples of the latter kind of variation can be found in some polyploid forms of *S. rubens*. The 16-ploid ($2n = 80$) and 20-ploid ($2n = 100$) cytotypes of *S. rubens* occur throughout the Mediterrean region and usually have small chromosomes and a symmetrical karyotype. In the eastern Mediterranean region the polyploids are sympatric with diploid ($2n = 10, 12, 14$) and tetraploid ($2n = 20$) plants which have much longer chromosomes (Hart 1987, Hart & Alpinar 1991b). The occurrence of polyploid plants with an asymmetrical karyotype containing some very long chromosomes (Fig. 1e), and also of plants with odd chromosome numbers ($2n =$ c. 76, c. 94), points towards frequent hybridization and allopolyploidy in this region. Similar asymmetrical karyotypes occur in artificial allopolyploids obtained from crosses between tetraploid ($2n = 20$) and 16-ploid ($2n = 80$)

Table 1. Chromosome numbers in the European *Sedum* species and in some related species from North Africa and the Near East (names marked with an asterisk). The numbers in this list have all been determined in plants collected in nature (Hart 1978, 1982a, 1983a, b, 1984, 1985, and unpubl., Castroviejo & Calvo 1981, Hart & Berg 1982, Hébert 1983, Hart & Alpinar 1991a, b, and unpubl.).

Sedum	*x* =	2*n* = 2*x*	3*x*	4*x*	5*x*	6*x*	7*x*	8*x*	9*x*-20*x*
acre	20	40	60	80	10	120	°	°	°
aetnense	13	26	°	52	°	°	°	°	°
album	17	34	51	68	85	102	136	°	°
alpestre	8	16	°	°	°	°	°	°	°
alsinefolium	10	20	°	°	°	°	°	°	°
amplexicaule	12	24	36	48	60	72	°	96	°
andegavense	25	50	°	°	°	°	°	°	°
anglicum	12	°	°	48	°	°	°	c. 144	°
annuum	11	22	°	°	°	°	°	°	°
apoleipon	22	44	°	°	°	°	°	°	°
arenarium	12	24	°	48	°	°	°	°	°
atratum	9	18	°	36	°	°	°	°	°
borissovae	13	26	°	°	°	°	°	°	°
brevifolium	18	36	°	72	°	°	°	°	°
caeruleum	13	26	°	°	°	°	°	°	°
caespitosum	6	12	°	24	°	°	°	°	°
candollei	11	22	33	°	°	°	°	°	°
cepaea	10<-11	20, 22	°	44	°	°	°	°	°
confertiflorum	6	12	°	°	°	°	°	°	°
creticum	11	22	°	°	°	°	°	°	°
dasyphyllum	14	28	42	56	70	84	°	°	°
forsterianum	12	24	36	48	60	72	84	96	°
fragrans	13	26	°	°	°	°	°	°	°
granatense	14	28	°	56	°	°	°	°	°
grisebachii	8	16	°	32	°	°	°	°	°
gypsicola	17	34	°	68	°	102	°	°	°
hirsutum	9<-10	18, 20	°	°	°	60	°	°	°
hispanicum	7	14	°	28	°	°	°	°	°
laconicum	8	16	°	32	°	°	°	°	°
lagascae	15	30	°	°	°	°	°	°	°
litoreum	10	20	°	40	°	60	°	°	°
magellense	14<-15	28, 30	°	°	°	°	°	°	°
melanantherum	13	26	°	°	°	°	°	°	°
monregalense	15	30	°	°	°	°	°	°	°
montanum	17	34	51	68*	°	°	°	°	°
subsp. *orientale*	(49)	°	°	°	°	c. 98	°	°	°

Sedum	x=	$2n = 2x$	$3x$	$4x$	$5x$	$6x$	$7x$	$8x$	$9x$-$20x$
mucizonia	9->10->11	18, 20, 22	°	°	°	°	°	°	°
multiceps *	29	58	°	°	°	°	°	°	°
nevadense	—	°	°	°	°	°	°	°	°
obtusifolium *	5<- 6	12	°	°	°	30	°	°	°
ochroleucum	17	34	°	68	°	102	°	°	°
pallidum	10	20	40	60	°	°	°	°	°
pedicellatum	11<-14	22, 28	°	°	°	°	°	°	°
pilosum *	6	12	°	°	°	°	°	°	°
pruinatum	13	26	°	°	°	°	°	°	°
rubens	5	10, 12	14	20	°	°	°	40, 42	60, 80, 100
rupestre	(56)	°	°	°	°	88	°	112	120
subsp. *erectum*	16	°	°	64	°	96	°	°	°
samium	9	18	°	°	°	°	°	°	°
sediforme	16	32	48	60, 64	80	96	°	128	c. 144, 176
sempervivoides *	7	14	°	°	°	°	°	°	°
sexangulare	37	74	111	148	185	°	°	°	°
stefco	7	14	°	°	°	°	°	°	°
stellatum	5	10	°	°	°	°	°	°	°
steudelii *	6	12	°	°	°	°	°	°	°
stoloniferum *	7	14	°	°	°	°	°	°	°
subulatum	9	18	°	°	°	°	°	°	°
tristriatum	11	22	°	44	°	°	°	°	°
tuberiferum	16	32	°	°	°	°	°	°	°
tuberosum *	23	46	°	°	°	°	°	°	°
tymphaeum	7	14	°	°	°	°	°	°	°
ursi *	6	12	°	°	°	°	°	°	°
urvillei	16	32	48	64	80	96	112	128	°
villosum	15	30	°	°	°	°	°	°	°

plants.

The variation in DNA amount of 2C nuclei is proportionally related to the size of the chromosomes and karyotypes (compare Fig. 1 and Table 3). The amount of DNA per 2C nucleus is very low in many *Sedum* species. It is extremely low in the diploid cytotypes of *S. album* and *S. obtusifolium*, which have the lowest values reported so far for angiosperms (Bennet & Smith 1976).

Because of their enormous diversity chromosome numbers are of little use to determine relationships among taxa above the species level in *Sedum*. On the other hand, chromosome numbers have proved to be extremely useful to delimit the species. Almost 90 % of the European species can be defined and recognized unambiguously by a unique combination of morphological characters and chromosome numbers. In addition cytological characters, such as chromosome size, karyotype symmetry, and amount of DNA per nucleus, usually fully agree with this species concept. Furthermore, chromosome changes such as polyploidy and dysploidy, in combination with other evidence, can be used to indicate the direction of evolution (Jones 1970).

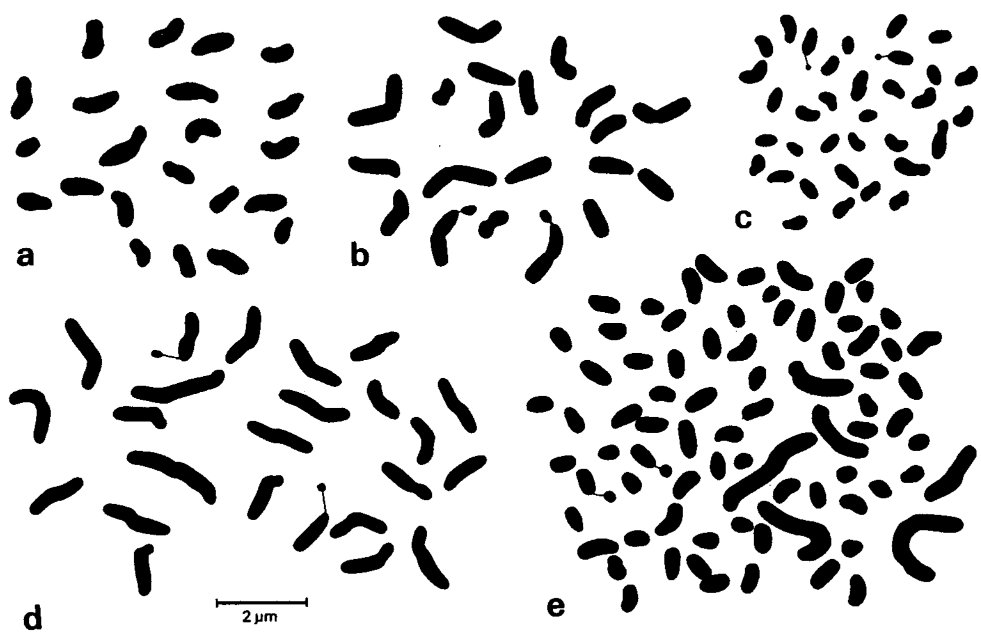

Fig. 1. Chromosome complements of some European *Sedum* species. **a, b:** two diploid cytotypes of *S. cepaea*, $2n = 22$ and $2n = 20$, respectively, from central Greece; **c:** diploid *S. album*, $2n = 34$, from Spain; **d:** diploid *S. forsterianum*, $2n = 24$, from Spain; **e:** 16-ploid *S. rubens*, $2n = 80$, from the East Aegean region (after Hart & Alpinar 1991b).

3. Hybridization

The use of crossing data is widely accepted in assessing the genetic identity of species (biological species concept) as well as in evaluating the relationships between species. A hybridization program has been started involving all European *Sedum* species. So far about 30 % of the 1431 possible interspecific combinations between the 54 European species of *Sedum* have been tested (not counting reciprocal crosses and the inevitable extra combinations due to infraspecific cytological variation). Furthermore, several crosses with species from Anatolia, Israel, and North Africa have been made. Initially the experiments were designed to test the validity of existing infrageneric classifications (e.g., Berger 1930, Fröderström 1932, Borissova 1969), but crosses between unrelated species have also been tried regularly.

Table 2. Relative length of the chromosomes (haploid set) of the two diploid cytotypes of *Sedum cepaea* (mean calculated from 12 metaphase plates from four different plants of each cytotype). SD = standard deviation.

2*n*	Mean relative length of chromosomes												Total	SD
20	7.2	6.2	5.5	5.3	5.0	4.8	4.6	4.4	4.0	—	3.5	—	50.5	0.25
22	—	6.5	5.5	5.1	4.9	4.7	4.6	4.3	4.1	3.8	3.6	3.4	50.5	0.30

Table 3. Basic and somatic chromosome numbers, and amounts of DNA (picograms per 2C nucleus) with standard deviation (SD), of nine Eurasiatic species of *Sedum*.

Sedum	*x*	2*n*	DNA	SD
ser. *Propontica*				
stellatum	5	10	0.59	0.04
obtusifolium	6	12	0.42	0.05
stoloniferum	7	14	0.63	0.08
ser. *Rupestria*				
forsterianum	12	24	0.92	0.01
rupestre subsp. *erectum*	16	64	2.07	0.09
sediforme	16	32	1.16	0.04
montanum	17	34	1.05	0.06
ochroleucum	17	34	0.91	0.01
ser. *Alba*				
album	17	34	0.29	0.02

The results of a particular cross can be affected by many factors and a negative result does not necessarily imply that the species involved are reproductively isolated (Ornduff 1969). However, it may be safely assumed that taxa which could be easily hybridized, a single crossing involving only a few flowers producing large numbers of viable seeds, are genetically more closely related than taxa which could not be hybridized at all, not even by trying each combination repeatedly with several plants from different origins as well as with different cytotypes, and with large numbers of flowers being used in each experiment.

The results of the crossing experiments in the *S. acre* group may serve as an example to demonstrate the significance of hybridization patterns in evolutionary studies on European *Sedum* species (Table 4). The *S. acre* group, as originally conceived by Webb (1964), contains the perennial, small herbaceous European *Sedum* species resembling *S. acre* in habit, size and shape of the leaves, inflorescences, and flowers, as well as in the bright yellow petals. To this group I have added three annual *Sedum* species, i.e. *S. annuum*, *S. litoreum*, and *S. samium*, and two perennial North African *Sedum* species, *S. multiceps* and *S. tuberosum*, which closely resemble *S. acre* in habit as well as in the size, shape, and colour of their flowers (Hart 1978, 1982a, 1983a, b).

The results of the crosses between the 14 species of the *S. acre* group thus redefined are summarized in Table 4. 12 of the 14 species have been tested for self-compatibility. The selfings all produced seeds, usually in considerable quantities, except in *S. urvillei* which performed below average. Fertility of the progeny of selfings was usually high, except in the hybrids with odd ploidy levels. Of the 91 possible interspecific combinations between the 14 species of the *S. acre* group 60 % have been tested. The success of the crosses varied widely, but the variation shows a quite distinctive pattern. *S. acre*, *S. litoreum*, and *S. samium* are reproductively completely isolated, and can only breed with themselves, whereas the other 11 species are interfertile in various degrees. They form a comparium, i.e. "a group of species which have the potency to hybridize" (Danser 1929). In contrast to the highly fertile intraspecific hybrids the interspecific hybrids are sterile or their fertility is very much reduced, at least at the diploid level.

The genetic relationships among the 14 species of the S. acre group as indicated by their hybridization patterns deviate in many respects from previous phylogenies and classifications based on morphological characters (Hart 1978, 1982a). Over-emphasis on vegetative characters like habit and growth form has deluded many taxonomists in the assessment of the taxonomic positions of *S. acre*, the annual species, and *S. tuberosum*. The isolated position of *S. acre* in the hybridization diallel contrasts sharply with the generally accepted view that this species is closely related to the other perennial species of the *S. acre* group (Boissier 1872, Fröderström 1932, Webb 1964). The obviously diverging genetic affinities of the four yellow-flowered *Sedum* species contradict their incorporation in *S.* sect. *Epeteium* (Boissier 1872, Praeger 1928, Berger 1930) together with a large number of presumably equally unrelated species. Until recently the resemblance between the thickened monopodial rhizome of *Rhodiola* and *S. tuberosum* has prevented many systematists to appreciate the equally obvious differences between the two taxa and to fully perceive the genetic relationships between the latter and other species included in the *S. acre* group.

The results of the whole hybridization program, which in addition to 53 European *Sedum* species (*S. nevadense* was not available) involved 8 *Sedum* species from Anatolia and North Africa, agree with the results described for the *S. acre* group. Selfings were always highly successful and their progeny was fully fertile. In contrast, the interspecific hybrids, at least at the diploid level, were usually completely sterile. The interspecific crosses which have been performed with these 61 species so far indicate the presence of 29 comparia in this assemblage. 17 comparia contain only a single species, though quite often several cytotypes, whereas the remaining 12 comparia vary in size from 2 to 11 species and may contain up to 25 cytotypes. Further experiments may reduce the number of comparia, especially of the monotypic ones, or else may add to some of them species from the Near East and North Africa which have not yet been incorporated into the

Table 4. Hybridization diallel of the species of the *Sedum acre* group. The first figure indicates the number of flowers used in each combination, the second figure (after the colon) the mean number of viable seeds per flower produced in each cross.

Sedum	x	*acre* 20	*alpe* 8	*gris* 8	*laco* 8	*annu* 11	*bori* 13	*tu-f* 16	*urvi* 16	*apol* 22	*tu-s* 23	*mult* 29	*sexa* 37	*sami* 18	*lito* 10
acre	20	91:21	10:0	21:0	—	16:0	—	—	16:0	—	—	—	5:0	—	—
alpestre	8		14:47	5:0	—	1:0	—	—	1:13	7:18	7:84	6:20	—	5:0	5:0
grisebachii	8	14:0	22:2	42:45	19:2	22:0	12:1	—	7:0	5:2	—	7:0	18:2	2:0	—
laconicum	8	2:0	5:27	15:1	13:16	—	—	—	—	8:4	15:0	8:11	—	8:0	2:0
annuum	11	6:0	8:7	18:0	3:0	8:55	—	—	3:11	—	—	—	—	12:0	4:0
borissovae	13	5:0	5:6	12:0	7:16	3:0	5:7	5:8	17:2	—	—	—	22:6	—	—
tuberiferum	16	—	—	5:0	—	—	5:0	5:13	28:2	—	—	—	11:0	7:0	—
urvillei	16	40:0	—	34:0	—	—	3:0	—	70:4	—	—	—	10:0	—	—
apoleipon	22	—	7:11	2:0	2:11	2:0	—	—	—	—	—	—	—	1:0	—
tuberosum	23	—	2:0	2:0	—	3:0	—	—	—	—	—	2:20	—	—	—
multiceps	29	2:0	5:3	—	—	—	—	4:10	4:15	—	5:49	4:43	—	—	5:0
sexangulare	37	35:0	—	6:0	—	—	2:0	—	2:0	—	—	—	11:7	—	—
samium	9	—	6:0	—	6:0	8:0	—	—	5:0	—	7:0	—	—	5:20	—
litoreum	10	—	—	—	5:0	—	—	—	—	—	—	—	—	3:0	21:44

program.

The conclusions to be derived from the results of this hybridization program are that in *Sedum* artificial hybridization is an appropriate method to delimit species, and may further be useful to establish relationships between species, because certain groups of species apparently are separated by strong, effective hybridization barriers. These hybridization barriers, however, are neither correlated with the basic chromosome number and ploidy-level of the species, nor are they correlated with the distribution of the species. Whether the taxa are allopatric or sympatric or occur together in the same habitat apparently has no effect whatsoever on their hybridization pattern. The relation between the hybridization patterns of the species and morphological variation will be discussed in the following sections.

4. The series concept

Although the hybridization pattern of the European species of *Sedum* is apparently not correlated with the morphological characters traditionally used in infrageneric classifications, particularly with those relating to life-form and habit, some comparia agree completely or in part with the infrageneric taxa distinguished by Praeger (1921), Berger (1930), Fröderström (1932), and Borissova (1939, 1969). Because these authors most frequently attributed the rank of series to these groups of species I have classified the comparia at the same taxonomic level (Hart 1978, 1983b, 1985), except for *S.* ser. *Aithales* and *S.* ser. *Pedicellata* (see chapter 10).

In *Sedum* the series (comparia) clearly represent the evolutionary units immediately preceding the terminal taxa, i.e. the species and cytotypes. Morphologically *S.* ser. *Rupestria*, *S.* ser. *Alpestria* (including *S.* ser. *Mitia*), and *S.* ser. *Propontica* are very distinct and have been recognized for a long time already. The majority of the other series is also quite distinct and can be easily distinguished using different combinations of a variety of morphological characters. In addition the series can be defined cytologically and biochemically.

The morphological characters of which the character states appeared to be correlated with the hybridization patterns of the species have already been discussed at some length previously (Hart 1978, 1987, Hart & Koek-Noorman 1990), but it may be useful to mention them once more: (1) The insertion of the sepals (Fig. 2), which are either free and spurred at the base or basally fused with the receptacle. (2) The ornamentation of the testa (Fig. 3), which consists either of hexagonal cells with a single papilla in the centre or of longitudinal rows of transversely oblong cells with two papillae each. These papillae are often fused forming longitudinal ridges or costae. (3) The shape of the apex of the seed. This is either acute or has a small ridge encircling the tip which is called a corona. (4) The plants are either completely glabrous or have an indumentum which usually consists of simple glandular hairs. The hybridization patterns of the species and the states of these four characters are inversely related. When two species do not completely agree in the character states of all four characters interspecific hybrids could never be produced. The reverse, however, does not hold true. When species agree in the states of these four characters they can not always hybridize. Inspection of the hybridization diallel of the *S. acre* group (Table 2) shows that hybridization barriers between the species coincide indeed with a change of the character state of at least one of these four characters. All 14 species have seeds with a pointed apex, but *S. acre*, *S. litoreum*, and *S. samium* differ from the other 11 species with respect to the insertion of the sepals (*S. acre*), the ornamentation of the testa (*S. litoreum*), and the presence of an indumentum (*S. samium*).

A second independent set of characters related to the identity of the European series of *Sedum* are the size of the chromosomes (Fig. 1) and the amount of DNA per nucleus. In general the species of each series agree perfectly well in these two characters. A complete survey of DNA amounts per nucleus, however, is not yet available for all series. The figures presented in Table 3 clearly indicate the value of this character, though.

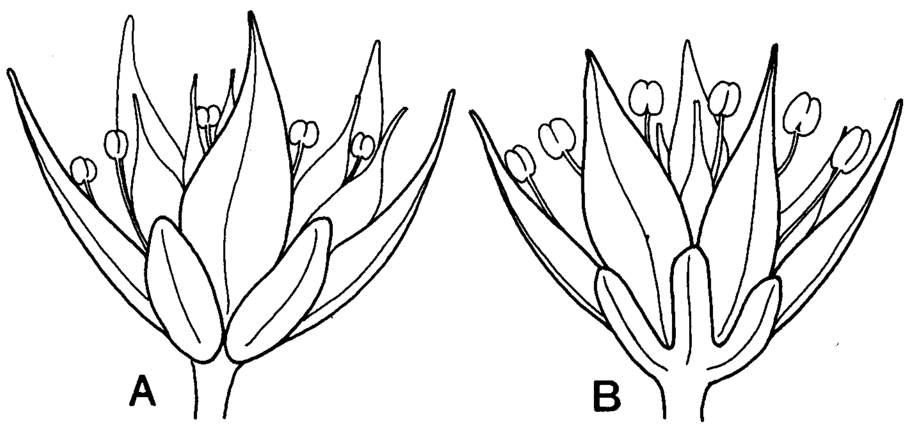

Fig. 2. Insertion of the sepals in *Sedum*. **A:** *S. acre*; **B:** *S. sexangulare* (after Fröderström 1932).

The third independent set of characters is the variation of chloroplast DNA. The results of some preliminary studies of restriction enzyme fragment patterns of chloroplast DNA of some 30 Eurasiatic species of *Sedum* clearly indicate that the genetic similarity, based on shared restriction fragments, is much greater among the species of each series than between species of different series.

5. Evolutionary trends

Although all series of *Sedum* can be delimited by a unique set of morphological characters (see chapter 10), many series still show a large amount of morphological variation, especially the large series. Much of this variation can be attributed to adaptations to different habitats. Quite often new, derived or specialized character states apparently evolved independently in different series. Many of these apomorphies have frequently been used in previous infrageneric classifications of *Sedum*, and some have even been considered to be of utmost taxonomic importance. Now that it has become clear that parallelism is the true nature of these apormophies, they can be evaluated accordingly and considered in their proper context. Very often these apomorphies represent an evolutionary trend restricted to a certain geographical region, though in most cases we do not yet know or understand the selective advantage of these features.

Annual and/or hapaxanth *Sedum* species are very common in Europe, and they amount to about 40 % of the species. In about one third of the European series of *Sedum* a close (phylo-)genetic relationship between annual and perennial species could be demonstrated, both forms occurring side by side. The species of the other 18 series are either strictly annual (9 series) or perennial (9 series). With the exception of *S. annuum* and *S. villosum*, which also occur in northern Europe, and *S. atratum*, which is restricted to high

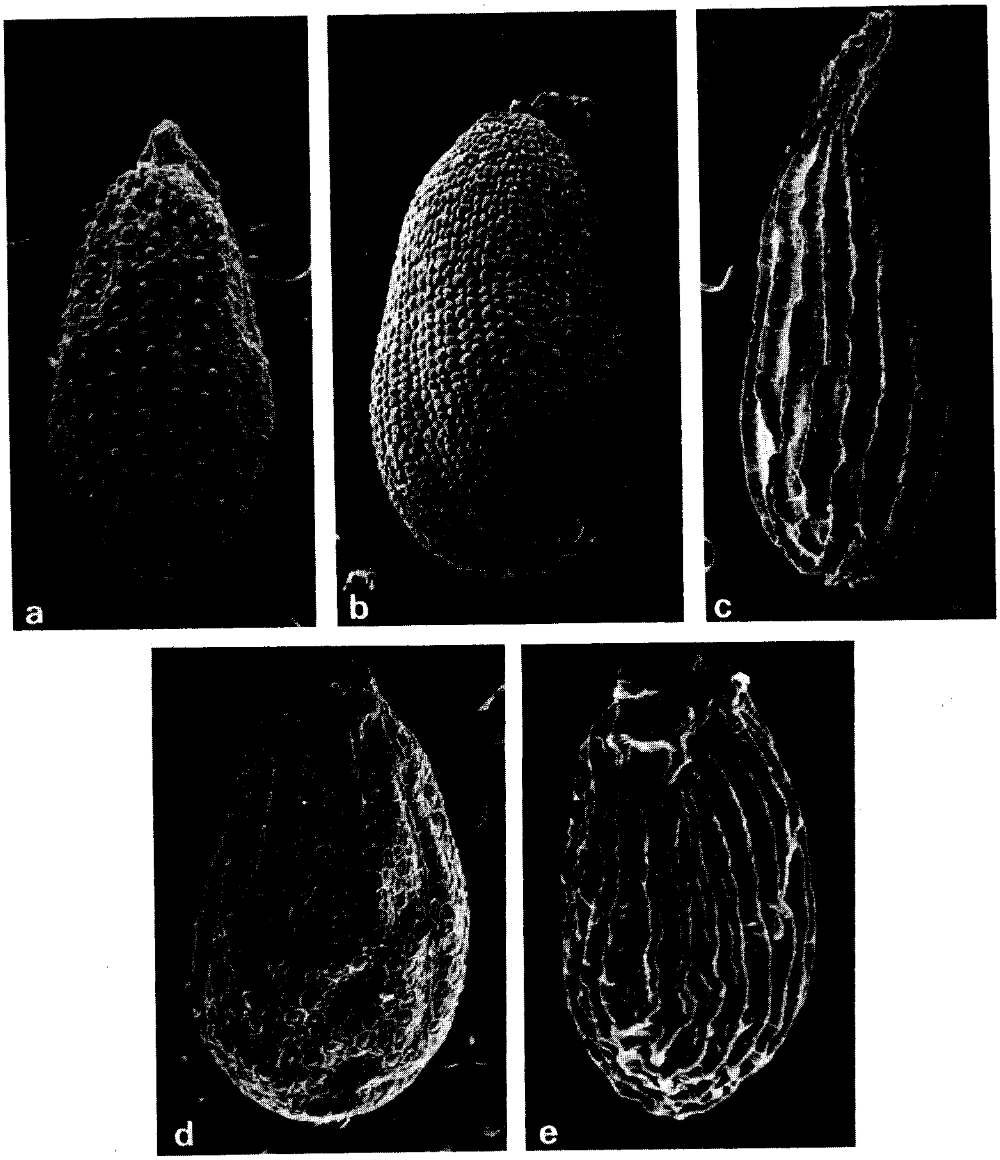

Fig. 3. Ornamentation of the testa and shape of the seeds in *Sedum*. **a:** *S. grisebachii*; **b:** *S. brevifolium*; **c:** *S. sediforme*; **d:** *S. arenarium*; **e:** *S. cepaea*. Reticulate (a, d), bipapillate (b), costate (c, e), apiculate (a-c), and coronate (d-e) seeds.

altitudes, the annual *Sedum* species are confined to lowland habitats in the Mediterranean region. In North America and Asia the number of annual *Sedum* species is much lower than in Europe and in *Sedum* the annual habit may well be an adaptation to the typical

Mediterranean climate. However, the annual habit is not the only way for a *Sedum* to survive the hot, dry Mediterranean summer. An alternative strategy to adapt to summer dryness is the production of subterranean propagules. *S. tuberiferum* of *S.* ser. *Alpestria* produces small tubers consisting of a swollen stem clothed with bracteate, white leaves, whereas the propagules of *S. obtusifolium* of *S.* ser. *Propontica* consist of short offshoots covered with tightly appressed, swollen, almost globular white leaves.

Rosettes have evolved in many *Crassulaceae* as an adequate adaptation to water stress, but in *Sedum* they are not very common. Conspicuous rosettes are characteristic features of the species of *S.* ser. *Sempervivoides* and *S.* ser. *Cepaea*. The rosettes of *S.* ser. *Alsinefolia* and *S.* ser. *Hirsuta* are somewhat less distinct. The dense clusters of leaves at the tips of the non-flowering shoots of *S. forsterianum* of *S.* ser. *Rupestria*, *S. laconicum* and *S. multiceps* of *S.* ser. *Alpestria*, can be regarded as intermediate stages.

A monopodial primary axis evolved independently in three *Sedum* species of the central Mediterranean region, i.e. in *S. tuberosum* of *S.* ser. *Alpestria* from Tunisia, in *S. tristriatum* of *S.* ser. *Cepaea* from Crete and the Peloponnisos, and in *S. tymphaeum* of *S.* ser. *Sempervivoides* from northern Greece. The monopodial, primary shoot of *S. tuberosum* has evolved into a tuberous rhizome which closely resembles a similar rhizome of many species of *Rhodiola* (Hart 1982a).

The typical *Sedum* flower is 5-parted, but in many series a change in the number of floral parts has occurred. *S.* ser. *Rupestria* is the best known example of *Sedum* with polymerous flowers. Most species of *S.* ser. *Rupestria* have 6- to 7-merous flowers, but the flowers of *S. amplexicaule* and *S. sediforme* sometimes consist of up to 12 parts. Both species were originally placed in *Sempervivum*. *S. hispanicum* of *S.* ser. *Glaucorubens* has 6- to 9-merous flowers. The second species of this comparium, however, *S. steudelii* has strictly 5-merous flowers. Hybrids between the two species are intermediate in this respect as could be expected. A reduction of the number of floral parts has also occurred several times, but is usually less obvious, most probably because a reduction of the number of floral parts most often occurs in inconspicuous and autogamous flowers. *S. aetnense*, *S. andegavense* and *S. stefco* have tetramerous flowers, though the terminal flower of the flowering shoot is quite often 5-merous. Some populations of *S. caespitosum* consist exclusively of plants with strictly tetramerous flowers.

The typical *Sedum* flower is choripetalous, but basally slightly connate petals are common throughout the genus. The petals of *S. alsinefolium* and *S. fragrans* of *S.* ser. *Alsinefolia* are fused for about one third. The flowers of *S. lagascae* and *S. villosum* of *S.* ser. *Subrosea* and of the polyploid form of *S. hirsutum* (*S. winkleri*) also have basally distinctly connate petals. The most spectacular examples of sympetalous flowers in European *Sedum* species, however, are provided by *S. candollei* of *S.* ser. *Pedicellata* and *S. mucizonia* of *S.* ser. *Dasyphylla*, which both have petals united for 2/3 or more of their length. Usually both species are classified in Mucizonia of subfamily *Cotyledonoideae* (Candolle 1828, Berger 1930, Webb 1964), but their hybridization patterns and the morphological features correlated with the hybridization patterns clearly indicate that they both evolved independently from different groups of *Sedum* in the western part of the Mediterranean region (see chapter 10). Here the unique sympetalous flower of the species of *Pistorinia* DC. should also be mentioned. The corolla tube of the flowers of *Pistorinia* may be up to 2 cm long, 3-5 times the length of the lobes, and is often quite narrow. As yet it is not possible to link *Pistorinia* with certainty to any group of *Sedum*, but most certainly the affinities of *Pistorinia* should be searched for in the *Sedoideae* rather than in the highly artificial *Cotyledonoideae* (Uhl 1963).

Flowers of *Sedum* are usually either yellow or white. Except for *S.* ser. *Rupestria* in which both colours occur, the species of each series all have flowers of the same basic colour. However, a considerable number of species of the groups with essentially white petals have developed pink or red flowers. The three species of *S.* ser. *Sempervivoides* are the most striking example. The flowers of *S. tymphaeum* are white, of *S. pilosum* pink, and the flowers of *S. sempervivoides* are brilliant red. In the eastern Mediterranean region pink flowers further occur in many populations of *S. pallidum* and *S. rubens* of *S.* ser. *Aithales*, and the three species of *S.* ser. *Propontica* have pink flowers too, though Greek populations of *S. stellatum* are predominantly white-flowered. The flowers of the West Mediterranean *S. lagascae* and *S. villosum* of *S.* ser. *Subrosea* are pink with a yellow base. Furthermore, the flowers of *S. candollei* of *S.* ser. *Pedicellata* are often pink or reddish.

In *Sedum* the colour of the anthers is either red or yellow. Red anthers usually occur in combination with white petals, whereas yellow flowers have stamens with yellow anthers. Some white-flowered plants lack the ability to synthesise anthocyanins, and consequently their anthers are yellow instead of red. The reverse development can be observed in some yellow-flowered species of the eastern Mediterranean region. In some populations of *S. grisebachii* and *S. laconicum* of *S.* ser. *Alpestria*, *S. litoreum* of *S.* ser. *Litorea*, and *S. samium* of *S.* ser. *Samia*, many plants have stamens with red anthers. This character combination is restricted to the Aegean region and is most prominent on Crete (100 % in some populations of *S. litoreum* on Crete).

A reduction of the number of epipetalous stamens, ultimately resulting in a haplostemonous flower, has occurred in the evolution of many *Sedum* species. In the European species a reduction of the number of stamens is always correlated with a tendency to autogamy or pseudocleistogamy, and involves changes in a whole series of correlated characters. Usually the autogamous plants have small, inconspicuous flowers, which hardly open during anthesis, small anthers (containing few pollen grains), and short styles. *S. aetnense* of *S.* ser. *Macrosepala*, *S. andegavense* of *S.* ser. *Pedicellata*, and *S. caespitosum* of *S.* ser. *Rubra* are completely autogamous and have strictly haplostemonous flowers. The turnover from the allogamous obdiplostemonous condition to the autogamous haplostemonous condition can be observed in *S. rubens* of *S.* ser. *Aithales* and *S. litoreum* of *S.* ser. *Litorea*. In both species the change in the mode of pollination runs parallel with an increasing degree of ploidy, thus clearly indicating the direction of the development (Hart 1985, and in prep., Hart & Alpinar 1991b).

The number of ovules per carpel varies from 10 to 20 in most species of *Sedum*. In some species the number of ovules is somewhat reduced, e.g. in *S. album* and *S. gypsicola* which often have only about 7 ovules in each carpel. A more drastic reduction has occurred in *S. melanantherum* of *S.* ser. *Melananthera* and *S. caeruleum* of *S.* ser. *Caerulea*. The carpels of *S. caeruleum* contain only 2 ovules, of which usually only 1 develops into a mature seed, whereas *S. melanantherum* has 2 to 4 ovules per carpel.

6. Centres of speciation

The European series of *Sedum* as presented here are comparia. The species of each series are therefore regarded to be genetically closely related, and consequently each series is considered to be monophyletic. With the use of the geographical distribution of the morphological and cytological variation within the species and series the centre of origin of the series has been determined. In all series of *Sedum* the area of maximum variation, that is the area with the highest number of species and/or cytotypes, coincides with the area of the diploid cytotypes with the lowest basic numbers. The latter are considered to represent the least advanced (oldest or most original) taxa, and usually also have a very limited distribution.

The centres of origin of several series of *Sedum* appear to be located in the same region, and for the European species of *Sedum* by and large three main and two secondary centres of origin can be indicated. By now the centre of origin of most European series of *Sedum* has been determined and can be assigned to one of the following three regions: (1) the West Mediterranean centre of origin which encompasses the Iberian Peninsula (Portugal and Spain) and northern Africa; (2) the East Mediterranean centre of origin, which encompasses the Aegean region (mainly Crete, the East Aegean Islands and western Turkey) and the southern Balkans; and (3) the Irano-Turanian centre of origin which encompasses the Caucasus and adjacent mountain ranges in eastern Anatolia and northern Iran. In addition to these three main centres secondary centres of speciation are located in the western Alps and northern Africa (Tunisia, Cyrenaica).

As an example of the assessment of the main and secondary centres of origin of the present European *Sedum* flora three series of *Sedum* have been chosen for discussion. The distribution patterns of the species and cytoytpes of *S.* ser. *Rupestria* of the West Mediterranean centre of origin, of *S.* ser. *Alpestria* of the East Mediterranean centre, and of *S.* ser. *Propontica* of the Irano-Turanian centre will be analyzed in some detail (Fig. 4a-c).

An instructive example of a group of *Sedum* species which evolved from the West-Mediterranean centre of origin is *S.* ser. *Rupestria* (Fig. 4a). Its 7 species are widely distributed throughout the Mediterranean region and central Europe, but most morphological and cytological diversity is found on the Iberian Peninsula. 6 of them occur in Portugal and Spain, and 17 out of a total of about 25 cytotypes so far reported for the series also occur on the Iberian Peninsula. Furthermore, the diploid cytotypes of the species with the lowest basic numbers, *S. amplexicaule* (x = 12), *S. forsterianum* (x = 12), and *S. pruinatum* (x = 13), are endemic to north-western Portugal and adjacent central Spain. Moreover, the diploid cytotype of *S. sediforme* (x = 16) is restricted to the Iberian Peninsula and adjacent southern France. The highest concentration of species of *S.* ser. *Rupestria* is found in north-western Portugal and adjacent Spain, and in the French-Italian Alps and the Cévennes (France). The latter two centres, however, contain fewer cytotypes, and diploid cytotypes only of *S. ochroleucum* (x = 17) and *S. montanum* (x = 17) of which the basic numbers are considered to be of secondary origin.

A western origin has been inferred for 8 more series, i.e. *S.* ser. *Alba*, *S.* ser. *Anglica*, *S.* ser. *Caerulea*, *S.* ser. *Dasyphylla*, *S.* ser. *Hirsuta*, *S.* ser. *Melananthera*, *S.* ser. *Pedicellata*, and *S.* ser. *Subrosea*. Most probably the species of *S.* ser. *Alsinefolia* and *S.* ser. *Monregalensia* evolved from the secondary centre of origin in the French-Italian Alps. The most striking example of a group of *Sedum* species originating from the East Mediterranean centre of origin is the large and diverse *S.* ser. *Alpestria* (Fig. 4b). Its 12 species are widely distributed throughout the Mediterranean region, western and central Europe and Anatolia, but most variation is encountered on the southern part of the Balkan Peninsula. 8 of them occur in Greece and adjacent Macedonia (southern Bulgaria and Yugoslavia), and three are endemic to this region. Furthermore, 15 out of the 23 cytotypes known for *S.* ser. *Alpestria* occur in the southern Balkans, and the distribution of the paleo-diploid taxa (x = 8) *S. alpestre*, *S. grisebachii*, and *S. laconicum*, is also restricted to the Balkans (Hart 1985). *S. alpestre* may appear to be an exception, but in the northern Balkans, Alps, Karpathians, and Pyrenees, this species is represented by the more advanced, predominantly autogamous form, whereas the ancestral allogamous form, *S. alpestre* var. *erythraeum*, is restricted to northern Greece and Macedonia. Only 4 species of *S.* ser. *Alpestria* do not occur on the Balkan Peninsula. *S. multiceps* (x = 29) and *S. tuberosum* (x = 23) are neo-endemics which evolved in the secondary centre of speciation in northern Tunisia and adjacent Algeria (Hart 1982a). *S. borissovae* is endemic to the

Ukraine, where it occurs solely on granitic outcrops (Webb 1964). It has a secondary basic number of $x = 13$. *S. ursi* ($x = 6$) is endemic to the mountains of western and southern Anatolia (Hart 1990, Hart & Alpinar unpubl.).

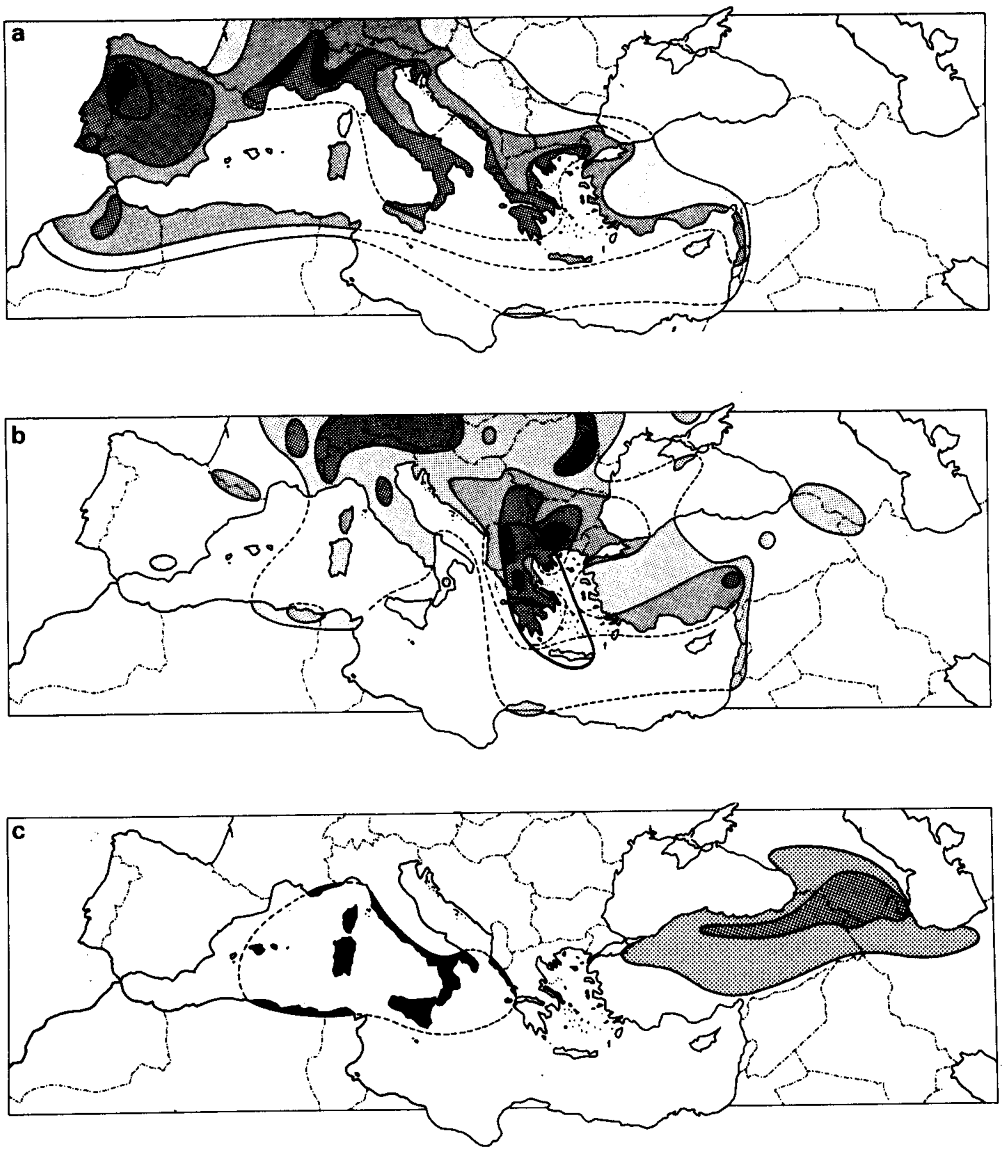

Fig. 4. Centres of origin of three European series of *Sedum*. **a**: distribution of *S*. ser. ***Rupestria***; **b**: distribution of *S*. ser. ***Alpestria***; **c**: distribution of *S*. ser. ***Propontica***. The four different shades of gray indicate the number of species per area, viz., 1, 2, 3, and 4-5 species (in order of increasing density). The distribution of *S. stellatum* (in **c**) is indicated with black. The distribution areas of the paleo-diploid cytotypes of *S*. ser. ***Rupestria*** and *S*. ser. ***Alpestria*** are indicated with a bold line.

Some 10 more series of *Sedum* have evolved from the East Mediterranean centre of origin. *S.* ser. *Aithales*, *S.* ser. *Confertiflora*, *S.* ser. *Macrosepala*, *S.* ser. *Rubra*, and *S.* ser. *Samia* evolved in the East Aegean region or southern Anatolia. *S.* ser. *Cepaea* and *S.* ser. *Litorea*, on the other hand, evolved in the South Aegean region. Both taxa are most diverse on Crete. Most probably the monotypic *S.* ser. *Magellensia*, *S.* ser. *Sedella*, and *S.* ser. *Stefco* originated in the southern Balkans.

As an example of the *Sedum* species originating from the Irano-Turanian centre of origin *S.* ser. *Propontica* was chosen (Fig. 4c). In contrast to the previous examples it is a small group (3 species), and its area is noticeably disjunct (Hart 1984). Two of the three species and three out of the four cytotypes known for this group occur in north-eastern Anatolia, the Caucasus and adjacent Iran. The third species, *S. stellatum*, is confined to the regions bordering the central part of the Mediterranean. The annual *S. stellatum* is predominantly autogamous and clearly advanced in comparison to the perennial and allogamous, Irano-Turanian *S. obtusifolium* and *S. stoloniferum*.

The other European *Sedum* species which evolved from the Irano-Turanian centre of origin belong to *S.* ser. *Sempervivoides*, which has a disjunct distribution pattern similar to *S.* ser. *Propontica*, and to *S.* ser. *Glauco-rubens* and *S.* ser. *Subulata*.

7. Relationships between the series

To determine the relationships between the series a cladistic analysis has been performed on a data set derived from the descriptions of the series in chapter 10 (22 characters and 54 character states). *Saxifraga aizoides* L. has been used as an outgroup. Although the data set is quite small the most parsimonious tree (Fig. 5) is completely resolved, but has very little structure. In addition to the distinct *S.* ser. *Rupestria* and *S.* ser. *Subulata* only two about equally large, though ill defined, groups are distinguished, i.e. *S.* ser. *Acria* to *S.* ser. *Aithales*, and *S.* ser. *Confertiflora* to *S.* ser. *Hirsuta*. These two groups differ in only one character, i.e., the position of the follicles. However, even this character does not discriminate perfectly between the two groups, the monotypic *S.* ser. *Melananthera* and *S.* ser. *Sedella* having both been placed in the wrong cluster.

Rather surprisingly, the results of this cladistic analysis almost perfectly match Fröderström's (1932) and Grulich's (1984) classifications of the European species of *Sedum*. However, Fröderström's and Grulich's classifications are both very artificial. They are based on a single character and must therefore be rejected, similar to the classifications of Koch (1843), Boissier (1872), Berger (1930), etc., which are primarily based on habit (annual vs. perennial).

In order to generate a classification of the European series of *Sedum* that would be more significant in the evolutionary sense, the weight attributed to the four characters of which the different states are correlated with the hybridization patterns of the species has been considered. These characters are highly significant in regard to the genetic relationships of the species, but they have additional value because the direction of the transformation of the states has been determined for three of them (Hart & Berendsen 1980, Hart & Koek-Noorman 1990). From an anatomical and ontogenetic point of view the free, spurred sepals, the reticulate testa, and the acute seed apex represent the primitive conditions, whereas the basally fused sepals, the costate testa, and the coronate seed apex are the derived or advanced character states. Furthermore, the presence of an indumentum is regarded as an advanced condition.

The tree in Fig. 6 is based on the same data set as the previous cladogram, but extra weight has been given to the four characters which are correlated with the hybridization patterns of the species. Although this weighting resulted in a substantial increase of the total length of the tree (to about 130 %), its consistency slightly increased. The structure of the cladogram also changed considerably. Biologically it is now much more significant, though in one place not completely resolved. Now there are two main groups, which are rather well defined: a large group comprising the specialized taxa, *S.* ser. *Litorea* to *S.* ser. *Magellensia*, and a smaller group in which the primitive character states predominate, *S.* ser. *Acria* to *S.* ser. *Samia*. The advanced taxa (21 series with 44 species) share an apomorphy for two characters. They all have a costate (orbipapillate) testa and sepals which are basally fused with the receptacle. Furthermore, the species of this group, except *S. atratum*, *S. caespitosum*, *S. litoreum*, *S. magellense* and *S. stefco*, are glandular-pubescent. The less advanced taxa (6 series and 18 species) share one plesiomorphy, the reticulate testa. With respect to the other characters which are correlated with the hybridization patterns the second group is rather diverse. There are homoplasies in *S.* ser. *Alpestria* (sepals basally fused), in *S.* ser. *Samia* (glandular-pubescent, sepals basally fused), and in *S.* ser. *Anglica* and *S.* ser. *Melananthera* (seeds coronate).

Neither the most parsimonious tree (Fig. 5) nor the second, weighted cladogram (Fig. 6) shows any resemblance whatsoever with the arrangement of the series according to their centre of origin (Fig. 4). On the contrary the series originating from each of the three Eurasiatic centres of origin are apparently randomly distributed among the two major clades in both trees. From this apparent contradiction different conclusions can be drawn.

If the taxa originating from each centre of origin are monophyletic, evolution has followed a similar course in all three centres with respect to the development of the characters correlated with the hybridization pattern of the species. Considering the high frequency of parallelism demonstrated previously for other characters, it may be quite reasonable to assume that evolution went along this course. However, when the *Sedum* floras of America and Asia are also taken into account this becomes less likely. In America as well as in Asia species occur which agree with each of the major groups of the two cladograms (ortho-verus kypho-carpic, and primitive versus advanced). The independent development of identical combinations of characters in at least four or five different places, on three continents, is not, however, a very convincing hypothesis.

On the other hand, if the taxa originating from each centre of origin do not share a common ancestor, the conclusion is inevitable that the *Sedum* floras of the three European centres of speciation (and also the *Sedum* floras of the two other continents) were already completely differentiated regarding the characters correlated with the hybridization pattern of the present species from the onset. Consequently the three main European centres of origin of the present *Sedum* flora represent fragments of an older now extinct *Sedum* flora. Accordingly the centres of origin may be identical with refugia for Mediterranean flora elements during the ice ages or even more distant geological events.

8. Conclusions

From the results and discussions in the preceding paragraphs the following story of evolution of *Sedum* in Europe emerges. The European *Sedum* flora in its present form descends from two related, but distinct ancestral groups. An ill-defined, somewhat loose group of species characterized by various combinations of primitive characters on one hand, and a rather distinct group of specialized species united by at least two synapomorphies on the other hand. This primeval European *Sedum* flora itself was a segregate of a more ancient *Sedum* flora which extended to America as well as to Asia and already consisted of the two aforementioned units throughout its range. On all three

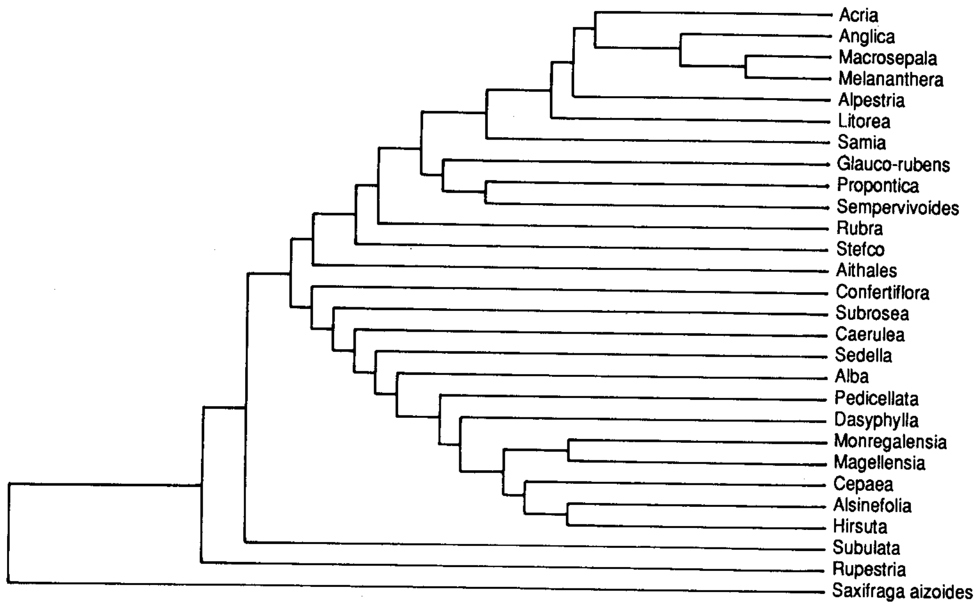

Fig. 5. Most parsimonious tree of the European series of *Sedum* based on the characters used in the descriptions of the series in chapter 10 (22 characters, 58 character states).

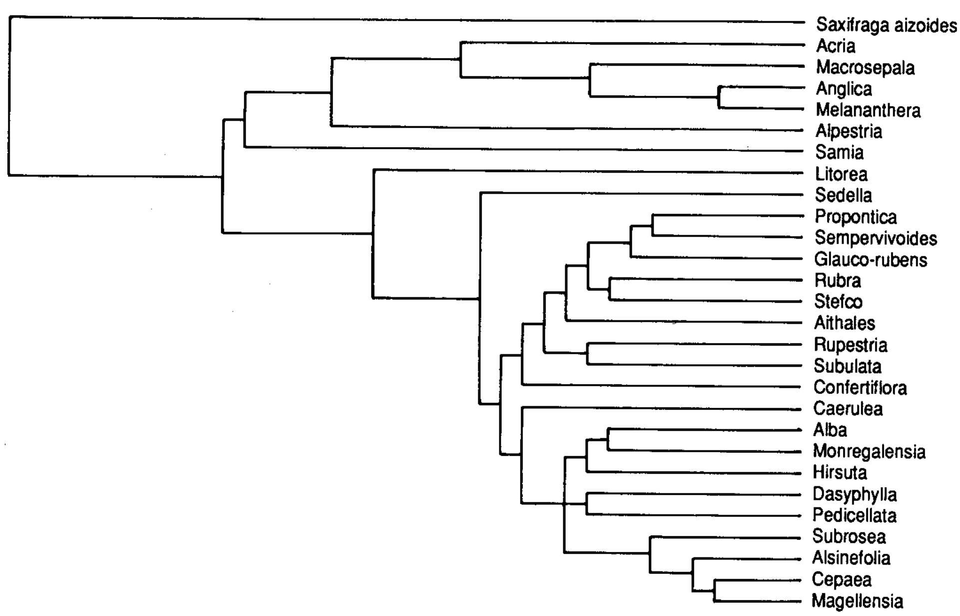

Fig. 6. Cladogram of the European series of *Sedum* based on the same data set as Fig. 5, but with the weight of the four characters which are correlated with the hybridization patterns of the species being enhanced: ornamentation of the testa (x6); insertion of the sepals (x5); shape of the seed apex (x4); presence or absence of an indumentum (x3).

continents the more advanced species were most successful and gave rise to numerous new taxa. Most prominent among these are of course the large and distinct groups defined by several synapomorphies such as for instance *Aeonium*, *Rosularia*, and *Sempervivum* in Europe, *Echeveria*, *Dudleya*, and *Pachyphytum* in America, and *Hylotelephium* and *Rhodiola* in Asia. In Europe, however, the ancient *Sedum* flora was reduced and its fragments became confined to three isolated areas (refugia) at some time during this period of proliferation and specialization. These three regions then became centres of origin when the species they held in turn started to spread and proliferate, before they reached their present distributions.

The terminal units of the evolution of *Sedum* in Europe, the species and cytotypes, are distinct and well defined. The evolutionary units directly preceding the terminal taxa are the comparia or series. The 54 European *Sedum* species are arranged in 27 series of different size, which can be defined by various combinations of autapomorphies. Most probably all series are monophyletic. They differ, however, in age because the hybridization barriers which separate them date back to different periods and to different events of reproductive isolation.

Crossability and interfertility have often been used to define generic limits, though these features alone are not sufficient to segregate or join genera (Stebbins 1950, Kruckeberg 1962, Ornduff 1969, Stace 1975, Powell 1985). In respect to crossability the European series of *Sedum* are similar to well defined comparia such as *Aeonium*, *Echeveria*, *Dudleya*, and *Sempervivum*, and it can be argued that the series of *Sedum* also merit generic rank. However, it is the amount of evolutionary divergence rather than the antiquity of the split (Cronquist 1969) which should determine the taxonomic position of a group, and the morphological differentiation among the series of *Sedum* is very small compared with other Crassulacean genera. The morphological distance between the primitive and advanced groups of *Sedum* is much less apparent than between the advanced groups of *Sedum* and more specialized genera such as *Aeonium* and *Sempervivum*, though in the evolutionary sense the latter genera and the advanced groups of *Sedum* are by and large equidistant to the primitive groups of *Sedum*. Consequently, nothing would be gained by treating the European series of *Sedum* as genera. In addition to many nomenclatural changes it would require the creation of new undefinable or paraphyletic taxa (subfamilies, tribes or subtribes) to indicate the relationships among these new genera (Funk 1985).

Rowley (1988) in a discussion of the classification of the *Sedoideae* and the status of the segregate genera of *Sedum* recommended the retention of "a united *Sedum*, embracing all the segregates, although retaining the most distinctive at the level of subgenera, sections and series". I have gladly accepted this advice, being sure that in following this point of view the stability of nomenclature is served best.

9. Key to the European series of *Sedum*

- Testa reticulate
  - Sepals basally free
    - Seeds apiculate. Plants glabrous throughout
      - Petals yellow — 1. *S.* ser. *Acria*
      - Petals white — 2. *S.* ser. *Macrosepala*
    - Seeds coronate. Plants glabrous. Petals white
      - Follicles stellate-patent, with lips — 3. *S.* ser. *Anglica*
      - Follicles erect — 4. *S.* ser. *Melananthera*
  - Sepals basally connate. Seeds apiculate. Petals yellow
    - Plants glabrous throughout — 5. *S.* ser. *Alpestria*
    - Plants glandular-pubescent (petals) — 6. *S.* ser. *Samia*
- Testa costate, rarely bipapillate. Sepals basally connate
  - Seeds apiculate
    - Plants glabrous throughout
      - Petals yellow — 7. *S.* ser. *Litorea*
      - Petals white
        - Follicles erect — 20. *S.* ser. *Sedella*
        - Follicles stellate-patent
          - Flowers 5-merous, haplostemonous — 18. *S.* ser. *Rubra*
          - Flowers 4-merous, obdiplostemonous — 22. *S.* ser. *Stefco*
    - Plants glandular-pubescent
      - Petals yellow or cream. Leaves mucronate — 19. *S.* ser. *Rupestria*
      - Petals white. Leaves not mucronate
        - Follicles erect
          - Ovules 1-2 per carpel. Flowers 6-9-merous — 10. *S.* ser. *Caerulea*
          - Ovules numerous. Flowers 5-merous
            - Flowers distinctly pedicellate
              - Leaves in whorls of 4 — 15. *S.* ser. *Monregalensia*
              - Leaves alternate or decussate
                - Basal leaves rosulate — 13. *S.* ser. *Hirsuta*
                - Basal leaves not rosulate
                  - Plants densely glandular-pubescent — 12. *S.* ser. *Dasyphylla*
                  - Plants sparsely glandular-pubescent
                    - Seeds oblong-elliptic — 9. *S.* ser. *Alba*
                    - Seeds pyriform — 16. *S.* ser. *Pedicellata*
            - Flowers sessile or subsessile
              - Plants annual — 11. *S.* ser. *Confertiflora*
              - Plants perennial. Roots tuberous — 23. *S.* ser. *Subulata*
        - Follicles stellate-patent or divergent
          - Follicles stellate-patent, with distinct lips
            - Flowers 5-merous. Plants perennial or biennial
              - Leaves flat, decussate, not rosulate — 17. *S.* ser. *Propontica*
              - Leaves semiterete, alternate, rosulate

21. *S.* ser. *Sempervivoides*

Flowers 5-7(-9)-merous. Plants usually annual
14. *S.* ser. *Glauco-rubens*

Follicles divergent, without distinct lips
8. *S.* ser. *Aithales*

Seeds coronate
Plants glandular-pubescent
Basal leaves rosulate
Pedicels long. Petals basally connate. Inflorescence lax
24. *S.* ser. *Alsinefolia*
Pedicels short. Petals free (when basally connate inflorescence very large) 25. *S.* ser. *Cepaea*
Basal leaves not rosulate 27. *S.* ser. *Subrosea*
Plants glabrous throughout. 26. *S.* ser. *Magellensia*

10. Conspectus

Sedum L. subg. ***Sedum*** (Clausen 1975, Ohba 1978).

Synonyms: *Cepaea* Fabricius (1759), type *S. cepaea* L. — *Enchylus* Ehrhart (1789), nom. ambig. (= *S. annuum* L.). — *Phedimus* Rafinesque (1817), lectotype *S. stellatum* L. — Aithales Webb & Berthelot (1836-1841), lectotype *S. rubens* L. — *Procrassula* Grisebach (1843), type *S. caespitosum* (Cav.) DC. — *Leucosedum* Fourreau (1868), lectotype *S. album* L. — *Sedella* Fourreau (1868), lectotype *S. atratum* L. — *Macrosepalum* Regel & Schmalhausen in Regel (1882), type *S. aetnense* Tin. — *Mucizonia* (DC.) Berger (1930), lectotype *S. mucizonia* (Ortega) Hamet — *Prometheum* (A. Berger) Ohba (1978), type *S. sempervivoides* Fischer ex MB. — *Pseudorosularia* Gurgenidze nom. illeg. (1978), *S. sempervivoides* Fischer ex MB. — *Asterosedum* Grulich (1984), type *S. stellatum* L. — *Oreosedum* Grulich (1984), type *S. album* L. — *Petrosedum* Grulich (1984), type *S. rupestre* L. — *Poenosedum* Holub (1984), type *S. tuberosum* Cosson & Letourn. — *Etiosedum* Löve & Löve (1985a), type *S. annuum* L. — Hjaltalinia Löve & Löve (1985a), type *S. villosum* L. — Helladia Král (1987), type *S. creticum* Presl.

S. sect. ***Sedum*** (the Eurasiatic species of *S.* subg. ***Sedum***, Hart 1982b).

Synonyms: *Umbilicus* sect. *Mucizonia* Candolle (1828), lectotype *S. mucizonia* (Ortega) Hamet — *S.* sect. *Cepaea* Koch (1843), lectotype *S. cepaea* L. — *S.* sect. *Seda-genuina* Koch (1843), nom. inval. — *S.* sect. *Epeteium* Boissier (1872), lectotype *S. hispanicum* L. (Borissova 1969) — *S.* sect. *Eusedum* Boissier (1872), nom. inval. — *S.* sect. *Sempervivoides* Boissier (1872), lectotype *S. pilosum* Fischer ex MB. (Borissova 1939) — *S.* sect. *Prometheum* Berger (1930), lectotype *S. sempervivoides* Fischer ex MB. (Ohba 1978) — *S.* sect. *Cyprosedum* Berger (1930), lectotype *S. lampusae* (Kotschy) Boiss. (Ohba 1978) — *S.* sect. *Eurasiatica Orthocarpia* Fröderström (1932), nom. inval. — *S.* sect. *Eurasiatica Kyphocarpia* Fröderström (1932), nom. inval. — *Rosularia* sect. *Sempervivoides* (Boiss.) Borissova (1939) — *S.* subg. *Spathulata* Borissova (1969), type *S. spurium* MB.

Testa reticulate, sepals free (spurred), seeds apiculate, glabrous:

1. *S*. ser. ***Acria*** Berger (1930), lectotype: *S. acre* L. (Borissova 1969).
Synonyms: *S*. subsect. *Acria* (A. Berger) Maire (1977), comb. inval.
Glabrous perennials. Leaves alternate, terete, ovate-oblong, obtuse. Flowers 5-merous, sessile. Sepals free. Petals free, yellow. Stamens 10, with yellow anthers. Follicles many-seeded, stellate-patent, with distinct lips. Seeds ovoid, with a reticulate testa and acute apex. $x = 20$.
Throughout Europe, North Africa, Anatolia.
S. acre L.

2. *S*. ser. ***Macrosepala*** (Regel & Schmalh.) Borissova (1939).
Basionym: *Macrosepalum* Regel & Schmalh. in Regel (1882).
Glabrous annual. Leaves alternate, semiterete to terete, oblong, acute. Flowers 4- or 5-merous, sessile. Sepals free. Petals free, white. Stamens 4 or 5, with red anthers. Follicles with 1-3 seeds, divergent, without lips. Seeds ovoid, with a reticulate testa and acute apex. $x = 13$.
Southern Europe, Anatolia, Iran.
S. aetnense Tineo (= *S. tetramerum* Trautv.; = *Macrosepalum turkestanicum* Regel & Schmalh. in Regel).

Testa reticulate, sepals free (peltate), seeds coronate, glabrous:

3. *S*. ser. ***Anglica*** Hart, ser. nov., typus *S. anglicum* Huds.
Plantae glabrae, annuae vel perennes. Sepala basin omnino libera. Petala alba. Folliculi stellato-patentes. Semina apice coronata, testa reticulata.
Glabrous annuals or perennials. Leaves alternate, terete, oblong to ovate, obtuse. Flowers 5-merous, sessile. Sepals free. Petals free, white. Stamens 10, with red anthers. Follicles many-seeded, stellate-patent or divergent, with inconspicuous lips. Seeds ovoid, with a reticulate testa and coronate apex. $x = 12$.
Western Europe, North Africa.
S. anglicum Hudson, *S. arenarium* Brot.

4. *S*. ser. ***Melananthera*** Hart, ser. nov., typus *S. melanantherum* DC.
Plantae glabrae, perennes. Sepala basin omnino libera. Petala alba. Folliculi erecti. Semina apice coronata, testa reticulata.
Glabrous perennials. Leaves alternate, semiterete, oblong, obtuse. Flowers 5-merous, sessile. Sepals free. Petals free, white. Stamens 10, with red anthers. Follicles with 2 or 3 seeds, erect, without lips. Seeds ovoid, with a reticulate testa and coronate apex. $x = 13$.
Spain, North Africa
S. melanantherum DC.

Testa reticulate, sepals united, seeds apiculate, glabrous:

5. *S*. ser. ***Alpestria*** Berger (1930), type *S. alpestre* Vill.
Synonyms: *S*. ser. *Mitia* Berger (1930), type *S. mite* Gilib. — *S*. ser. *Tuberosa* Berger (1930), type *S. tuberosum* Cosson & Letourn — *S*. subsect. *Mitia* (A. Berger) Maire (1977), comb. inval. — *S*. subsect. *Tuberosa* (A. Berger) Maire (1977), comb. inval.

Glabrous annuals or perennials. Leaves alternate, terete to semiterete, ovate to oblong, obtuse or subacute. Flowers 5-merous, sessile. Sepals basally fused with the receptacle. Petals free, yellow. Stamens 10, with yellow anthers (rarely red). Follicles many-seeded, stellate-patent, with distinct lips. Seeds ovoid, with a reticulate testa and acute apex. $x = 6$, 8, 11, 13, 16, 22, 23, 29, 37.

Throughout Europe, North Africa, Near East.

S. alpestre Vill., *S. annuum* L. [= *Enchylus annuus* (L.) Ehrhart, = *Etiosedum annuum* (L.) Á. Löve & D. Löve], *S. apoleipon* Hart, *S. borissovae* Balk., *S. grisebachii* Boiss. & Heldr., *S. laconicum* Boiss. & Heldr., *S. multiceps* Cosson & Durieu, *S. sexangulare* L. (= *S. mite* Gilib.), *S. tuberiferum* Stoj. & Stef., *S. tuberosum* Cosson & Letourn. [= *Poenosedum tuberosum* (Cosson & Letourn.) Holub], *S. ursi* Hart, *S. urvillei* DC.

Testa reticulate, sepals united, seeds apiculate, glandular pubescent:

6. ***S.*** ser. ***Samia*** Hart, ser. nov., typus *S. samium* Runemark & Greuter.

Plantae parce glanduloso-pubescentes. Sepala basin receptaculo adnata. Petala flava. Semina apice acuta, testa reticulata.

Sparingly glandular-pubescent annuals. Leaves alternate, terete, ovate to oblong, obtuse. Flowers 5-merous, sessile. Sepals basally fused with the receptacle. Petals free, yellow. Stamens 10, with red or yellow anthers. Follicles many-seeded, stellate-patent, with narrow lips. Seeds ovoid, with a reticulate testa and acute apex. $x = 9$.

Samos, Anatolia.

S. samium Runemark & Greuter.

Testa costate (bipapillate), sepals united, seeds apiculate, glabrous:

7. ***S.*** ser. ***Litorea*** Hart (1978), type *S. litoreum* Guss.

Glabrous annuals. Leaves alternate, semiterete, oblong, obtuse. Flowers 5-merous, sessile. Sepals basally fused with the receptacle. Petals free, yellow. Stamens 10 or less (5), with yellow or red anthers. Follicles many-seeded, divergent, often with distinct lips. Seeds ovoid, with a papillate testa and acute apex. $x = 10$.

East Mediterranean region to France.

S. litoreum Guss.

Testa costate, sepals united, seeds apiculate, glandular pubescent:

8. ***S.*** ser. ***Aithales*** (Webb & Berth.) Hart, stat. nov.

Basionym: *Aithales* Webb & Berthelot (1836-1841: 178. 1840). — Synonym: *S.* subsect. *Rubentia* Maire (1977), nom. inval.

Glandular-pubescent annuals or perennials. Leaves alternate or in whorls of 4, terete or semiterete, oblong-elliptical or spatulate, obtuse. Flowers 5-merous, sessile. Sepals basally fused with the receptacle. Petals free, white (rarely yellowish). Stamens 10 or less (5), with red anthers. Follicles many-seeded, divergent, without lips. Seeds ovoid, with a costate testa and acute apex. $x = 5$, 10.

Throughout the Mediterranean region, central Europe, Near East.

S. pallidum MB., *S. rubens* L. (= *Aithales rubens* (L.) Webb & Berth.). Note: The two species of *S.* ser. *Aithales* are almost indistinguishable at the diploid and tetraploid level, but so far have successfully resisted all attempts to be crossed (Hart 1985, Hart & Alpinar 1991b).

9. *S.* ser. ***Alba*** Berger (1930), type *S. album* L.

Synonym: *S.* subsect. *Alba* (A. Berger) Maire (1977), comb. inval.

Sparingly glandular-pubescent perennials. Leaves alternate, terete, oblong to circular, obtuse or rounded. Flowers 5-merous, pedicellate. Sepals basally fused with the receptacle. Petals free, white. Stamens 10, with red anthers. Follicles many-seeded, erect, without lips. Seeds oblong or ovoid, with a costate testa and acute apex. $x = 17$.

Throughout Europe, North Africa, Near East.

S. album L. [= *Leucosedum album* (L.) Fourr., = *Oreosedum album* (L.) Grulich], *S. gypsicola* Boiss. & Reuter.

10. *S.* ser. ***Caerulea*** Fröderström (1932), type *S. caeruleum* L.

Synonym: *S.* subsect. *Caerulea* (Fröderström) Maire (1977), comb. inval.

Usually sparingly glandular-pubescent annuals. Leaves alternate, terete, oblong, obtuse. Flowers 7-merous (6-9-merous), pedicellate. Sepals basally fused with the receptacle. Petals free, blue or white. Stamens 14 (12-18), with red anthers. Follicles erect, with 1 or 2 seeds. Seeds ovoid, with a costate testa and acute apex. $x = 13$.

West Mediterranean region.

S. caeruleum L.

11. *S.* ser. ***Confertiflora*** Hart, ser. nov., typus *S. confertiflorum* Boiss.

Plantae annuae, glanduloso-pubescentes. Folia oblonga vel linearia, obtusa vel subacuta. Flores 5-meri, sessiles. Sepala basin receptaculo adnata. Petala alba. Folliculi erecti, seminibus numerosis. Semina apice acuta, testa costata.

Sparingly glandular-pubescent annuals. Leaves alternate, terete, oblong to linear, subacute or obtuse. Flowers 5-merous, sessile or subsessile. Sepals basally fused with the receptacle. Petals free, white. Stamens 10, with red anthers. Follicles many-seeded, erect, without lips. Seeds ovoid, with a costate testa and acute apex. $x = 6$.

Anatolia.

S. confertiflorum Boiss.

12. *S.* ser. ***Dasyphylla***, ser. nov., Hart, typus *S. dasyphyllum* L.

Plantae glanduloso-pubescentes. Folia alterna vel decussata, obtusa vel subacuta. Flores 5-meri, pedicellati. Sepala basin receptaculo adnata. Petala fere omnino connata vel libera, alba. Folliculi erecti, seminibusnumerosis. Semina apice acuta, testa costata.

Often coarsly glandular-pubescent annuals or perennials. Leaves alternate or decussate, terete to semiterete, ovate to oblong, obtuse or subacute. Flowers 5-merous, pedicellate. Sepals basally fused with the receptacle, united. Petals free or connate, forming a long tube, white. Stamens 10, with red anthers (rarely yellow). Follicles many-seeded, erect, without lips. Seeds ovoid, with a costate testa and acute apex. $x = 7, 9, 10, 11$.

Central and Southern Europe, North Africa, Anatolia.

S. dasyphyllym L., *S. granatense* Pau, *S. mucizonia* (Ortega) Hamet, [= *Cotyledon hispidus* Lam., = *Mucizonia hispida* (Lam.) A. Berger, = *Umbilicus hispidus* (Lam.) DC.].

13. *S.* ser. ***Hirsuta*** Fröderström (1932), type *S. hirsutum* All.

Densely glandular-pubescent perennials. Leaves alternate, terete, oblong, obtuse, in a basal rosette. Flowers 5-merous, pedicellate. Sepals basally fused with the receptacle. Petals connate at the base, white. Stamens 10, with red anthers. Follicles many-seeded,

erect, without lips. Seeds ovoid, with a costate testa and acute apex. $x = 9, 10$.
South-western Europe, North Africa.
S. hirsutum All.

14. *S.* ser. ***Glauco-rubens*** Fröderström (1932), lectotype *S. hispanicum* L.
Synonym: *S.* ser. *Hispanica* Borissova (1969), type *S. hispanicum* L.
Glandular-pubescent annuals or perennials. Leaves alternate, terete or semiterete, oblong, subacute. Flowers 6- or 7-merous (rarely to 9-merous), sessile. Sepals basally fused with the receptacle. Petals free, white. Stamens 12 or 14, with red anthers. Follicles many-seeded, stellate-patent, with distinct lips. Seeds ovoid, with a costate testa and acute apex. $x = 7$.
Southern Europe, Near East.
S. hispanicum L., *S. steudelii* Boiss.

15. *S.* ser. ***Monregalensia*** Hart, ser. nov., typus *S. monregalense* Balbis.
Plantae glanduloso-pubescentes. Folia verticillata, subacuta. Flores 5-meri, pedicellati. Sepala basin receptaculo adnata. Petala alba. Folliculi erecti, seminibus numerosis. Semina apice acuta, testa costata.
Glandular-pubescent perennials. Leaves in whorls of 4, semiterete, oblong-elliptic, subacute. Flowers 5-merous, pedicellate. Sepals basally fused with the receptacle. Petals free, white. Stamens 10, with red anthers. Follicles many-seeded, erect, without lips. Seeds ovoid, with a costate testa and acute apex. $x = 15$.
Southern France, Italy.
S. monregalense Balb.

16. *S.* ser. ***Pedicellata*** Hart, ser. nov., typus *S. pedicellatum* Boiss. & Reuter.
Plantae parce glanduloso-pubescentes. Folia alterna vel decussata, obtusa vel rotundata. Flores 5-meri (raro 4-meri), pedicellati. Sepala basin receptaculo adnata. Petala alba. Folliculi erecti, seminibus numerosis. Semina pyriformia, apice acuta, testa papillosa vel costata.
Sparingly glandular-pubescent annuals or perennials. Leaves alternate or decussate, terete, ovate to oblong, obtuse or rounded. Flowers 5-merous (rarely 4-merous), pedicellate. Sepals basally fused with the receptacle. Petals free or basally connate, white or pink. Stamens 10 or 5(4), with red anthers (rarely yellow). Follicles many-seeded, erect, without lips. Seeds pyriform, with a costate or papillate testa and acute apex. $x = 11, 14, 18, 25$.
South-western Europe, North Africa.
S. andegavense (DC.) Desv., *S. brevifolium* DC., *S. candollei* Hamet, *S. pedicellatum* Boiss. & Reuter. Note: *S. brevifolium* agrees completely with the description of this series, but so far could not be hybridized with the other three species which form a true comparium.

17. *S.* ser. ***Propontica*** Berger (1930), lectotype *S. stoloniferum* S. G. Gmelin (Hart 1984).
Synonyms: *S.* ser. *Stolonifera* Fröderström (1932), type *S. stoloniferum* S. G. Gmelin — *S.* subsect. *Stellata* Maire (1977), nom. inval. — *S.* sect. *Stolonifera* (Fröderström) Ohba (1978).
Sparingly glandular-pubescent annuals or perennials. Leaves decussate, flat, elliptical to circular, shortly petiolate, dentate, acute. Flowers 5-merous, sessile. Sepals basally fused with the receptacle. Petals free, white or pink. Stamens 10, with red anthers. Follicles

many-seeded, stellate-patent, with distinct lips. Seeds ovoid, with a costate testa and acute apex. $x = 5, 7, 15$.

Central Mediterranean region, Anatolia, Iran.

S. stellatum L. [= *Asterosedum stellatum* (L.) Grulich, = *Phedimus stellatus* (L.) Rafin.], *S. stoloniferum* S. G. Gmelin, *S. obtusifolium* C. A. Meyer (= *S. proponticum* Aznav.).

18. *S.* ser. ***Rubra*** Borissova (1969), type *S. caespitosum* (Cav.) DC.

Glabrous annuals. Leaves alternate, terete, ovate to elliptical, obtuse. Flowers 5-merous (rarely 4-merous), subsessile. Sepals basally fused with the receptacle. Petals free, white. Stamens 5 (or 4), with red anthers. Follicles many-seeded, stellate-patent, without lips. Seeds ovoid, with a costate testa and acute apex. $x = 6$.

Mediterranean region, Near East.

S. caespitosum (Cav.) DC. (= *Crassula caespitosa* Cav., = *Procrassula magnolii* Griseb.).

19. *S.* ser. ***Rupestria*** Berger (1932), type *S. rupestre* L.

Synonym: *S.* subsect. *Rupestria* (A. Berger) Maire (1977), comb. inval.

Glandular-pubescent perennials. Leaves alternate, terete, linear to oblong, mucronate. Flowers 7-merous (5-12-merous), sessile. Sepals basally fused with the receptacle. Petals free, yellow or white (cream-coloured). Stamens 14 (10-24), with yellow anthers. Follicles many-seeded, erect, without lips. Seeds oblong, with a costate testa and acute apex. $x =$ 12, 13, 14, 16, 17.

Throughout Europe, North Africa, Near East.

S. amplexicaule DC., *S. forsterianum* Sm., *S. montanum* Song. & Perrier, *S. ochroleucum* Chaix, *S. pruinatum* Brot., *S. rupestre* L. [= *S. reflexum* L., = *Petrosedum reflexum* (L.) Grulich], *S. sediforme* (Jacq.) Pau.

20. *S.* ser. ***Sedella*** (Fourr.) Hart, stat. nov.

Basionym: *Sedella* Fourreau (1868: 384).

Glabrous annuals. Leaves alternate, terete, oblong or elliptical, obtuse to rounded. Flowers 5-merous, sessile or subsessile. Sepals basally fused with the receptacle. Petals free, white (or cream-coloured). Stamens 10, with red anthers. Follicles many-seeded, divergent, with inconspicuous lips. Seeds ovoid, with a costate testa and acute apex. $x = 9$ (8).

Mountains of southern Europe.

S. atratum L. [= *Sedella atrata* (L.) Fourr.].

21. *S.* ser. ***Semperviviodes*** (Boiss.) Fröderström (1932).

Basionym: *S.* sect. *Sempervivoides* Boissier (1872).

Finely glandular-pubescent annuals or perennials. Leaves alternate, semiterete, oblong, acute or subacute, in a basal rosette. Flowers 5-merous shortly pedicellate. Sepals basally fused with the receptacle. Petals free, white, pink or red. Stamens 10, with red anthers. Follicles many-seeded, stellate-patent, with distinct lips. Seeds ovoid, with a costate testa and acute apex. $x = 6, 7$.

Mountains of Central Greece, Anatolia, Iran.

S. pilosum Fischer ex MB. [= *Pseudorosularia pilosa* (MB.) Gurg., = *Rosularia pilosa* (MB.) Borissova], *S. sempervivoides* Fischer ex MB. (= *Prometheum sempervivoides* (MB.) Ohba, = *Pseudorosularia sempervivoides* (MB.) Gurg.], *S. tymphaeum* Quézel & Contandriopoulos.

22. ***S.*** ser. ***Stefco*** Hart, ser. nov., typus *S. stefco* Stef.

Plantae glabrae. Folia obtusa. Flores 4-meri, breviter pedicellati. Sepala basin receptaculo adnata. Petala alba. Folliculi stellato-patentes, sine labiis secus suturam. Semina apice acuta, testa costata.

Glabrous perennials. Leaves alternate, terete, ovate to oblong, obtuse. Flowers 4-merous, shortly pedicellate. Sepals basally fused with the receptacle. Petals free, white. Stamens 8, with red anthers. Follicles many-seeded, stellate-patent, without lips. Seeds ovoid, with a costate testa and acute apex. $x = 7$.

Southern Balkans.

S. stefco Stef.

23. ***S.*** ser. ***Subulata*** Hart, ser. nov., typus *S. subulatum* (C. A. Meyer) Boiss.

Plantae perennes, parce glanduloso-pubescentes, radicibus tuberosis. Folia acuta. Flores 5-meri, sessiles. Sepala basin receptaculo adnata. Petala alba. Folliculi erecti, seminibus numerosis. Semina apice acuta, testa costata.

Sparingly glandular-pubescent perennials with tuberous roots. Leaves alternate, terete, linear to oblong, acute. Flowers 5-merous, sessile. Sepals basally fused with the receptacle. Petals free, white. Stamens 10, with red anthers. Follicles many-seeded, erect, without lips. Seeds oblong to ovoid, with a costate testa and acute apex. $x = 9$.

Southern Russia, Anatolia, Iran.

S. subulatum (C. A. Meyer) Boiss.

Testa costate, sepals united, seeds coronate, glandular pubescent:

24. ***S.*** ser. ***Alsinefolia*** Berger (1930), type *S. alsinefolium* All.

Densely glandular-pubescent annuals or perennials. Leaves alternate, flat, oblong to spatulate or petiolate, obtuse to subacute, in a basal rosette. Flowers 5-merous, pedicellate. Sepals basally fused with the receptacle. Petals basally connate, white. Stamens 10, with red anthers. Follicles many-seeded, erect, without lips. Seeds ovoid, with a costate testa and coronate apex. $x = 10, 13$.

French-Italian Alps.

S. alsinefolium All., *S. fragrans* Hart.

25. ***S.*** ser. ***Cepaea*** (Koch) Fröderström (1932).

Basionym: *S.* sect. *Cepaea* Koch (1843).

Glandular-pubescent annuals or perennials. Leaves alternate or in whorls of 4, flat, oblong to spatulate or petiolate, obtuse to subacute, in a basal rosette. Flowers 5-merous, shortly pedicellate. Sepals basally fused with the receptacle. Petals free or basally connate, white or pink. Stamens 10, with red anthers. Follicles many-seeded, erect, without lips. Seeds ovoid, with a costate testa and coronate apex. $x = 10, 11$.

Central and southern Europe, Cyprus, Anatolia.

S. cepaea L. (= *Cepaea caesalpini* Fourr.), *S. creticum* C. Presl [=*Helladia cretica* (Presl) Kral], *S. cyprium* Jackson & Turrill, *S. lampusae* (Kotschy) Boiss., *S. microstachium* (Kotschy) Boiss., *S. tristriatum* Boiss. & Heldr.

26. ***S.*** ser. ***Magellensia*** Hart, ser. nov., typus *S. magellense* Ten.

Plantae glabrae, caulibus repentibus vel ascendentibus. Folia alterna vel decussata, plana vel semiteretia, late elliptica. Sepala basin receptaculo adnata. Petala alba. Semina apice coronata, testa costata.

Glabrous perennials, with creeping and ascending shoots. Leaves decussate or alternate, broadly elliptical, semiterete or flat, obtuse. Flowers 5-merous, pedicellate. Sepals basally fused with the receptacle. Petals free, white. Stamens 10, with red anthers. Follicles many-seeded, erect, without lips. Seeds ovoid, with a costate testa and coronate apex. $x = 14, 15$.

Mountains of southern Italy, southern Balkans, Crete, Anatolia.

S. magellense Ten.

27. *S.* ser. ***Subrosea*** Hart, nom. nov.

Replaced synonym: *S.* sect. *Villosa* Clausen (1975), type *S. villosum* L. [non *S.* ser. *Villosa* Borissova (1969), type *S. selskanianum* Regel & Maak.]. — Synonym: *S.* subsect. *Paniculata* Battand. & Trabut ex Maire (1977), nom. nud.

Densely glandular-pubescent annuals. Leaves, alternate, terete, oblong to linear, subacute. Flowers 5-merous, pedicellate. Sepals basally fused with the receptacle. Petals free, white or pink. Stamens 10, with red anthers. Follicles many-seeded, erect, without lips. Seeds ovoid, with a costate testa and coronate apex. $x = 15$.

Western Europe, North Africa.

S. lagascae Pau, *S. nevadense* Cosson, *S. villosum* L. [= *Hjatalinia villosa* (L.) Á. Löve & D. Löve].

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