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Cytotaxonomic studies in *Rosularia* (Crassulaceae)

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Abstract

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The 15 species of *Rosularia* cytologically studied differ conspicuously in the size of their chromosomes, basic number and level of polyploidy. Two groups can be distinguished; 6 species have the basic number $x = 7$ (or the secondary number $x = 13$), relatively long chromosomes (on average more than 1.5 microns) and are predominantly polyploid ($2n = 14, 26, 28, 56, 70, 84$ and 104), whereas the other 9 species have the basic number $x = 9$ (or the secondary number $x = 8$), chromosomes less than 1 micron long and they are mainly diploid ($2n = 18, 36$ and 128). The evolutionary relationships between these two groups and the systematic position of some taxa recently included in *Rosularia* are briefly discussed.

Introduction

De Candolle (1828) classified the Old World rosette-forming Crassulaceae with a distinctly gamopetalous corolla in section *Rosularia* of the genus *Umbilicus* DC. However, gamopetalous flowers and rosettes have developed independently in many groups of Crassulaceae (Berger 1930, Uhl 1961a) and plants sharing these characters are not necessarily closely related. Stapf (1923) regarded *U.* sect. *Rosularia* as a distinct genus. Berger (1930) removed *Rosularia* from the other gamopetalous Crassulaceae and included it in the predominantly choripetalous subfamily Sedoideae. He distinguished two sections, viz. sect. *Rosularia* with about 25 species in Asia Minor and the Himalaya, and the monotypic sect. *Ornithogalopsis* Berger for *R. paniculata* (Regel & Schmalh.) Berger from northern Iran, Afghanistan and adjacent regions of the U.S.S.R. Borissova (1939, 1969) added the two Irano-Turanian species of *Sedum* sect. *Sempervivoides* Boiss. (= *S.* sect. *Prometheum* Berger) and *Sempervivella alpestris* (Kar. & Kir.) Berger (= *Umbilicus alpestris* Kar. & Kir.) from the Himalaya to *Rosularia*. She distinguished 4 sections in the genus. Jansson & Rechinger (1970) further added *Sedum adenotrichum* Wall. ex Edgew. (incl. var. *viguieri* Hamet) to *Rosularia*. Ohba (1978), on the other hand, excluded the two species of *S.* sect. *Sempervivoides* (= *Prometheum* (Berger) Ohba) from *Rosularia*, but

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added *Sempervivella sedoides* (Decne.) Stapf, the monotypic genus *Afrovivella* Berger from Ethiopia and *Sedum* sect. *Monanthella* Berger from Morocco. In his revision of *Rosularia* (in press) Eggli accepted Ohba's delimitation of the genus, though he included two more species of *Sedum* from SE Europe and Morocco, viz. *S. hirsutum* All. and *S. wilczekianum* Font Quer. In all, he distinguished 25 species in the genus *Rosularia* (including 11 subspecies and 2 varieties) which he arranged in 4 sections. In contrast to the preceding authors, Hamet (1929) and Fröderström (1930–1932) did not recognize the genus *Rosularia*. They included it in *Sedum* and assigned the species to different infrageneric groups.

Cytologically the family Crassulaceae is about the most variable group of plants imaginable. Especially within the genus *Sedum* L. (350–500 species) the variation seems infinite. Every basic chromosome number from $x=4$ to $x=37$ has been reported and many higher basic numbers also occur (Uhl 1963, 't Hart 1985). Many species comprise a polyploid series, sometimes of considerable length, and furthermore, dysploidy and amphiploidy are common phenomena in many taxa. Because of their enormous diversity, cytological characters can be successfully used to delimit species and all kinds of infraspecific taxa within the Sedoideae, but they are usually of very little help for defining higher taxa. However, the other subfamilies of the Crassulaceae, and some of the genera of the Sedoideae which are apparently transitional to the other subfamilies, show less cytological variation and in these groups chromosome studies have been very useful for clarifying taxonomic relationships (Uhl 1961 a, b, Uhl & Moran 1953, 1973, Friedrich 1973).

Except for two undocumented reports of $n=ca. 52$ and $n=64$ by Uhl (1961 b) for *R. pallida* (= *R. aizoon*) and *R. sedoides* [*Sempervivella alba* (Edgew.) Stapf] respectively, virtually nothing was known about the cytology of *Rosularia* s.l. The present cytological investigations were carried out in conjunction with a systematic study of *Rosularia* by the junior author (Eggli in press). To this purpose he assembled a sizable collection of generally well-documented living plants which enabled us to make this survey.

Material and methods

The majority of the plants studied were collected in nature by the authors themselves, but some were obtained from other sources (table 3). The plants were cultivated in the temperate greenhouses of the Botanic Gardens of the University and the Städtische Sukkulenten-Sammlung at Zürich and/or the University at Utrecht. Voucher specimens of the plants studied are or will be deposited either in the herbarium of the Institute of Systematic Botany, Zürich (Z) or in that of the Institute of Systematic Botany at Utrecht (U). Chromosome numbers were determined in root-tip mitoses ('t Hart 1978). Drawings were made with the use of a Zeiss Camera Lucida and auxiliary magnification systems (magnification ca. 9000). The nomenclature proposed by Eggli (in press) is used throughout.

Results

The karyotypes of the 15 species and 9 subspecies of *Rosularia* that were cytologically investigated differ in many respects. Most conspicuous were the differences in the size and number of the chromosomes, the basic chromosome number and the level of ploidy. The results are summarized in table 1.

Tab. 1. The average length of the chromosomes, the basic numbers and the somatic chromosome numbers of 15 species of the genus *Rosularia* (DC.) Stapf.

Length in μ	x =	<i>Rosularia</i>	2n =							
			2 ×	4 ×	6 ×	8 ×	10 ×	12 ×	14 ×	16 ×
> 1.5	7 (13)	<i>aizoon</i>	14	26, 28			70			
		(13) <i>alpestris</i> ssp. <i>alpestris</i>		26, 28						
		<i>chrysantha</i>						84		
		(13) <i>rechingeri</i>								c. 104
		<i>serpentinica</i> var. <i>serpentinica</i>				56				
		var. <i>gigantea</i>		28						
		var. (Elmali)							112	
< 1	9	spec. (Murat Dağı)			56					
		<i>adenotricha</i> ssp. <i>adenotricha</i>	18	36						
		ssp. <i>viguieri</i>	18							
		<i>blepharophylla</i>	18							
		<i>elymaitica</i>	18							
		<i>globulariifolia</i>	18							
		<i>haussknechtii</i>	18							
		<i>lineata</i>	18							
		(8) <i>sedoides</i>								128
		<i>sempervivum</i> ssp. <i>sempervivum</i>	18							
		ssp. <i>amanensis</i>		36						
		ssp. <i>glaucophylla</i>		36						
		ssp. <i>kurdica</i>	18							
		ssp. <i>libanotica</i>	18							
		ssp. <i>persica</i>	18							
		ssp. <i>pestalozzae</i>		36						
		<i>serrata</i>	18							

a. Size of the chromosomes

Like the chromosomes of almost all Crassulaceae the chromosomes of *Rosularia* are small or very small, usually less than 2.5 microns long. Nevertheless, the species differ conspicuously with respect to the size of their chromosomes, which allows to distinguish two groups. The chromosomes of 16 taxa (9 species and 7 subspecies) were very small (fig. 1 d–k). Depending on the degree of condensation their length varied from about 0.85–1.25 micron for the longest chromosome and from about 0.35–0.6 micron for the smallest. On average the chromosomes of this group were less than 1 micron long. The length of the chromosomes of the other 8 taxa (6 species and 2 subspecies) varied from about 1–1.5 micron for the smallest chromosome to about 2.5 microns for the longest (fig. 1 a–c). On average the chromosomes of this group were more than 1.5 microns long.

Although the centromeres and the individual chromatids of the chromosomes of most species of *Rosularia* were usually indistinguishable, the often somewhat elliptical or ovate shape of the chromosomes indicated a distal position of the centromere. Most probably the small chromosomes are predominantly acrocentric or telocentric. The karyotypes of most plants were rather symmetrical. In the plants with long chromosomes



Fig. 1. Metaphase plates from root-tips of *Rosularia*. – a, *R. aizoon* (Fenzl) Berger, $2n=14$ (Eggli 931) – b, *R. alpestris* (Kar. & Kir.) Boriss. ssp. *alpestris*, $2n=28$ (HtH 30403) – c, id, $2n=26$ (HtH 30523) – d, *R. serrata* (L.) Berger, $2n=18$ (HtH 30206) – e, *R. globulariifolia* (Fenzl) Berger, $2n=18$ (HtH 30204) – f, *R. adenotricha* (Wall.) Jansson ssp. *viguieri* (Hamet) Jansson, $2n=18$ (HtH 30519) – g, *R. haussknechtii* (Boiss. & Reuter) Berger, $2n=18$ (Eggli 983) – h, *R. sempervivum* (Bieb.) Berger ssp. *sempervivum*, $2n=18$ (HtH 30540) – i, *R. sempervivum* ssp. *kurdica* Eggli, $2n=18$ (Eggli 882) – j, *R. sedoides* (Decne.) Ohba, $2n=128$ (HtH 30531) – k, *R. elymaitica* (Boiss. & Hausskn.) Berger, $2n=18$ (Eggli 886).

as well as the plants with small chromosomes the longest chromosome was generally about twice as long as the smallest, and the extremes were usually linked by an almost continuous series of intermediates (fig. 1). However, in a few taxa the variation in the length of the chromosomes is distinctly discontinuous. For example, *R. elymaitica* (Boiss. & Hausskn.) Berger (fig. 1 k) and *R. sempervivum* (Bieb.) Berger ssp. *persica* (Boiss.) Eggli have four conspicuously large chromosomes. The other subspecies of *R. sempervivum*, on the other hand, usually have six or eight long chromosomes, but these are less distinct (fig. 2 h, i). Furthermore, the forms of *R. alpestris* ssp. *alpestris* with the chromosome number $2n=28$ have two pairs of chromosomes of about 1 micron which are much smaller than the others (fig. 1 b).

b. Chromosome numbers and polyploidy levels

In 22 plants of the 6 species with long chromosomes (average about 1.5 microns) the chromosome numbers $2n=14, 26, 28, 56, 70, 84, 104$ and 112 were found (table 3). These are all multiples of 7, except for the numbers $2n=26$ and 104 . In this group the tetraploid and higher levels of ploidy prevail. The diploid cytotype ($2n=14$) is rare, having so far only been found in three populations of *R. aizoon* (Fenzl) Berger from eastern Anatolia. On the other hand, the chromosome number $2n=28$ was found in 3 species, the numbers $2n=26$ and 56 in two species each. The other chromosome numbers were each found only in a single species. Within *R. aizoon* and *R. serpentinica* (Werdermann) Muirhead occur large polyploid series with the numbers $2n=14, 28$ and 70 and $2n=28, 56$ and 112 , respectively.

In 45 plants of the 9 species with small chromosomes (on average less than 1 micron) the chromosome numbers $2n=18, 36$ and 128 were found (table 3). The first two numbers are multiples of 9 and the third a multiple of 8. Except for *R. sedoides*, all species are diploid and have the chromosome number $2n=18$. In addition the tetraploid chromosome number $2n=36$ was found in *R. adenotricha* ssp. *adenotricha* and in *R. sempervivum* ssp. *amanensis* Eggli, ssp. *glaucophylla* Eggli and ssp. *pestalozzae* (Boiss.) Eggli. The chromosome number $2n=128$ was only found in *R. sedoides*. This species is most probably 16-ploid.

c. Dysploidy and variation in the size of the chromosomes

A comparison of the karyotypes of the two tetraploid cytotypes, with the chromosome number $2n=26$ and $2n=28$, respectively (table 1), of *R. aizoon* and *R. alpestris* ssp. *alpestris* showed that the differences in chromosome number are correlated with differences in the length of some chromosomes. The plants of *R. alpestris* with the chromosome number $2n=26$ have one pair of extra long chromosomes which are not found in the karyotypes of the plants with the chromosome number $2n=28$ (fig. 1 b, c). These extra long chromosomes have probably resulted from the fusion of two pairs of small

Tab. 2. Mean relative length of the chromosomes (haploid set) of the karyotypes of the two tetraploid cytotypes of *Rosularia alpestris* ssp. *alpestris* in figure 1.

2n	Length of the chromosomes (%)															tot.	EE
28	—	5.0	4.3	4.1	3.9	3.8	3.6	3.6	3.5	3.3	3.2	3.1	3.0	2.9	2.7	50.0	0.2–0.5
26	5.6	4.6	4.3	4.2	4.1	3.9	3.7	3.6	3.5	3.4	3.3	3.1	—	2.9	—	50.2	0.3–0.6

Tab. 3. Chromosome numbers, origin and collection numbers of the plants studied (HtH numbers refer to the collection in Utrecht, the other numbers to plants cultivated at Zürich).

Rosularia adenotricha (Wall.) Jansson ssp. *adenotricha*

2n = 18. **Afghanistan: prov. Paktia**; Sirkai Kotal, soil slopes, 3000 m, *Hedge & Wendelbo W8902*, ex Roy. Bot. Gard. Edinburgh 691360.

2n = 36. **India: Himachal Pradesh**; Simla distr.; Kufri-Jail road, ca. 2000 m, *Sarkaria s.n.*, ex International Succulent Institute (ISI) 1223, HtH 30404.
Nepal: N of Tianiri, Bheri river, *Bruyns 2495*.

R. adenotricha (Wall.) Jansson ssp. *viguieri* (Hamet) Jansson

2n = 18. **Afghanistan**: Hindarkush, Salang pass, on limestone, 3500–4200 m, *Furse 8782*, ex Roy. Bot. Gard. Edinburgh 671127, HtH 30519.

R. aizoon (Fenzl) Berger

2n = 14. **Turkey: prov. Erzincan**; Munzur Dağları, N side, above Uluçinar, among limestone pebbles in much degraded pasture, *Eggli 982*; **prov. Erzurum**; S side of Çoruh Dağları, Erzurum – Ispir, between Kirkik and Ispir, near highest point of pass, limestone and volcanic debris, 2200 m, *Eggli 931*; **prov. Gümüşane – Erzurum**; Kopdagi Geçidi, highest point of pass, on limestone conglomerate, 2400 m, *Eggli 965*.

2n = 26. **Turkey: prov. Van**; Menengene Dağı, between Van and Başkale, near Güzeldere Geçidi, cracks of limestone, 2900 m, *Eggli 872*; Menengene Dağı, between Van and Başkale, near Güzeldere Geçidi, in cracks of a dark rock, 2900 m, *Eggli 873*; **prov. Van**; Kavuşahap Dağları, Arnas Dağı, between Van and Çatak, turnoff to Bahçesaray, 2–3 km E of highest point of pass, on whitish dolomite rocks and in cracks, 2750–2850 m, *Eggli 876, 877, 878*.

2n = 28. **Turkey: prov. Bitlis**; W end of Kavuşahap Dağları, Hanemir Dağı, SE of Küçüküsu, above Oboskü, cracks of limestone rocks, 2500 m, *Eggli 863*; **prov. Van**; Mengene Dağı, between Van and Başkale, on a small hill near Güzeldere Geçidi, limestone, 2900 m, *Eggli 870*.

2n = 70. **Turkey: prov. Içel**; above Arslanköy, 2200 m, *Eggli 809*, HtH 30520; summit of hill 2 km NW of Arslanköy, 2600 m, *Peat 112.5.76*, ex Roy. Bot. Gard. Edinburgh 763186, HtH 30526.

R. alpestris (Kar. & Kir.) Boriss. ssp. *alpestris*

2n = 26. **Pakistan: Hazara**; Kaghan Valley, *Swedish Exped. Pakistan 282*, ex Roy. Bot. Gard. Kew 438-83-05864, HtH 30523.

2n = 28. **India: Kashmir**; Ladakh area, near the village of Haloti, 2960 m, *Gubler s.n.*, HtH 30403; Zozila (Zojilla), *Anonymus s.n.*, HtH 30522, 30499.

R. blepharophylla Eggli

2n = 18. **Turkey: prov. Diyarbakir**; 2–3 km SW of Ergani, in crevices and cracks of a greyish-white limestone hill, 810 m, *Eggli 851* [type collection], HtH 30521.

R. chrysantha (Boiss.) Tahkt.

2n = 84. **Turkey: prov. Isparta**; Dedegöl Dağı, steppe, 1800 m, *Sorger 70-46-88*, ex Roy. Bot. Gard. Edinburgh 702507, HtH 30525.

R. elymaitica (Boiss. & Hausskn.) Berger

2n = 18. **Turkey: prov. Van**; Arnas Dağı, between Van and Çatak, 8 km N of Çatak, limestone, 1850 m, *Eggli 886*.

Tab. 3. (continued)

R. globulariifolia (Fenzl) Berger

- 2n=18. **Turkey: prov. Antalya;** ruins of Phaselis S of Kemer, on limestone walls, 't Hart 30204; 8 km S of the turnoff to Cirali E of the main road from Anatalya to Kumluca, limestone, 600 m, *Eggli* 748; **prov. İçel;** Cilician Gates, near Tasobaşı, 10 km N of Pozanti along the road to Tarsus, limestone, *Eggli* 814.

R. haussknechtii (Boiss. & Reuter) Berger

- 2n=18. **Turkey: prov. Erzincan;** Munzur Dağları, N slope, above Uluçınar, in limestone crevices, 1800 m, *Eggli* 983.

R. lineata (Boiss.) Berger

- 2n=18. **Israel:** Upper Galilee, vic. of Kibbutz Yiftach, ca. 3 km from Lebanese border, *Shaw & Horovitz s.n.*, ex Roy. Bot. Gard. Kew *s.n.* [type collection of *R. setosa*], HtH 30527.

R. rechingeri Jansson

- 2n=c. 104. **Kurdistan** (Turkey, Iraq or Iran): exact provenance unknown, HtH 30530.

R. sedoides (Decne.) Ohba

- 2n=128. **India Kashmir;** vic. of Lake Gangabal, *Synge & Polunin s.n.*, ex Roy. Bot. Gard. Kew 294-77-02211, HtH 30531.

R. sempervivum (Bieb.) Berger ssp. *sempervivum*

- 2n=18. **Armenian S.S.R.:** Between Yerevan and Ghepard, near Garni, valley of the river Azam, basalt, 1250 m, *Eggli* 541, HtH 30539; NE part of Nakhichevan, Kafansky region, ex Hort. Bot. Yerevan, *Eggli* 521, HtH 30541; Ashtarak valley W of Yerevan, *Eggli* 573. **Turkey: prov. Van;** Artos Dağ, N slopes above Gevaş, 2900 m, *McNeill* 774, ex Roy. Bot. Gard. Edinburgh 560410, HtH 30540.

R. sempervivum (Bieb.) Berger ssp. *amanensis* Eggli

- 2n=36. **Turkey: prov. Hatay;** Gavur Dağları, between Dörtöl and Hassa, *Ern & Krone* 7022, ex Hort. Bot. Berlin 247-22-81-24.

R. sempervivum (Bieb.) Berger ssp. *glaucophylla* Eggli

- 2n=36. **Turkey: prov. Adana;** vic. of Pozanti, *Aberdeen Univ. Amanus Exp. I1.547*, ex Roy. Bot. Gard. Edinburgh 711816, HtH 30533; **prov. İçel;** Bolkar Dağları, N of Arslanköy, limestone, 1650 m, *Eggli* 784, HtH 30532; above Arslanköy, ca. 2000 m, *Eggli* 801.

R. sempervivum (Bieb.) Berger ssp. *kurdica* Eggli

- 2n=18. **Turkey: prov. Van;** Kavuşahap Dağları, Arnas Dağı, between Van and Çatak, turnoff to Bahcesaray, 15 km E of pass, above Yukari Narlıca, limestone, 2350 m, *Eggli* 882.

R. sempervivum (Bieb.) Berger ssp. *libanotica* (Labill.) Eggli

- 2n=18. **Turkey: prov. Gaziantep;** 39 km E of Bahçe, between Osmaniye and Gaziantep, limestone, 900 m, *Eggli* 835.

R. sempervivum (Bieb.) Berger ssp. *persica* (Boiss.) Eggli

- 2n=18. **Iran: prov. Kordestān;** Zagros Mts., 21 km S of Baneh along the road to Dezh Shāhpur (Marivam), 1700 m, *Fliegner & Simmons* 491, ex Roy. Bot. Gard. Kew 456-77-04282, HtH 30534; **prov. Mazandaran;** Elburz Mts., W of Rudbarak towards Mt. Takht-i-Suleiman, 1775 m, *Fliegner & Simmons* 359, ex Roy. Bot. Gard. Kew 456-77-06735, HtH 30529.

Lebanon – Syria: Jebel esh-Sheikh (Mt. Hermon), 1800 m, *Liston s.n.*, HtH 30535.

Turkey: prov. Elazığ; ca. 22 km N of Elazığ along the road to Tunceli, above pumping station of Keban Barajı, basaltic rocks, 900 m, *Eggli* 1003.

Tab. 3. (continued)

-
- R. sempervivum* (Bieb.) Berger ssp. *pestalozzae* (Boiss.) Eggli
 2n=36. **Turkey: prov. Adana;** Kaypak, *Aberdeen Univ. Amanus Exp. 11.688*, ex Roy. Bot. Gard. Edinburgh s.n. HtH 30536; N of Pozanti, *Aberdeen Univ. Amanus Exp. N2854*, ex Roy. Bot. Gard. Edinburgh 711804, HtH 30538; **prov. İçel;** 28 km E from Gazipaşa along the road to Anamur, dark limestone, 450 m, *Eggli 761*, HtH 30544.
- R. sempervivum* (Bieb.) Berger ssp.
 2n=18. **Turkey: prov. Bitlis;** W end of Kavuşsahap Dağları, Hanemir Dağı SE of Küçükusu, above Oboskü, cracks of limestone rocks, 2300 m, *Eggli 861*; **prov. Tunceli;** between Erzincan and Tunceli, ca. 30 km N of Tunceli, green schist, 1050 m, *Eggli 989*.
 2n=36. **Turkey: prov. Erzincan;** N side of Munzur Dağları, above Uluçınar, in limestone crevices, 1800 m, *Eggli 975*.
- R. serpentinica* (Wedermann) Muirhead var. *serpentinica*
 2n=56. **Turkey: prov. Muğla;** Sandras Dağları, above Ağla, 1600 m, *Eggli 729*.
- R. serpentinica* (Wedermann) Muirhead var. *gigantea* Eggli
 2n=28. **Turkey: prov. Muğla;** in a narrow valley ca. 3 km N of Marmaris, E of the road to Muğla (at the very first sharp bend in the road), at the base of serpentine rocks facing N, 150 m (locus classicus), 't Hart 30205.
- R. serpentinica* (Wedermann) Muirhead var.
 2n=112. **Turkey: prov. Elmalı;** highest point of pass N of Çölhisar in the direction of Karacula, *Koenen s.n.*, ZSS 87-2121.
- R. serrata* (L.) Berger
 2n=18. **Greece: Crete; Nom. Chanion;** Akrotiri, Katholikon, near Gouvernetou monasteri, 100–150 m, 't Hart 27234; Gorge of Samaria, 5 km N of Agia Roumeli, 200 m, 't Hart 27235; Gorge of Samaria, on rocks S of Xyloskala, 1150–1200 m, 't Hart 27236; **Nom. Lasithiou;** near Lassithi pass, *B. Egli 150361*; on a dry-stone wall S of Orino, 600–650 m, 't Hart 27237; **Nom. Rethymnis;** Idi Mts. Nida plain, rocks near the entrance to Ideon Antron, 1600 m, 't Hart 27238; **Samos;** pine woods 1 km W of Moni Zood. Pigis, 200 m, 't Hart 28301; Pírgos, on walls, ca. 350 m, 't Hart 28314; Mt. Kerkis, E slopes, 500 m E of Moni Koim. Theotokou on rocks along the road to Kozmadhei, 700 m, 't Hart 28296. **Turkey: prov. Denizli;** slopes above Pamukkale, limestone 500 m, *Eggli 688*; **prov. Muğla;** on limestone cliffs 11.5 km N of Marmaris along the road to Muğla, 50–100 m, 't Hart 30206; on limestone rocks 2 km S of Kızılağaç, 20 km S of Muğla, 600 m, 't Hart 30207; ancient site of Pinara, 330 m, *Eggli 739*.
- R. spec.* (Murat Dağı)
 2n=56. **Turkey: prov. Kutahya;** Murat Dağı, on rocky igneous slopes, 2100 m, *Davis s.n.*, ex Roy. Bot. Gard. Edinburgh 622740, HtH 30542.
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chromosomes which are still present in the cytotype with the chromosome number 2n=28 (table 2). Among the European Sedoideae descending dysploid changes of the basic number are quite common. In some cases the dysploid change could be demonstrated to have resulted from chromosome fusion rather than from the loss of chromosomes (aneuploidy), e.g. in the diploid *S. cepaea* L. ('t Hart 1985 and in prep.).

Of *R. rechingeri* Jansson only plants of a single collection are presently available for investigation. They have the chromosome number 2n=104 and the chromosomes are all rather long. The basic number x=13 in this cytotype most probably originated from a

dysploid change in the chromosome number of a tetraploid ancestor similar to the cytotypes with the chromosome number $2n=26$ of *R. aizoon* and *P. alpestris*.

The chromosomes of *R. sedoides* are very small, on average about 0.4 to 1.1 microns (fig. 1 j). Although the chromosomes of this highly polyploid cytotype differ considerably in length the variation is rather gradual and the karyotype of *R. sedoides* is no more asymmetrical than those of *R. elymaitica* and *R. sempervivum* ssp. *persica* of the group of species with small chromosomes (fig. 1 d–i, k).

Discussion

In contrast to the confusing diversity of chromosome numbers and basic numbers in the majority of groups of the Sedoideae, the cytological variation in *Rosularia* shows a very clear pattern. The 15 cytologically studied species (including 9 subspecies) can be divided into two very distinct groups which differ strikingly in the size of their chromosomes, basic number and levels of ploidy; 6 species have the basic number $x=7$ (or the secondary basic number $x=13$), long chromosomes (average 1.5 microns) and are completely or predominantly polyploid, whereas the other 9 species have small chromosomes (average less than 1 micron), the basic number $x=9$ and are mainly diploid, except for a few tetraploid forms of *R. adenotricha* and *R. sempervivum* and the highly polyploid ($16x$) *R. sedoides* which has the (probably secondary) basic number $x=8$.

Especially the uniformity of these two groups in regard to their basic number and the size of their chromosomes strongly suggest that each group has evolved independently over a very long period. However, morphologically the two groups are much less differentiated and none of the four most recent infrageneric classifications of the genus completely agrees with the cytological data. Most sections distinguished by Berger (1930), Borissova (1939, 1969) and Jansson and Rechinger (1970) comprise species of both groups. In his revision of the genus (in press) Eggli arranged the species in four sections. Of the species with the basic number $x=7$ he placed *R. aizoon*, *R. chrysantha*, *R. rechingeri* and *R. serpentinica* in *R. sect. Chrysanthae* Eggli and *R. alpestris* in *R. sect. Ornithogalopsis*. Except for *R. adenotricha*, he included all species with the basic number $x=9$ in *R. sect. Rosularia*. The former he placed in *R. sect. Sempervivella* (Stapf.) Jansson, in which in addition to *R. sedoides* he also included the genus *Afrovivella*, *Sedum* sect. *Monanthella* Berger and *S. hirsutum* and *S. wilczekianum*. Of these four sections only *R. sect. Sempervivella* is heterogeneous with respect to the basic numbers of the species, of which so far only three have been cytologically studied, viz. *R. sedoides* ($x=8$), *R. adenotricha* ($x=9$) and *S. hirsutum* ($x=10$).

Although so far only two-thirds of the species of *Rosularia* have been cytologically studied it is already quite clear that the variation in basic number and chromosome size is rather limited within this genus. Consequently these cytological characters can be very useful for determining the relationships between the taxa as well as their systematic position within the genus. Furthermore, the cytological characters may help to solve some of the controversies about the systematic position of a number of taxa which from a morphological point of view have been regarded as closely related to *Rosularia*. For instance, they strongly support the transfer of *Sempervivella alpestris* and *Sedum adenotricha* to *Rosularia* (Borissova 1939, Jansson & Rechinger 1970, Ohba 1978, Eggli in press). However, opinions still diverge about the systematic position of the species of *R. sect. Sempervivoides* (Boiss.) and *R. sect. Sempervivella* (Borissova 1939, Ohba 1978, Eggli l.c.) and our chromosome studies may stimulate further systematic and evolutionary investigations.

Borissova (1939, 1969) and Jansson & Rechinger (1970) transferred *Sedum sempervivoides* Fisch. ex Bieb. and *S. pilosum* Fisch. ex Bieb. of *S. sect. Sempervivoides* to *Rosularia*. On the other hand, Ohba (1978) placed the two species in *Prometheum* Ohba and Eggli (l.c.) also excluded them from *Rosularia*. Both species are strictly hapaxanth, predominantly biennial and are restricted to the Irano-Turanian region. The perennial *S. tymphaeum* Quezel & Contandriopoulos, which is endemic to a few mountain peaks in central and northern Greece, is closely related to *S. sempervivoides* and *S. pilosum* ('t Hart 1986a, b, Hagemann & 't Hart 1986). The three species can be easily hybridized and they agree in the character states of the four morphological characters which in other species of *Sedum* proved to be strictly correlated with the hybridization patterns of the species ('t Hart 1986a). *S. sempervivoides* and *S. tymphaeum* have the chromosome number $2n=14$, whereas *S. pilosum* has the chromosome number $2n=12$ (Moran 1972, 't Hart 1985 and unpubl.). Accordingly, the basic number of this group should be $x=7$, rather than $x=6$. The chromosomes of all three species are relatively long, about 1.5–2 microns or more. In regard to their basic number and the size of their chromosomes these three species very much resemble the species of *Rosularia* with the basic number $x=7$ and except for their ploidy level and some morphological features (see Eggli in press), there is no reason why they should not be included in *Rosularia*.

Uhl (1961) reported the chromosome number $n=64$ for *R. sedoides*. The chromosome number $2n=128$ found by us fits in nicely with this report. Uhl's plant most probably descended from the clone of stoloniferous plants which are widely cultivated in Western Europe. Morphologically and cytologically our plant agrees very well with this cultivated form. It is a vigorous grower producing numerous long runners with a terminal rosette and this highly developed capacity for vegetative propagation agrees very well with its polyploid ($16x$) condition. Non-stoloniferous forms of *R. sedoides* also occur and in fact seem to be more common in nature (Ohba 1977, 1980, Eggli in press). Diploid and/or tetraploid cytotypes of the species may very well occur among the non-stoloniferous forms. For example, in *Sedum amplexicaule* DC. a similar morphological differentiation has been found which is partly correlated with the differences in ploidy level ('t Hart 1978, 1986). Ohba (1977) considered *R. sedoides* to be closely related to *R. alpestris* ($x=7$), but the shape and size of its chromosomes rather suggest affinities with the species with the basic number $x=9$. The apparently intermediate position of *S. sedoides* may indicate an amphiploid origin. However, the karyotype of *R. sedoides* would be much more asymmetrical if it comprised chromosomes of both types. Furthermore, interspecific hybrids in *Rosularia* have so far only been reported between taxa with the same basic number (Eggli l.c.). A more plausible explanation for the origin of the basic number $x=8$ of *R. sedoides* is that it resulted from a decreasing dysploid change in a diploid or tetraploid ancestor from the group with the basic number $x=9$. Although the karyotype of *R. sedoides* is somewhat asymmetrical, the length of its chromosomes is on average much less than 1 micron (about 0.4 to 1.1 microns). The karyotype of *R. sedoides* much more resembles the karyotype of a plant with the basic number $x=9$ after the fusion of a few chromosomes than a karyotype resulting from the combination of sets of chromosomes with the basic numbers $x=7$ and $x=9$, respectively. However, in contrast to the species with the basic number $x=7$ dysploidy and polyploidy are absent or relatively rare among the species of *Rosularia* with the basic number $x=9$. So far, however, the cytological data on *R. sedoides* are still too scanty to arrive at a definite conclusion as to its affinities.

Of the rosulate and gamopetalous North African and SW European Sedoideae which Ohba (1978) and Eggli (in press) included in *Rosularia* only *Sedum hirsutum* is cytolog-

ically well-known. In *S. hirsutum* ssp. *hirsutum* the chromosome numbers $2n=18$ and $2n=20$ have been found ('t Hart unpubl.), in ssp. *baeticum* Rouy the chromosome numbers $2n=58$ (Aparicio 1987) and $2n=60$ ('t Hart unpubl.). The chromosomes of *S. hirsutum* are rather small, about 1 micron or less, except for one pair of about 1.2 microns in the plants of the cytotype with the chromosome number $2n=18$. The cytotype with the chromosome number $2n=18$ is the most common and widely distributed in Europe (Portugal, Spain and southern France) and it is considered to be the most advanced of the two cytotypes. It most probably originated from a descending dysploid change, i.e. from the fusion of 2 pairs of chromosomes, in an ancestral plant with the chromosome number $2n=20$. Since within this species complex no plants with the chromosome number $2n=10$ have so far been found, the basic number of *S. hirsutum* s.l. is considered to be $x=10$ and the dysploid change most probably occurred at the diploid level. Although the average length of the chromosomes of *S. hirsutum* agrees with those of the species of *Rosularia* with the basic number $x=9$ they are more slender. Since, in addition, *S. hirsutum* differs from these species in its basic chromosome number and the frequent occurrence of polyploidy and dysploidy, its inclusion in *Rosularia* is questionable in this respect.

Cytologically the two groups of species in *Rosularia* differ considerably and it is therefore difficult to determine their evolutionary relationships. According to Jones (1978) karyotype evolution in plants is a kind of cyclic process in which periods of rapid change and a general increase of chromosome material (abrupt speciation, polyploidy etc.) alternate with periods in which more gradual and less drastic alterations leading to an over-all reduction of the size of the karyotype prevail (Robertsonian translocations, deletions and other kinds of rearrangements). In this concept the species of *Rosularia* with the basic number $x=7$ would be in the phase of rapid proliferation of chromosome material whereas those with the basic number $x=9$ clearly exemplify the opposite situation. Since the position of both groups within this cycle of continuous transgressions in size and numbers of chromosomes merely emphasizes their distinctness, it becomes even more difficult to understand how and when their karyotypes evolved from a common ancestor. Cytological differences such as found between the two groups of *Rosularia* are quite common in *Sedum* and, for instance among the European species of *Sedum*, considerable cytological differences between usually rather small groups of species often reflect an intricate web of evolutionary relationships which in many cases has turned out to be much more complicated than the generally accepted classifications suggested.

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