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The evolution of the *Sedum acre* group *(Crassulaceae)*

Abstract

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The *Sedum acre* group comprises the small, herbaceous, perennial and annual, yellow-flowered, Eurasian *Sedum* species, except for *S. assyriacum* and *S. nanum* from the Near East, and the North African species of *S.* sect. *Monanthella;* in total, 16 species belonging to four comparia, or series:. *S.* ser. *Acria*, ser. *Alpestria*, ser. *Litorea*, and ser. *Samia*. Recent phytochemical and molecular studies indicate that the *S. acre* group is probably paraphyletic, though it belongs to a distinct and doubtless monophyletic lineage of the *Sedoideae*, the so-called *S. acre* lineage. A cladistic analysis of 62 morphological characters of the 16 species of the group is presented. The significance of the resulting phylogeny is discussed in relation to cytological and phytochemical data and the distribution of the taxa.

Introduction

The Eurasian *Sedum* flora comprises some 16 species resembling *S. acre* L. in habit and gross morphology. They are up to 10 (rarely 15) cm tall and have imbricate, terete or semiterete, obtuse, green or glaucous leaves c. 5-10(-20) mm long, cincinniform inflorescences with starry, 5-merous, yellow flowers, and stellately patent or divergent follicles with small lips along the ventral suture. The yellow-flowered *Sedum* species resembling *S. acre* are most abundant in the Mediterranean and Euxine regions. They occur from Morocco and southern (or central) Europe to Anatolia and the Caucasus. Their presence is most prominent, however, on the Balkan peninsula and in the Aegean region, where 12 of the 16 species occur.

In an account of the yellow-flowered species resembling *Sedum acre* of the Southern Balkans, the Bulgarian botanist Stefanov (1950) used the informal name *Cincinnisedum* to denote this group of species. In *Flora europaea* Webb (1964) used the casual name *S. acre* group to indicate the perennial species of Stefanov's *"Cincinnisedum"*. 't Hart (1978, 1983, 1991) extended the *S. acre* group to include the annual as well as perennial Eurasian *Sedum* species with yellow flowers resembling *S. acre.* In the present concept the *S. acre* group comprises all small herbaceous yellow-flowered Eurasian *Sedum* species except *S. assyriacum* Boiss. and *S. nanum* Boiss. from the Near East and the North

African species of *S.* sect. *Monanthella* A. Berger: *S. jaccardianum* Maire & Wilczek, *S. modestum* Ball, and *S. pubescens* Vahl (= *S. gattefossei* Batt.), all of which have orthocarpic follicles (Fröderström 1932).

Genetic relationships between the species of the *Sedum acre* group have been determined by hybridisation experiments ('t Hart 1978, 1982, 1991), which revealed that the group comprises four comparia, i.e. species potentially able to hybridize among each other (Danser 1929). Three comparia are monotypic: *S.* ser. *Acria* A. Berger (*S. acre*), ser. *Litorea* 't Hart (*S. litoreum* Guss.), and ser. *Samia* 't Hart (*S. samium* Runemark & Greuter). The fourth comparium, *S.* ser. *Alpestria* A. Berger, comprises 11 species: *S. alpestre* Vill., *S. annuum* L., *S. apoleipon* 't Hart, *S. borissovae* Balk., *S. grisebachii* Boiss. & Heldr., *S. laconicum* Boiss. & Heldr., *S. multiceps* Coss. & Dur., *S. sexangulare* L., *S. tuberiferum* Stoj. & Stef., *S. tuberosum* Coss. & Letourn., and *S. urvillei* DC. Two newly described species from Anatolia, *S. euxinum* 't Hart & Alpınar and *S. ursi* 't Hart, have tentatively been added to *S.* series *Alpestria* ('t Hart 1990, 't Hart & Alpınar 1991).

Although our knowledge of the morphology, cytology, and chemistry of the species of the *Sedum acre* group has much increased recently, the phylogeny of the group is still largely unknown. To improve our understanding of the evolution of the group a cladistic analysis of 62 morphological characters of the 16 species has been performed. The signifiance of the resulting phylogeny is discussed in relation to biosystematic and phytogeographical data.

Systematic position of the *Sedum acre* group

The Eurasian *Sedum* flora comprises two main groups which differ in the states of four characters in a way that appears to be correlated with the hybridization patterns of the species. The most important of these characters are ornamentation of the testa and mode of insertion of the sepals ('t Hart 1991, 't Hart & Koek-Noorman 1989). The advanced taxa all have costate (or bipapillate-celled) testa and sepals that are basally fused with the receptacle, whereas the primitive taxa have a reticulo-papillose testa and usually basally free (spurred) sepals.

Table 1. Alkaloids of the Eurasian primitive taxa (series) of *Sedum* (after Stevens & al. 1992, 1993). – 1 = pyrrolidines (norhygrine); 2-6 = piperidines [2 = pelletierine; 3 = sedridine; 4 = N-methyl pelletierine; 5 = 1-(2-N-methylpiperidyl)-propan-2-ol; 6 = sedamines (8-phenyl piperidines) & hydroxysedamines]; 7 = 2,6-disubstituted piperidines (sedacrine, sedinine, sedinon). ++ = present, + = traces, – = absent.

Sedum	1	2	3	4	5	6	7
ser. *Acria*	–	+	++	–	–	++	++
ser. *Alpestria*	++	+	+	++	++	–	–
ser. *Samia*	++	+	+	+	+	–	–
ser. *Litorea*	+	++	+	++	+	–	–
ser. *Macrosepala*	++	+	+	–	++	–	–
ser. *Anglica*	–	–	+	+	++	–	–
ser. *Melananthera*	+	++	+	++	++	–	–

The species of the *Sedum acre* group have a reticulo-papillose testa and accordingly belong to the clade of primitive taxa, except for *S. litoreum*, which has bipapillate testa cells and is accordingly included in the clade of advanced species ('t Hart 1991). In addition to the *S. acre* group the clade of primitive taxa also comprises four white-flowered Eurasian species with basally free sepals and reticulate seeds, placed in *S.* ser. *Anglica* 't Hart (*S. anglicum* Huds. and *S. arenarium* Brot.), ser. *Macrosepala* (Regel & Schmalh.) Boriss. (*S. aetnense* Tin.), and ser. *Melananthera* 't Hart (*S. melanantherum* DC.).

Analysis of chloroplast DNA restriction site variation of Eurasian *Sedoideae* supports the distinction of these two lineages (Ham 1994). The advanced species with basally fused sepals and costate seeds constitute the major, though cladistically weakly supported, group. The taxa in which the primitive character states predominate form a very distinct lineage, with *Sedum acre* branching off at its base. This so-called "*S. acre* lineage" comprises the primitive Eurasian series with reticulate seeds, *S.* ser. *Alpestria*, ser. *Anglica*, ser. *Macrosepala*, ser. *Melananthera*, and ser. *Samia*, as well as Asian and American species with reticulo-papillate seeds. In addition, it comprises the Eurasian *S. litoreum* which has a bipapillate testa cells.

The distribution of alkaloids in Eurasian *Sedoideae* corroborates the subdivision of *Sedum* inferred from chloroplast DNA analysis (Stevens & al. 1992, 1993). Only species with a reticulate testa and *S. litoreum* contain alkaloids (Table 1). Furthermore, when qualitative as well as quantitative aspects are taken into account the distribution of the alkaloids in the European *Sedum* species fully agrees with the infrageneric classification based primarily on hybridization patterns ('t Hart 1991, Stevens & al. 1993).

In conclusion, it is clear that the *Sedum acre* group is not a monophyletic taxon, though it is part of an apparently monophyletic "*S. acre* lineage" (Ham 1994). Most probably the *S. acre* group shares a common ancestor with other primitive series, such

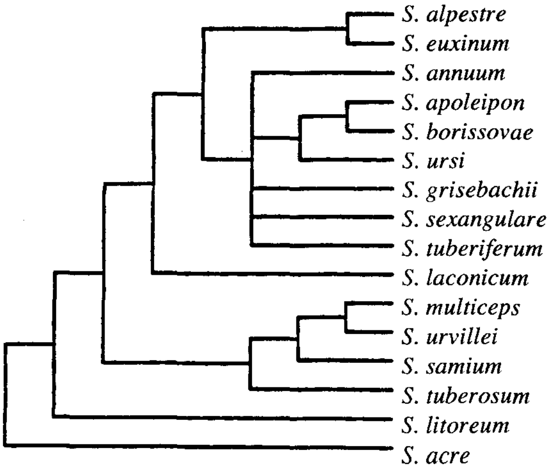


Fig. 1. Strict consensus tree of the *Sedum acre* group resulting from the analysis of 62 morphological characters and using *S. acre* as the outgroup (4 equally parsimonious trees).

Table 2. The characters, character states, and data matrix used in the cladistic analyses. All characters were unordered in the analysis. Species: 1 = *Sedum acre*; 2 = *S. alpestre*; 3 = *S. annuum*; 4 = *S. apoleipon*; 5 = *S. borissovae*; 6 = *S. euxinum*; 7 = *S. grisebachii*; 8 = *S. laconicum*; 9 = *S. multiceps*; 10 = *S. sexangulare*; 11 = *S. tuberiferum*; 12 = *S. tuberosum*; 13 = *S. ursi*; 14 = *S. urvillei*; 15 = *S. samium*; 16 = *S. litoreum*. Missing characters are indicated with question marks.

		1111111
N°	Characters and their states Species N°:	1234567890123456
1	Non-flowering shoots: (1) present, (2) absent	1121111111111122
2	Phyllotaxis: (1) 3/5, (2) 5/8, (3) 8/13	11?211223?2121??
3	Leaves on flowering shoot, insertion: (1) imbricate, (2) divergent, (3) squarrose	2121222123131223
4	Leaves on flowering shoot, length in mm: (1) < 5, (2) 5-10, (3) > 10	1221123322232223
5	Leaves on flowering shoot, width in mm: (1) < 1.5, (2) 1.5-2.5, (3) > 2.5	3221232221223233
6	Leaves on flowering shoot, outline: (1) linear, (2) oblong-elliptic, (3) ovate	3221221212222322
7	Leaves on flowering shoot, cross-section: (1) semiterete, (2) elliptical	1222222212222112
8	Leaves on flowering shoot, colour: (1) green, (2) glaucous or pruinose	1112211221112211
9	Leaves on flowering shoot, tip: (1) round, (2) obtuse, (3) acute	2112212332212323
10	Leaves on flowering shoot, ornamentation of tip: (1) glabrous, (2) mamillate, (3) papillate	1112213331122211
11	Leaves on flowering shoot, margin: (1) round, (2) obtuse, (3) acute	1222212232232232
12	Leaves on flowering shoot, margin: (1) glabrous, (2) papillate	1111111121121111
13	Leaves on flowering shoot, spur length in mm: (1) < 0.6, (2) 0.6-1.2, (3) > 1.2	2121212221322221
14	Leaves on flowering shoot, spur outline: (1) transverse oblong, (2) quadrate, (3) triangular	3111211211321211
15	Dead leaves: (1) not persistent, (2) persistent	1112111121111211
16	Dead leaves: (1) whitish, (2) brown or blackish, (3) grey	12?22??2222?23??
17	Inflorescence branches: (1) 2 (on average), (2) 3 or more	1121112122222221
18	Inflorescence, main branch; length in cm: (1) < 1, (2) 1-2.5, (3) > 2.5	2122222122232333
19	Inflorescence, primary branch; length in mm: (1) < 3, (2) 3 or more	2122222122221222
0	Inflorescence primary branch; diameter in mm: (1) < 1, (2) 1-2, (3) > 2	2111122222232222
21	Recaulescence upper leaf of flowering shoot: (1) 0-35 %,(2) 35-100 %	1221221212222223
22	Lower bract; recaulescence: (1) 0-50 %, (2) 50-100 %	2222221212222223
23	Lower bract; length in mm: (1) < 3.5, (2) 3.5 or more	1211122222221222
24	Lower bract; outline: (1) oblong-elliptic, (2) ovate	2111212111111211
25	Upper bract; length in mm: (1) < 4, (2) 4-5, (3) > 5	1221123232231323
26	Upper bract; outline: (1) oblong-elliptic, (2) ovate	2111112111111211
27	Upper bract; tip: (1) rounded to obtuse, (2) acute	1111111221111212
28	Spur upper bract; length in mm: (1) < 1.5, (2) 1.5 or more	1111111112121211
30	Subsidiary inflorescences: (1) few or none, (2) many	1111112211112111
31	Flower number: (1) less than 13, (2) more than 13	1121112122212212
32	Central flower: (1) 5-parted, (2) 6- 7-parted	1211111122121111
33	Pedicel. length: (1) < 0.5, (2) 0.5-1.0, (3) > 1.0	3222222212211222
34	Pedicel diameter in mm: (1) 1.0 or less, (2) more than 1.0	2111111221121122
35	Largest sepal; length in mm: (1) < 3.3, (2) 3.3 or more	2111112221121222
36	Largest sepal; width: (1) less than 1.8 mm, (2) 1.8 mm or more	2111111111121211
37	Largest sepal; outline: (1) oblong, (2) triangular-ovate	1112211211221211
38	Largest sepal; tip: (1) rounded, (2) obtuse, (3) acute	2212212231221323
39	Smallest sepal; length in mm: (1) < 2.4, (2) 2.4-3.6, (3) > 3.6	2211121221132112
40	Smallest sepal; width in mm: (1) 1.2 or less, (2) more than 1.2	1111111111121211
41	Petal length in mm: (1) < 5.5, (2) 5.5-6.5, (3) > 6.5	3112111122131231

		1111111
N°	Characters and their states	Species N°: 1234567890123456
42	Petals; width in mm: (1) < 1.5, (2) 1.5-2.5, (3) > 2.5	3212121222231221
43	Filament length in mm: (1) < 3.5, (2) 3.5-4.5, (3) > 4.5	3111111122131221
44	Filaments; connate part in mm: (1) < 0.5, (2) 0.5-1.0, (3) >1.0;	3222111121121111
45	Anther length in mm: (1) < 0.8, (2) 0.8-1.5, (3) > 1.5	2122111121232212
46	Anther width in mm: (1) < 0.8, (2) 0.5-0.6, (3) < 0.6	2112122121133222
47	Anther colour: (1) yellow, (2) red/yellow	1111111211111122
48	Squamae: (1) quadrate, (2) oblong	1211121111112111
49	Style length: (1) < 1.0 mm, (2) 1.0 mm or more	2112111122121222
50	Ovary length in mm: (1) < 2.5, (2) 2.5-3.5, (3) > 3.5	2112122232232331
51	Ovary width in mm: (1) < 1.5, (2) 1.5 or more	1111111121121221
52	Ovary base: (1) broad (sessile), (2) contracted (stipitate)	1211121111112222
53	Ovules per carpel: (1) less than 15, (2) more than 15	1221122221221221
54	Ripe follicles, position: (1) divergent, (2) stellate patent	2212222222222211
55	Ripe follicles, length in mm: (1) < 3.6, (2) 3.6 or more	21111112?1121222
56	Ripe follicles, colour: (1)yellowish or pale brown, (2)reddish- to dark brown	1112222222222221
57	Ripe follicles, lips ventral suture, width in mm: (1)< 0.4, (2)0.4-0.6, (3)> 0.6	33122223?1231311
58	Ripe follicles, lips ventral suture; colour: (1) whitish, (2) brown	12121211?2122111
59	Seeds, length in mm: (1) < 6.5, (2) 6.5-7.5, (3) > 7.5	1112321121112323
60	Seeds, length/width ratio: (1) < 2.0, (2) 2.0-2.5, (3) > 2.5	2321322211112113
61	Seeds, outline: (1) oblong elliptic, (2) ovoid	2112111222212222
62	Seeds, testa colour: (1) orange to red, (2) pale brown	1213332222233313

as *S.* ser. *Anglica*, ser. *Macrosepala*, and ser. *Melananthera*. The results of the hybridization experiments and the phytochemical analyses, however, strongly suggest that the 13 species of *S.* ser. *Alpestria* constitute a natural, or monophyletic, taxon.

Cladistic analysis of morphological characters

The phylogeny of the 16 species of the *Sedum acre* group is inferred from a cladistic analysis of 62 vegetative, floral and seed characters (Table 2). Of these 62 characters, 30 are quantitative. In the final analysis, *S. acre* was used as the outgroup, because of all the species of the group it has retained the greatest number of plesiomorphic characters ('t Hart 1992). It is completely glabrous, has free (spurred) sepals, and reticulate seeds with an acute apex. Furthermore, chloroplast DNA restriction site analysis places it at the base of the "*S. acre* lineage", as sister group to all other primitive Eurasian *Sedum* species (Ham 1994).

The data set was analysed with PAUP version 3.0s (Swofford 1991) under the Wagner parsimony criterion. The characters were treated unordered. The cladistic analysis resulted in 4 equally parsimonious trees with a length of 254 steps. The strict consensus tree is presented in Fig. 1. *Sedum acre* serves as the outgroup. Within the ingroup five clades are distinguished: two monotypic lineages *(S. litoreum* and *S. laconicum)* and three larger clades with the remaining 13 species, of which 4 form the *S. tuberosum* clade *(S. multiceps, S. samium, S. tuberosum,* and *S. urvillei),* 2 the *S. alpestre* clade *(S. alpestre* and *S. euxinum),* and 7 the *S. grisebachii* clade *(S. annuum, S. apoleipon, S. borissovae, S. grisebachii, S. ursi, S. sexangulare,* and *S. tuberiferum).*

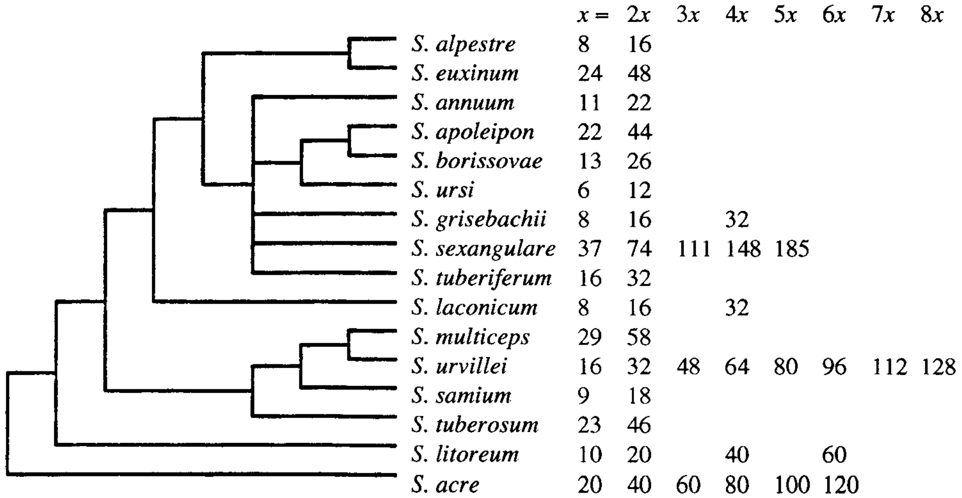
The result of the cladistic analysis by and large agrees with the classification of the species of the *Sedum acre* group based on hybridization patterns, except for *S. samium* which is placed in the *S. tuberosum* clade within *S.* ser. *Alpestria.*

When only the 13 species of the comparium *Sedum* ser. *Alpestria* are considered (*S. litoreum* and *S. samium* being excluded) the topology of the tree (not shown) remains essentially the same. Only the position of the *S. alpestre* clade changes: it becomes attached to the basal polytomy of the *S. grisebachii* clade.

The whole tree, however, is not very robust. A bootstrap analysis (100 replications) only supports the *Sedum alpestre* clade (52 % confidence) in the complete analysis, whereas only the *S. tuberosum* clade gets support (62 % confidence) when *S. litoreum* and *S. samium* are omitted.

Cytological variation and triterpenoid distribution

Cytologically the *Sedum acre* group is extremely variable (Fig. 2). Somatic chromosome numbers range from $2n = 12$ to $2n = 185$, and basic numbers from $x = 6$ to $x = 37$. Intraspecific polyploidy occurs in six species ('t Hart 1978, 't Hart & Ham 1992). Euploid autopolyploid series up to the tetraploid level have been reported in *S. grisebachii, S. laconicum,* and *S. sexangulare* (including a pentaploid), up to the hexaploid level in *S. acre* and *S. litoreum,* and to the octoploid level in *S. urvillei.* Only in *S. laconicum* is polyploidy accompanied by morphological and geographical differentiation. In Greece and on Crete the diploid form, subsp. *laconicum,* occurs, whereas the tetraploid form which has pale yellow flowers, subsp. *pallidum,* occurs in the Near East ('t Hart & Ham 1992).



	$x =$	$2x$	$3x$	$4x$	$5x$	$6x$	$7x$	$8x$
S. alpestre	8	16						
S. euxinum	24	48						
S. annuum	11	22						
S. apoleipon	22	44						
S. borissovae	13	26						
S. ursi	6	12						
S. grisebachii	8	16		32				
S. sexangulare	37	74	111	148	185			
S. tuberiferum	16	32						
S. laconicum	8	16		32				
S. multiceps	29	58						
S. urvillei	16	32	48	64	80	96	112	128
S. samium	9	18						
S. tuberosum	23	46						
S. litoreum	10	20		40		60		
S. acre	20	40	60	80	100	120		

Fig. 2. Cytological variation within the *Sedum acre* group in relation to phylogeny.

Of the 13 different basic chromosome numbers among the 16 species of the *Sedum acre* group, x = 6, 8, 9, 10, 11, and 13 may be regarded as primary base numbers, whereas x = 16, 20, 22, 23, 24, 29 and 37 are most probably secondary base numbers (Grant 1971). Only a single cytotype is known for each of the three species with an even secondary base number, *S. apoleipon* (x = 22), *S. euxinum* (x = 24), and *S. tuberiferum* (x = 16), and they are therefore considered to be diploid ('t Hart 1978, 1983, 't Hart & Alpınar 1992). The even basic numbers of *S. acre* (x = 20) and *S. urvillei* (x = 16) are almost certainly of a secondary nature, because plants with chromosome numbers of $2n$ = 60 and $2n$ = 48, respectively, show all the characteristics of triploids. They are usually completely sterile, and larger than their diploid ancestors ('t Hart 1971, 1978). The high frequency of secondary basic numbers indicates that polyploidy may have contributed substantially to speciation and evolution in the *S. acre* group.

The relation of chromosome numbers with the cladogram is rather peculiar. At first sight the different primary and secondary basic numbers appear to be randomly distributed over the five major clades (Fig. 2). However, all clades comprise at least one species with a primary basic number, whereas three clades also comprise secondary basic numbers. This pattern in combination with the large number of high and odd secondary basic numbers strongly suggests that reticulation played a major role in the evolution of the group.

Several species of the *Sedum acre* group have glaucous or pruinose leaves due to a conspicuous layer of epicuticular wax. The composition of the wax is rather uniform, though very complex, except for the triterpenoid fraction the composition of which is often species-specific (Stevens & al. 1994). Similar to the distribution of the secondary basic numbers the triterpenoid variation shows a rather erratic pattern (Fig. 3). The

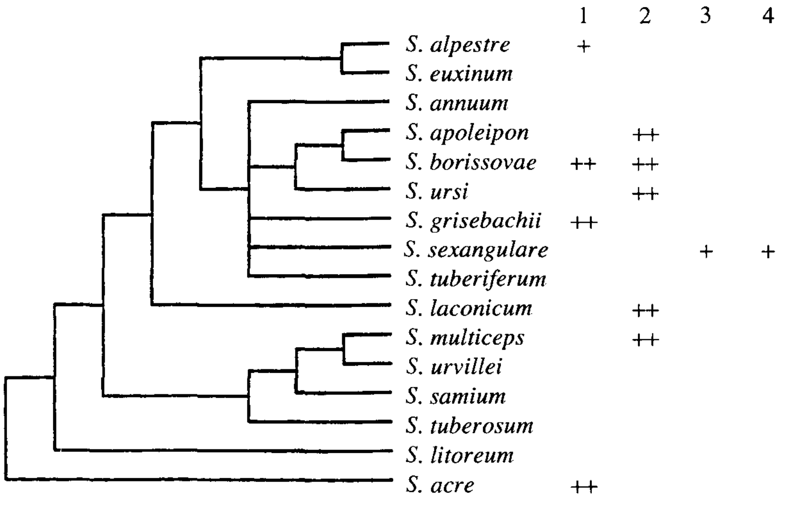


Fig. 3. Distribution of triterpenoid compounds of the epicuticular wax layer within the *Sedum acre* group in relation to phylogeny (Stevens & al. 1994, and unpubl.). - 1, 2 = unidentified lupanes; 3 = ursanes (α-amyrin); 4 = oleanes (β-amyrin); ++ = present, + = traces.

Table 3. Distribution of the species of the *Sedum acre* group. * = narrow endemics

Distribution area	*Sedum*
Endemic to the Balkans	*S. apoleipon* *
Endemic to the Balkans	*S. grisebachii*
Endemic to the Balkans	*S. tuberiferum* *
Endemic to the Ukraine	*S. borissovae* *
Balkans + N.W. & Central Europe	*S. sexangulare*
Balkans + Near East	*S. laconicum*
Balkans + Near East	*S. urvillei*
Balkans + N.W. & Central Europe + Near East	*S. alpestre*
Balkans + N.W. & Central Europe + Near East	*S. annuum*
Endemic to N.E. Anatolia	*S. euxinum* *
Endemic to S.W. Anatolia and the E. Aegean	*S. samium* *
Endemic to S. and C. Anatolia	*S. ursi*
Endemic to North Africa	*S. multiceps* *
Endemic to North Africa	*S. tuberosum* *
Throughout the Mediterranean region	*S. litoreum*
Europe + Near East + North Africa	*S. acre*

occurrence of the group of three yet unidentified lupanes both in species with primary and secondary basic numbers supports the hypothesis of speciation through reticulate evolution.

Geographical distribution of the species

The geographical distribution of the species of the *Sedum acre* group varies considerably (Table 3). *S. acre* occurs throughout the area of the group, but the other species all have more restricted distributions. Seven of the nine species designated as endemics may be regarded as narrow endemics (Table 3). The distribution of the species shows little correlation with the phylogeny of Fig. 2, though one may note that each of the five main lineages of the cladogram comprises at least one widespread species. The *S. tuberosum* clade comprises the two highly polyploid N African narrow endemics, *S. multiceps* and *S. tuberosum*, in addition to a narrow endemic of SW Anatolia, the diploid *S. samium*, and the widely distributed polyploid *S. urvillei*. The *S. alpestre* clade comprises two alpine species: the diploid *S. alpestre* ranges from the Pyrenees to Anatolia and is replaced by the highly polyploid, endemic *S. euxinum* in NE Anatolia. The *S. grisebachii* clade comprises three narrow endemics, *S. apoleipon*, *S. borissovae*, and *S. tuberiferum;* two widespread species, *S. annuum* and *S. sexangulare;* and two somewhat less restricted endemics, *S. grisebachii* and *S. ursi*, growing in the Balkans and southern to central Anatolia, respectively. Two narrow endemics, *S. apoleipon* and *S. tuberiferum*, and the widespread *S. sexangulare* are highly polyploid.

The centre of speciation of the *Sedum acre* group is most probably located on the Balkan peninsula or in the Aegean region ('t Hart 1991). This area comprises more species and endemic taxa than any other region. Furthermore, the diploid cytotypes of all species of the *S. acre* group which comprise an autopolyploid series occur on the Balkans.

Conclusions

Although the phylogeny of the *Sedum acre* group is still far from fully resolved, some conclusions about the evolutionary relationships among the species can already been drawn.

Notwithstanding their great overall morphological similarity, the *Sedum acre* group with its 16 species is probably not a monophyletic taxon, but a paraphyletic group within the monophyletic "*S. acre* lineage". However, the largest group of species within the *S. acre* group, *S.* ser. *Alpestria*, appears to be monophyletic.

The centre of origin of *Sedum* ser. *Alpestria*, and probably of the whole *S. acre* group, is located on the Balkan peninsula or in the Aegean region. During their migration away from the centre of origin diploids often became polyploid. For example, the diploid *S. alpestre* gave rise to the hexaploid *S. euxinum* in the east, and similarly the diploid *S. laconicum* gave rise to the tetraploid subsp. *pallidum* in Israel and Lebanon.

Reticulation has been an important feature in the evolution of the group, and has occurred throughout its distributional area. Reticulation resulted in large number of allopolyploid narrow endemics in the centre as well as at the borders of the total range. *Sedum apoleipon* and *S. tuberiferum* are instances of narrow endemics from the very centre of the area, whereas *S. multiceps* and *S. tuberosum* are good examples of allopolyploid endemics at the southern outskirts. In only one case reticulation resulted in a highly successful neo-species: *S. sexangulare* originated somewhere on the Balkans and successively spread all over Europe, where it is often found growing together with *S. acre*, the founder of the whole group.

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