H. 't Hart

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

Abstract


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. sect. Acria*, *sect. Alpestris*, *sect. Litorea*, and *sect. 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 *Sedoidae*, 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 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


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 significance of the resulting phylogeny is discussed in relation to biosystematic and phyto-geographical 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.

<table>
<thead>
<tr>
<th>Sedum</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>ser. Acria</td>
<td>-</td>
<td>+</td>
<td>++</td>
<td>-</td>
<td>+</td>
<td>++</td>
<td>++</td>
</tr>
<tr>
<td>ser. Alpestria</td>
<td>++</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>++</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ser. Samia</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ser. Litorea</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ser. Macrosepaia</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>++</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ser. Anglica</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>++</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>ser. Melananthera</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>++</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
The species of the *Sedum acre* group have a reticulo-papilllose 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. Alpestris*, *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).](image)
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. tuberosum; 13 = S. urvillei; 15 = S. samium; 16 = S. litoreum. Missing characters are indicated with question marks.

<table>
<thead>
<tr>
<th>N°</th>
<th>Characters and their states</th>
<th>Species N°:</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Non-flowering shoots: (1) present, (2) absent</td>
<td>1234567901234567</td>
</tr>
<tr>
<td>2</td>
<td>Phyllotaxis: (1) 3/5, (2) 5/8, (3) 8/13</td>
<td>12111112</td>
</tr>
<tr>
<td>3</td>
<td>Leaves on flowering shoot, insertion: (1) imbricate, (2) divergent, (3) squarrose</td>
<td>212122</td>
</tr>
<tr>
<td>4</td>
<td>Leaves on flowering shoot, length in mm: (1) &lt; 5, (2) 5-10, (3) &gt; 10</td>
<td>123222</td>
</tr>
<tr>
<td>5</td>
<td>Leaves on flowering shoot, width in mm: (1) &lt; 1.5, (2) 1.5-2.5, (3) &gt; 2.5</td>
<td>222222</td>
</tr>
<tr>
<td>6</td>
<td>Leaves on flowering shoot, outline: (1) linear, (2) oblong-elliptic, (3) ovate</td>
<td>111111</td>
</tr>
<tr>
<td>7</td>
<td>Leaves on flowering shoot, cross-section: (1) semiterete, (2) elliptical</td>
<td>111111</td>
</tr>
<tr>
<td>8</td>
<td>Leaves on flowering shoot, colour: (1) green, (2) glaucous or pruinose</td>
<td>211111</td>
</tr>
<tr>
<td>9</td>
<td>Leaves on flowering shoot, tip: (1) round, (2) obtuse, (3) acute</td>
<td>111111</td>
</tr>
<tr>
<td>10</td>
<td>Leaves on flowering shoot, ornamentation of tip: (1) glabrous, (2) mamillate, (3) papillate</td>
<td>111111</td>
</tr>
<tr>
<td>11</td>
<td>Leaves on flowering shoot, margin: (1) round, (2) obtuse, (3) acute</td>
<td>122222</td>
</tr>
<tr>
<td>12</td>
<td>Leaves on flowering shoot, glabrous, (2) papillate</td>
<td>111111</td>
</tr>
<tr>
<td>13</td>
<td>Leaves on flowering shoot, spur length in mm: (1) &lt; 0.6, (2) 0.6-1.2, (3) &gt; 1.2</td>
<td>212122</td>
</tr>
<tr>
<td>14</td>
<td>Leaves on flowering shoot, spur outline: (1) transverse oblong, (2) quadrat, (3) triangular</td>
<td>311111</td>
</tr>
</tbody>
</table>

15 Dead leaves: (1) not persistent, (2) persistent
16 Dead leaves: (1) whitish, (2) brown or blackish, (3) grey
17 Inflorescence branches: (1) 2 (on average), (2) 3 or more
18 Inflorescence, main branch; length in cm: (1) < 1, (2) 1-2.5, (3) > 2.5
19 Inflorescence, primary branch; length in mm: (1) < 3, (2) 3 or more
20 Inflorescence primary branch; diameter in mm: (1) < 1, (2) 1-2, (3) > 2
21 Rec caulusescence upper leaf of flowering shoot: (1) 0-35 %, (2) 35-100 %
22 Lower bract; recaulusescence: (1) few or none, (2) many
23 Lower bract; length in mm: (1) < 3.5, (2) 3.5 or more
24 Lower bract; outline: (1) oblong-elliptic, (2) ovate
25 Upper bract; length in mm: (1) > 4, (2) 4-5, (3) > 5
26 Upper bract; outline: (1) oblong-elliptic, (2) ovate
27 Upper bract; tip: (1) rounded to obtuse, (2) acute
28 Spur upper bract; length in mm: (1) < 1.5, (2) 1.5 or more
30 Subsidiary inflorescences: (1) few or none, (2) many
31 Flower number: (1) less than 13, (2) more than 13
32 Central flower: (1) 5-parted, (2) 6-7-parted
33 Pedicel length: (1) < 0.5, (2) 0.5-1.0, (3) > 1.0
34 Pedicel diameter in mm: (1) 1.0 or less, (2) more than 1.0
35 Largest sepal; length in mm: (1) < 3.3, (2) 3.3 or more
36 Largest sepal; width: (1) less than 1.8 mm, (2) 1.8 mm or more
37 Largest sepal; outline: (1) oblong, (2) triangular-ovate
38 Largest sepal; tip: (1) rounded, (2) obtuse, (3) acute
39 Smallest sepal; length in mm: (1) < 2.4, (2) 2.4-3.6, (3) > 3.6
40 Smallest sepal; width in mm: (1) 1.2 or less, (2) more than 1.2
41 Petal length in mm: (1) < 5.5, (2) 5.5-6.5, (3) > 6.5
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) sepalas, 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).

\[
x = 2x \quad 3x \quad 4x \quad 5x \quad 6x \quad 7x \quad 8x
\]

- S. alpestre: \(8 \quad 16\)
- S. euxinum: \(24 \quad 48\)
- S. annuum: \(11 \quad 22\)
- S. apoleipon: \(22 \quad 44\)
- S. borissovae: \(13 \quad 26\)
- S. ursi: \(6 \quad 12\)
- S. grisebachii: \(8 \quad 16 \quad 32\)
- S. sexangulare: \(37 \quad 74 \quad 111 \quad 148 \quad 185\)
- S. tuberiferum: \(16 \quad 32\)
- S. laconicum: \(8 \quad 16 \quad 32\)
- S. multiceps: \(29 \quad 58\)
- S. urvillei: \(16 \quad 32 \quad 48 \quad 64 \quad 80 \quad 96 \quad 112 \quad 128\)
- S. samium: \(9 \quad 18\)
- S. tuberosum: \(23 \quad 46\)
- S. litoreum: \(10 \quad 20 \quad 40 \quad 60\)
- S. acre: \(20 \quad 40 \quad 60 \quad 80 \quad 100 \quad 120\)

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 & Alpmar 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 unpub.).](image)

- 1 = unidentified lupanes; 3 = ursanes (\(\alpha\)-amyrin); 4 = oleanes (\(\beta\)-amyrin); ++ = present, + = traces.
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.

References


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