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Biosystematic studies in *Sedum* (Crassulaceae) from Turkey. 4. The cytology of *Sedum* subsect. *Spathulata* Boriss.

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SUMMARY

The diploid cytotypes of the species of *Sedum* series *Involucrata* and *S.* series *Propontica* of *S.* subsect. *Spathulata* differ more than five-fold in nuclear DNA amount, even though some occur in similar habitats and sometimes in mixed populations. Morphologically the two series are quite similar, but the basic chromosome numbers and karyotypes differ considerably, and they are probably only distantly related. The dysploid series in *S.* series *Propontica*, ranging from $x=7$ to $x=5$, is not a result of a simple series of successive Robertsonian translocations, but involves different kinds of chromosomal rearrangements as well. The 2C value of *S. obtusifolium* ($x=6$) with the chromosome number $2n=30$ would indicate an octoploid ($8x$) level of ploidy, but the karyotype structure offers no explanation for the implicit loss of 18 chromosomes.

Key-words: Crassulaceae, *Sedum* sect., *Spathulata*, nuclear DNA content, chromosome numbers, cytogeography.

INTRODUCTION

Maximowicz (1884) first used the name *Sedum* series *Involucrata* to denote a small group of perennial Caucasian *Sedum* species which closely resemble *S. spurium* Bieb. (=*S. involucratum* Bieb.). They have creeping and rooting non-flowering shoots with decussate, succulent flat, spathulate to broadly elliptic or orbicular, usually crenate or dentate leaves, rather dense, cymose or (sub-)corymbose inflorescences with large, showy, 5-merous, obdiplostemonous flowers, distinctly unequal sepals, and pinkish, red or white petals. Because of this unique combination of a large number of characters the group is generally regarded as a very distinct and natural taxon, though opinions about its systematic position vary considerably (Maximowicz 1884; Borissova 1939, 1969; Ohba 1978; Grulich 1984; 't Hart 1984).

Berger (1930) separated *S. obtusifolium* C.A. Meyer (=*S. proponticum* Azn.) from *S.* series *Involucrata* because of its peculiar, subterranean propagules with densely imbricate, small, white leaves (Praeger 1921), which enable the plant to survive the Mediterranean summer droughts. He classified it in the monotypic *S.* series *Propontica*. Fröderström (1932) classified the species of *S.* series *Involucrata* into two series

Table 1. Chromosome numbers in *Sedum* sect. *Spathulata* Boriss

Sedum	2*n*=	References
S. series *Involucrata* Maxim.		
S. spurium Bieb.	28	Baldwin 1935; Löve & Löve 1985a; Appendix.
	42	Zhukova 1967; Appendix.
S. series *Propontica* Berger		
S. obtusifolium C.A. Meyer	12*	Appendix.
	30	't Hart & Alpınar 1991; Appendix.
S. stellatum L.	10	Baldwin 1939, 1940; 't Hart 1984; Löve & Löve 1985a; Appendix.
S. stoloniferum Gmelin	14	't Hart 1984; Appendix.
	28	Baldwin 1935.

*Number reported for first time.

according to the position of the ripe follicles. Borissova (1939, 1969) adopted Berger's classification, but united the two series into *S.* subsect. *Spathulata* of *S.* sect. *Sedum* (=*S.* sect. *Seda genuina* Koch). Ohba (1978) raised *S.* subsect. *Spathulata* to the rank of subgenus, and Grulich (1984) finally merged Borissova's two series into the genus *Asterosedum* Grulich. To this new genus he also added the annual *S. stellatum* L. from the central Mediterranean region. The results of hybrization experiments with *S. spurium* and *S. stoloniferum* strongly support Fröderström's classification of the species into two series ('t Hart 1984). Further hybridization experiments also indicated a close genetic relationship between *S. stellatum* and *S. stoloniferum*, and the former has consequently been classified in *S.* series *Propontica*.

Cytologically *S.* subsect. *Spathulata* (including *S. stellatum*) is rather diverse and in this respect agrees very well with the rest of the genus *Sedum*. So far six different cytotypes have been reported for four species (see Table 1). In this paper we present the results of a cytological study of 41 plants of four species of *S.* subsect. *Spathulata*, which were recently collected in Anatolia, Greece, and the Caucasus.

MATERIAL AND METHODS

All plants used in this study were collected in nature and for further investigations cultivated in the temperate greenhouse of the Botanic Garden at Utrecht. The origin of the plants and their collection and accession numbers are listed in the appendix.

Chromosome numbers were determined in root tip mitoses ('t Hart & Eggli 1988). Root tips were fixed in Karpechenko's fixative, dehydrated, embedded in paraffin, and sectioned at 15 μm. The sections were stained according to Heidenhain's haematoxylin method and made permanent with DEPEX. Drawings of karyotypes were made with the use of a Zeiss microscope and camera lucida (total magnification *c.* 9000 times).

The amount of DNA per nucleus was determined in interphase nuclei of root tips fixed in formaldehyde and stained with Feulgen according to the method described by Greilhuber (1988). The stained root tips (*c.* 3 mm long) were twice washed in tap water for 15 min, macerated with 2% pectinase and 0·5% cellulase for 10 min at 27°C, and then

squashed in 45% acetic acid. After removal of the cover glass the slides were twice cleared in SO_2 water for 50 s, rinsed in distilled water, dehydrated in absolute alcohol, and finally made permanent in Euparal. The slides were stored in the dark. The relative amounts of DNA per nucleus were measured with the IBAS image analysis system (Kontron, Eching, Germany). The microscopical image (objective 40 ×, green filter) was scanned and the image was corrected for shading. Of each slide (root tip) the internal optical density (IOD) of at least 100 randomly selected nuclei was measured (Krug 1980). The measured values were arranged in 13–20 classes. To determine the 2C DNA amount the mean was calculated of the values of 2–6 classes around the median of the G1 phase. Of each plant two root tips (replications) were measured.

To convert the IOD values into absolute amounts of DNA per nucleus, *Sedum rupestre* L. subsp. *rupestre* (accession number *HRT-22976*) was used as a standard in all experiments. The amount of DNA per nucleus of the standard plant (4·58 pg) was calibrated with *Allium cepa* (33·55 pg; van 't Hof 1965).

RESULTS

Chromosome numbers

The results of our chromosome counts of 41 plants of the four species of *S.* subsect. *Spathulata* are summarized in Table 1. The diploid chromosome number $2n=12$ of *S. obtusifolium* is reported here for the first time. The other chromosome numbers agree with previous reports for these species.

Baldwin (1935) reported the tetraploid chromosome number $2n=28$ for a cultivated plant of *S. stoloniferum* of unknown origin. The drawing of the karyotype of *S. stoloniferum* which accompanies Baldwin's report, however, is almost identical to the karyotype of *S. spurium* in the same figure. Both karyotypes consist of chromosomes of about 2–3·5 μm which are typical of *S. spurium* (compare Fig. 2e of the present article). Almost certainly Baldwin's report of *S. stoloniferum* is based on a wrongly identified plant of *S. spurium*. Considering the enormous cytological diversity within *Sedum* in general, the tetraploid cytotype of *S. stoloniferum* may quite well occur somewhere, though we found only diplopid plants ($2n=14$) in a representative sample from the central and western part of the distribution area of the species ('t Hart 1984; Appendix).

Cytogeography

The distribution of the species and cytotypes of *S.* subsect. *Spathulata* in Anatolia is presented in Fig. 1. *S. spurium* is a Caucasian element and occurs only in north-eastern Anatolia between approximately 1000 and 3000 m. The plants in the western part of the distribution area in Anatolia usually have red or pink flowers, whereas the plants in the far north-eastern part (prov. Kars) have pure white flowers. Cytologically, however, the two taxa are completely identical. They are both diploid, except for one triploid ($2n=42$), red flowered plant from Gümüşane (Appendix). *S. stoloniferum* is a euxine element. It is bound to the regions with high rainfall on the northern slopes of the mountains bordering the Black Sea. It occurs from sea-level up to 2300 m (on Şavval Tepe) and often grows in mesic conditions (woods and forest margins). The occurrence of *S. stoloniferum* on the Amanus Mountains (prov. Hatay) is quite remarkable, but a similar characteristic disjunct distribution is known for other euxine species (Davis 1965,

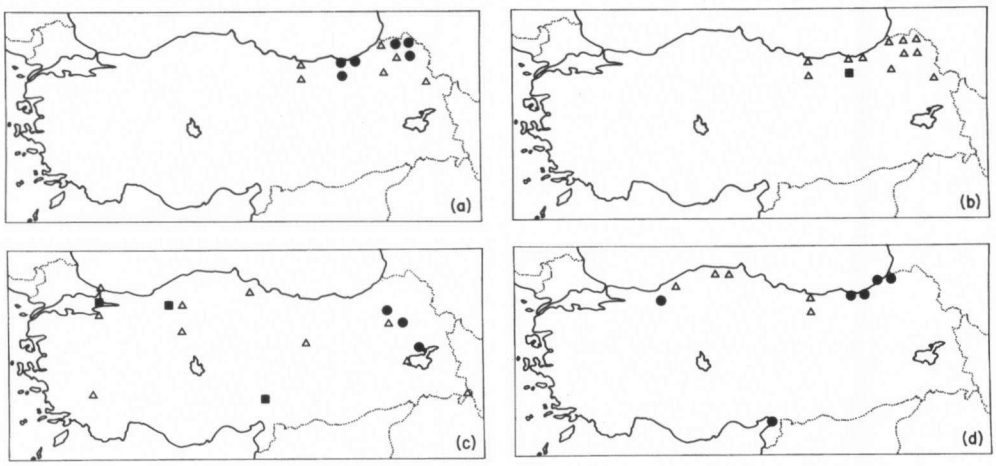

Fig. 1. Distribution of the cytotypes of three species of *Sedum* subsect. *Spathulata* in Turkey (see 't Hart & Alpınar 1991). (a) *S. spurium*, $2n=28$ [●]; (b) id., $2n=42$ [■]; (c) *S. obtusifolium*, $2n=12$ [●] and $2n=30$ [■]; (d) *S. stoloniferum*, $2n=14$ [●]. The open triangles indicate locations of herbarium specimens (Chamberlain 1972, and the authors' own collections).

1971; Quézel 1986). *S. obtusifolium* occurs throughout the larger part of Anatolia as well as in northern Iran and the Caucasus. We found it from sea-level in north-west Turkey (prov. Kocaeli) up to 2150 m in eastern Anatolia (prov. Ağri). The diploid plants ($2n=12$) were all collected east of the Anatolian diagonal, whereas the polyploid plants ($2n=30$) occurred west of this imaginary line (Ekim & Güner 1986).

Morphologically the two cytotypes differ; the diploid plants are smaller, and their leaves are spatulate or oblong-elliptic, whereas the polyploid plants have oblong-elliptic to orbicular leaves.

Amount of DNA per nucleus

The amounts of DNA per 2C nucleus of 6 cytotypes of 4 species of *S.* subsect. *Spathulata* are presented in Table 2. The variation among the taxa is conspicuously discontinuous and the species fall into two distinct groups. *S. obtusifolium* ($2n=12$), *S. stellatum* ($2n=10$) and *S. stoloniferum* ($2n=14$) have about 0·4–0·6 pg DNA per nucleus at the diploid level, whereas *S. spurium* ($2n=28$) has about 5–8 times more DNA (3·5 pg). The differences between the 2C values of the diploid cytotypes of *S. obtusifolium, S. stellatum* and *S. stoloniferum* are highly significant ($P<0·01$), but the differences in the 2C values among the plants of each cytotype are not significant.

Karyotypes

The karyotypes of the species and cytotypes of *S.* subsect. *Spathulata* differ considerably (Fig. 2). Similar to the variation in nuclear DNA content, two groups can be distinguished.

The karyotype of *S. spurium* (Fig. 2e) is fairly symmetrical, with predominantly sub-metacentric or metacentric chromosomes of about 1·6–3·1 μm. The total length of the chromosome complement of the diploid cytotype of *S. spurium* amounts to *c.* 64 μm.

Table 2. Mean nuclear DNA content (2C values) for six cytotypes of four species of *Sedum* subsect. *Spathulata*

Species	2*n*=	Accession number	DNA values: Replicates 1	2	$\bar{x}$	Mean	*L*
S. obtusifolium	12	31290	0·46	0·46	0·46		
		31405	0·36	0·41	0·39	0·42	± 0·08
	30	30254	1·67	1·80	1·74		
		31755	1·63	1·67	1·65	1·69	± 0·12
S. stellatum	10	29024	0·57	0·64	0·61		
		31486	0·56	0·57	0·57	0·59	± 0·06
S. stoloniferum	14	31374	0·57	0·63	0·60		
		31647	0·74	0·59	0·67	0·63	± 0·12
S. spurium	28	30408	3·37	3·68	3·53		
		30409	3·58	3·61	3·60		
		31187	3·40	3·74	3·57		
		31393	3·19	3·79	3·49	3·54	± 0·17
	42	31341	5·49	5·78	5·64	5·64	± 1·84

L indicates the 95% confidence limits of the mean.

The karyotypes of the diploid cytotypes of *S. obtusifolium* (2*n*=12), *S. stellatum* (2*n*=10) and *S. stoloniferum* (2*n*=14) resemble each other to some extent (Fig. 2a,c,d). In contrast to *S. spurium* they have small chromosomes of about 1–2 μm. The total length of the chromosome complements of these three taxa is presented in Table 3. The differences in total chromosome length between the three species are highly significant ($P<0·01$). The total length of the chromosome complements of these three cytotypes is positively correlated with the amount of DNA per nucleus ($P<0·01$). The karyotypes of the three diploid cytotypes are about equally symmetrical, but the karyotype of the polyploid cytotype of *S. obtusifolium* is conspicuously asymmetrical.

DISCUSSION

The results of our cytological studies clearly show that the species of *S.* subsect. *Spathulata* fall into two distinct groups which correspond with the serial classification based on the position of the ripe follicles and the hybridization patterns of the species (Fröderström 1932; 't Hart 1984). The two groups differ significantly in basic chromosome number, amount of DNA per nucleus, and karyotype characteristics. The nuclear DNA content in *S.* series *Involucrata* is about 3·5 pg at the diploid level (2C), the basic chromosome number is $x=14$, and the chromosomes are large and metacentric or sub-metacentric. The nuclear DNA content of the species of *S.* series *Propontica*, on the other hand, is about 0·4–0·6 pg at the diploid level (2C), there are three basic numbers, $x=5$, $x=6$ and $x=7$, and the chromosomes are rather small, about 1 to 2 μm.

Considerable variation in nuclear DNA amounts and chromosome size among congeneric taxa at the diploid level is quite common in angiosperms (Bennett *et al.* 1982; Narayan 1982; Laurie & Bennett 1985; Price 1988). However, the five- to seven-fold

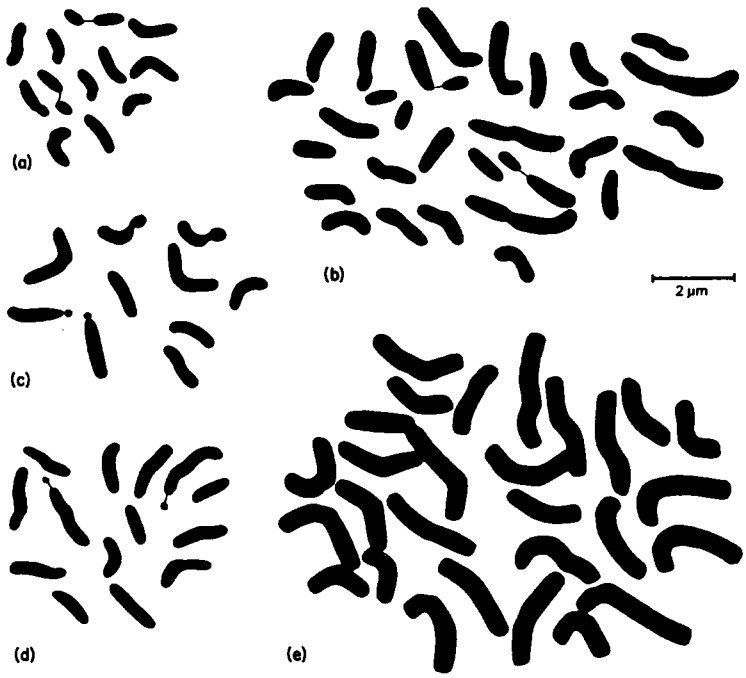

Fig. 2. Somatic metaphase plates of five cytotypes of *Sedum* subsect. *Spathulata*. (a) *S. obtusifolium* C.A. Meyer, $2n=12$ [*HRT-31405*]; (b) *S. obtusifolium*, $2n=30$ [*HRT-30254*]; (c) *S. stellatum* L., $2n=10$ [*HRT-29024*]; (d) *S. stoloniferum* Gmelin, $2n=14$ [*HRT-31374*]; (e) *S. spurium* Bieb., $2n=28$ [*HRT-31393*].

Table 3. Mean total length of the chromosome complements (µm) of the diploid cytotypes of three species of *Sedum* series *Propontica*

Species	$2n=$	Accession number	Metaphase 1	Metaphase 2	Metaphase 3	$\bar{x}$	Mean	L
S. obtusifolium	12	31290	13·1	14·4	16·3	14·6		
		31405	13·0	14·0	14·1	13·7	14·2	± 1·3
S. stellatum	10	29024	14·0	14·1	14·5	14·2		
		31486	16·2	16·8	17·2	16·7	15·5	± 1·5
S. stoloniferum	14	31374	18·2	18·6	19·3	18·7		
		31647	16·0	18·7	20·2	18·3	18·5	± 1·5

L indicates the 95% confidence limits of the mean.

difference in the amount of nuclear DNA and the related variation in chromosome size between the species of *S.* subsect. *Spathulata* are rather extreme. A similar, though somewhat less extreme, variation in chromosome size occurs within another group of morphologically apparently closely related Crassulaceae, i.e. *Rosularia* (DC.) Stapf. ('t Hart & Eggli 1988; Eggli 1988). The species of *R.* sect. *Chrysanthae* Eggli and *R.* sect. *Ornithogalopsis* Berger have a basic number of $x=7$ and large chromosomes (average

length >1·5 μm), whereas the species of *R.* sect. *Rosularia* and *R.* sect. *Sempervivella* (Stapf) Jansson have a basic number of $x=9$, and very small chromosomes (average length <1 μm).

The nuclear DNA amounts of the diploid cytotypes of *S.* series *Propontica* rank among the smallest so far recorded for angiosperms, and they are much smaller than the DNA amounts per nucleus reported for other Crassulaceae (Bennett 1972; Bennett & Smith 1976; Bennett *et al.* 1982). In many groups of angiosperms the nucleotype is considered to be positively correlated with latitude, altitude, life cycle and/or minimum generation time (Bennett 1972; Grime & Mowforth 1982; Laurie & Bennett 1985; Rayburn *et al.* 1985; Kenton *et al.* 1986). However, in the species of *S.* subsect. *Spathulata* no such correlation could be observed. On the contrary, at several locations in north-eastern Anatolia diploid *S. spurium* ($2n=28$) and *S. stoloniferum* ($2n=14$) grow in close proximity (Yağmurdere, 1750 m, prov. Gümüşane; Sümela Monastery, 1250 m, prov. Trabzon), or even intermingled (Kirklar Dağı, Sivrikaya, 1850 m, prov. Rize). These mixed populations make one wonder about the significance of the five- to six-fold difference in nuclear DNA amount between these two congeneric and morphologically very similar diploid species, which grow in the same habitat and compete for the same resources (Thomas 1971; Narayan 1983).

The hybridization pattern of the species of *S.* subsect. *Spathulata s.l.* fully agrees with the cytological differences between *S.* series *Involucrata* and *S.* series *Propontica.* Although *S. spurium* and *S. stoloniferum* grow in close proximity or even in mixed populations, natural hybrids have never been reported. *S. stellatum* and *S. stoloniferum*, on the other hand, can be very easily hybridized experimentally, but crosses between these two species and *S. spurium* have not been successful so far ('t Hart 1984). These results corroborate the observation that substantial differences in genome size (2C values and/or chromosome size) affect crossability or hybrid vigour and viability (Laurie & Bennett 1985; Flavell 1986).

At first sight the evolutionary relationship between the three species of *S.* series *Propontica* seems to be determined by a simple series of dysploid changes resulting from two successive Robertsonian translocations. Beginning with the least specialized, perennial *S. stoloniferum* ($2n=14$) these would have led to the most specialized, annual *S. stellatum* ($2n=10$), via the somewhat less advanced, perennial *S. obtusifolium* ($2n=12$). The differences between the species in 2C values and total length of their chromosome complements, by and large agree with the supposed dysploid changes. However, the similarity of their karyotypes, which are about equally symmetrical, and the significant decrease in the 2C values indicate that the process of speciation has most likely been more intricate.

The amount of nuclear DNA in the plants of *S. obtusifolium* with the chromosome number $2n=30$ is almost exactly four times the amount of DNA in the diploid ($2n=12$) plants (Table 2). However, the chromosome number and chromosome morphology do not agree with an octoploid condition ('t Hart & Alpınar 1991). If the plants are really octoploid the modification of the karyotype would have involved several Robertsonian translocations (without notable change of the amount of nuclear DNA) resulting in a reduction of the presumed octoploid chromosome number by 18. The asymmetry of the karyotype of the plants seems to support this idea to some extent. An alternative mode of origin for the plants with the chromosome number $2n=30$ would be allopolyploidy. However, with respect to the identical, peculiar habit of the two cytotypes of this species, an allopolyploidy origin seems quite unlikely.

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APPENDIX

Origin, collection number, accession number of the cytologically investigated plants. The AH numbers refer to plants collected for the project 'Biosystematic studies in *Sedum* of Turkey' ('t Hart & Alpınar 1991).

Sedum obtusifolium C.A. Meyer, $2n=12$.
Turkey: prov. Ağrı; 41 km S of Horasan, 1 km W of Tahir, 2150 m, *AH-296* [*HRT-31160*]; **prov. Erzurum**; valley of the River Tortum, 30 km N of Erzurum along the road to Artvin, 1900 m, *AH-541* [*HRT-31405*]; **prov. Van**; 20 km N of Erçis along the road to Patnos, 1900 m, *AH-426* [*HRT-31290*].

S. obtusifolium C.A. Meyer, $2n=30$.
Turkey: prov. Bolu; 20 km S of Gerede, W of the road to Kızılcahaman, 1350 m, *AH-33* [*HRT-30254*]; **prov. Kocaeli**; near Yelkenkaya along the road to Bayramoğlu, S of the road Istanbul–Izmit, 50 m, *AH-107* [*HRT-30842*]; **prov. Malatya**; near Kargaçayiri, 25 km S of Geben along the road to Andlrin, 1200 m, *AH-667* [*HRT-31755*].

Sedum spurium Bieb., $2n=28$.
Turkey: prov. Artvin; near Cam Gecidi 28 km ESE of Şavşat along the road to Ardahan, 2300 m, *AH-529* [*HRT-31393*]; **prov. Gümüşane**; N of Vaudağı Geçidi, 35 km S of Gümüşane W of the road to Bayburt, 1700 m, *AH-470* [*HRT-31334*]; **prov. Kars**; castle of Kars, 1800 m, *AH-323* [*HRT-31187*]; near the river Mezra, 15 km N of Kars along the road to Susuz, 1650 m, *AH-328* [*HRT-31192*]; 5 km N of Susuz, along a small tributary of the River Kars, 1850 m, *AH-331* [*HRT-31195*]; Gölgeli, 41 km N of Susuz, 1900 m, *AH-335* [*HRT-31199*]; 5 km E of Ardahan along the road to Kars, 1900 m, *AH-339*, [*HRT-31203*]; 8 km E of Çıldır along the northern shores of Lake Çıldır, 2050 m, *AH-342* [*HRT-31206*]; **prov. Rize**; Kırklar Dağı, near Ovitdağı Geçidi, 2650 m, *AH-506* [*HRT-31370*]; Kırklar Dağı, near Sivrikaya N of Ovitdağı Geçidi E of the road to Rize, 1850 m, *AH-511* [*HRT-31375*]; **prov. Trabzon**; Altındere Vadisi Milli Parki, 5 km S of Meyem Ana Monastery, 1650 m, *AH-498* [*HRT-31362*]. **USSR: Armenia**; Ceceros–Lagusskaya, valley of Dzhairachi, 150 km on the road from Tbilisi to Ordzhorikidze, 1050 m, U. Eggli *UE-448* [*HRT-30408*]; Sevan, on Sevan peninsula in Lake Sevan, *c.* 2000 m, C.C. Beerg *s.n.* [*HRT-18461, HRT-18462*]; **Georgia**: Kazbegi rayon, above the village of Kazbegi, 1900 m, U. Eggli *UE-387* [*HRT-30409*].

S. spurium Bieb., $2n=42$.
Turkey: prov. Gümüşane; 2·5 km S of Kostandağı Geçidi, along a small stream 17 km SW of Yağmudere, 2000 m, *AH-477* [*HRT-31341*].

Sedum stellatum L., $2n=10$.
Greece: Kefalonia, ep. Kranaias; NE of Argostoli, near the crossroads at the eastern shore of the Koutavos laguna, 25 m, A.R. Schouten *ST8*, [*HRT-29024*]; NE of Argostoli, 3 km E of the

Koutavos laguna near the road to Ayia Varvara, 100 m, A.R. Schouten *ST9* [*HRT-29025*]; near the church of Ayia Varvara E of Argostoli, 70 m, A.R. Schouten *ST10* [*HRT-29026*]; above Argostoli, along the road to Spilaio, *c.* 80 m, A.R. Schouten *ST14* [*HRT-29028*]; **ep. Samis**; vic. of Lake Avythos near Ayios Nikolaos, 280 m, A.R. Schouten *ST11* [*HRT-29027*]; **Ithaki, ep. Ithakis**; W of Vathy along the road to Arethousa Spring, 150 m, A.R. Schouten *ST16* [*HRT-29024*]. **Italy: Sardinia;** near the coast at Porto Alabae (vic. of Bosa), A. Mayer *s.n.* [*HRT-31486*].

Sedum stoloniferum Gmelin, $2n=14$.
Turkey: prov. Artvin; 4 km N of Arhavi along the road to Rize (74 km), near the sea, *AH-516* [*HRT-31380*]; Alaca Dağı, near Saz 24 km SWS of Murgul, 1850 m, *AH-519* [*HRT-31383*]; Alaca Dağı, Şavval Tepe, near Çamurlu Yayla, 2300 m, *AH-523* [*HRT-31387*]; **prov. Bolu**; about 3 km S of Yedigöller Milli Parkı, along the road to Bolu, 1450 m, *AH-118* [*HRT-30853*]; 1–2 km N of Sarımıstan, along the road from Bolu to Yedigöller Milli Parkı, along the road to Bolu, 1450 m *AH-118* [*HRT-30853*]; 1–2 km N of Sarımıstan, along the road from Bolu to Yedigöller Milli Parkı, 1700 m, *AH-125* [*HRT-30860*]; **prov. Gümüşane**; 1·5 km N of Yağmudere along the road to Araklı, 1750 m, *AH-493* [*HRT-31357*]; **prov. Hatay**; 13 km NNE of Belen, along the road from Atik Yayla to the military post, 1650 m, *AH-563* [*HRT-31647*]; **prov. Rize**; Kırklar Dağı, near Sivrikaya N of Ovitdağı, Geçidi, E of the road to Rize, 1850 m, *AH-510* [*HRT-31374*]; valley of the River Iyidere near Kalkandere along the road to Rize, 50 m, *AH-515* [*HRT-31379*]; **prov. Trabzon**; near Sümela Monastery, 1250 m, *AH-494* [*HRT-31358*]; 10 km N of Macka along the road to Meyem Ana Monastery (Sümela), 750 m, *AH-501* [*HRT-31365*]; 2 km W of Of, near the sea along the road to Sürmene, *AH-502* [*HRT-31366*].