

## ***SEDUM INCE (CRASSULACEAE), A NEW SPECIES FROM SOUTHERN ANATOLIA***

H. 'T HART\* & K. ALPINAR†

The newly described white-flowered annual *Sedum ince* closely resembles *S. eriocarpum* and the annual forms of *S. hispanicum* (*S. longibracteatum*), but differs from the former by its alternate instead of verticillate leaves, and from the latter by the 5-merous instead of 6–9-merous flowers and the ripe follicles which are divergent instead of patent and lack the distinct lips along the ventral suture. Molecular phylogenetic analyses indicate that *S. ince* is but distantly related to *S. eriocarpum* as well as to *S. hispanicum*. It belongs to a cytological distinct lineage of *Sedum* subgenus *Gormania* sporting a basic chromosome number of  $x = 7$ . Within this lineage, however, *S. ince* holds a unique position and consequently it is classified in the monotypic *S. series Elegans*.

**Keywords.** Chloroplast DNA, *Crassulaceae*, flora of Turkey, new species, *Sedum*.

### **INTRODUCTION**

In contrast to the *Crassulaceae* floras of Mexico, South Africa and Asia, the Mediterranean *Crassulaceae* flora comprises a high number (20%) of strictly annual species (Böttcher & Jäger, 1984; 't Hart, 1996). Annual *Crassulaceae* are usually quite variable in habit and gross morphology due to a direct response to variation in edaphic conditions during early development. However, most annual Mediterranean species are quite distinct and can be easily distinguished by different combinations of morphological characters, except for the species of the species-aggregate including the white-flowered *S. hispanicum* L. and *S. rubens* L. More than 20 segregate species and subspecies have been described for this aggregate from the Aegean region and Near East. However, there is little consensus on the validity and taxonomic status of most segregate taxa so far (Boissier, 1872; Rechinger, 1943; Chamberlain, 1972; 't Hart & Alpinar, 1991a; 't Hart, 1996). Cytologically the *S. hispanicum-rubens* aggregate is extremely variable, comprising at least 25 different cytotypes ('t Hart & Alpinar, 1991b; 't Hart & van Ham, 1991; 't Hart, 1996).

As part of a biosystematic study of Turkish *Sedum* ('t Hart & Alpinar, 1991a) we collected a large number of plants of these critical, white-flowered, annual *Sedum* taxa throughout the larger part of Turkey. In addition to the common and widely distributed *S. eriocarpum* Sibth. & Sm., *S. hispanicum*, *S. pallidum* M. Bieb. (although predominantly perennial this species also belongs to this aggregate; 't Hart & Alpinar,

\* Department of Plant Ecology and Evolutionary Biology, University of Utrecht, Padualaan 8, 3584 CH Utrecht, the Netherlands.

† Department of Pharmaceutical Botany, Faculty of Pharmacy, Istanbul University, 34452 Istanbul, Turkey.

1991b), *S. steudelii* Boiss., and *S. rubens* we collected a white-flowered, annual *Sedum*, that differed from the aforementioned species by a unique combination of flower, fruit and seed characters. We found it in southern Anatolia only (Table 1) and named it *Sedum ince*. The name of the new species is derived from the Turkish word 'ince' which means elegant (Latin: *gracilis*) and refers to the habit of the plants which have delicate, slender stems, relatively long pedicels, and small flowers.

***Sedum ince* 't Hart & Alpinar, sp. nov.**

*Sedum annum* gracile, *S. eriocarpum* et *S. hispanicum* proximum, a primo foliis alternis, flosculis minoribus, folliculis laeibus, seminibus pallide brunneis, a postremo floribus pentameris, folliculis suberectis ad divergentibus differt.

Type: cultivated at Utrecht Botanic Garden from seeds collected in Turkey [prov. Konya, Aydos Dağı 19km SE of Ereğli, near Sinanlı along the road to the village of Delimahmutlu, rocky limestone slopes near a graveyard, 1350m, 1991, *Alpinar & 't Hart AH793*], 25 v 1992 [holo. ISTE (72678), iso. U (HRT-32001)].

Erect, usually simple, slender annual to 7 or rarely 10cm high, glandular pubescent, especially in upper part. *Leaves* alternate, sessile with a very short, truncate spur, oblong to linear, to 10mm long, rounded, terete, grey-green or glaucous-white. *Inflorescence* cymose with 11–13(4–18) flowers on 2 or 3, suberect, monochasial branches, rarely with subsidiary branches. *Bracts* 1, leaf-like. *Peduncles* slender, 1–1.5mm long. *Flowers* 5-merous, with 10 stamens. *Sepals* broadly sessile, basally connate, triangular, 0.6–0.8mm long, acute. *Petals* basally free, ovate-oblong to elliptic, 3.5–5mm long, acuminate, white sometimes tinged red. *Filaments* white, glabrous. *Anthers* oblong-globose, red. *Styles* distinct, c.0.8mm long. *Nectary scales* cuneate to quadrate-oblong, denticulate, yellow. *Follicles* suberect or divergent, smooth, pale brown. *Seeds* ovoid, pale brown, costate, apex acute.  $2n=14$ .

#### TAXONOMIC POSITION OF *SEDUM INCE*

##### *Cytological and morphological data*

We collected seeds of *Sedum ince* at 5 locations (Table 1) on rocky or gravelly, limestone soils at 1350–1850m altitude. Seeds of Mediterranean, annual *Sedum* species usually germinate within 3–7 days in high numbers when sown in the greenhouse in early spring. Seeds of *S. ince*, however, did not germinate that easily. They need a prolonged cold treatment (vernalization) and so far only seeds of accession HRT-32001 have germinated after spending a winter in a cold frame. The seedlings were subsequently brought into the greenhouse and cultivated like other annual *Sedum*.

At first sight flowering plants of *Sedum ince* (Fig. 1) are almost indistinguishable from *S. eriocarpum* subsp. *orientale* 't Hart ('t Hart, 1996) or the strictly annual form of *S. hispanicum* from southern Anatolia (Hatay) and the Near East (Israel, Lebanon, Syria and Saudi Arabia), which is also known as *S. longibracteatum* Fröd.

TABLE 1. Origin of the plants (HRT numbers refer to the accession-numbers of plants cultivated at the Utrecht Botanic Gardens and voucher specimens of the cultivated plants in the Utrecht herbarium; the ISTE numbers refer to voucher specimens in the herbarium of the Istanbul Faculty of Pharmacy). Accessions marked with an asterisk (HRT numbers) have been used in the chloroplast DNA analyses

Species	Origin
<i>Phedimus spurius</i> (M. Bieb.) 't Hart	Turkey (Ardahan); Yalnızçam Geçidi, 2300m, HRT-31393*, ISTE 61127.
<i>Prometheum aizoon</i> (Fenzl) 't Hart	Turkey (Kahramanmaraş); Berit Dağı, c.2500m, HRT-31740*, ISTE 62223.
<i>Prometheum sempervivooides</i> (M. Bieb.) H. Ohba	Turkey (Erzurum); Delibaba gorge, 17km E of Horasan along the road to Ağrı, 1750m, HRT-31153*, ISTE 60785.
<i>Rosularia sempervivum</i> (M. Bieb.) A. Berger	Turkey (Hatay); village of Arpaluşağı, between Kırıkhan and Hassa, 900m, HRT-31674*, ISTE 62120.
<i>Sedum acre</i> L.	Turkey (Bolu); 6km W of Mengen along the road to Dirgine, 200m, HRT-30869*, ISTE 59479.
<i>Sedum album</i> L.	Spain (Teruel); 9km SE of Albarracin, 1350m, HRT-29329*.
<i>Sedum eriocarpum</i> Sibth. & Sm. subsp. <i>orientale</i> 't Hart, 2n=14	Turkey (Muğla); 21km N of Kalkan along the road to Gölbent, 150m, HRT-30294.
<i>Sedum eriocarpum</i> Sibth. & Sm. subsp. <i>orientale</i> 't Hart, 2n=20	Turkey (Manisa); Kırkağaç Dağı, above Kırkağaç, 950m, HRT-32487*, ISTE 65296.
<i>Sedum hispanicum</i> L.	Turkey (Denizli); Honaz Dağı, 12km N of Honaz, 1550m, HRT-32538*, ISTE 65355.
<i>Sedum ince</i> 't Hart & Alpinar	Turkey (Bolu); Yedigöller Milli Parkı, 1150m, HRT-30865*, ISTE 59475.
	Greece (Thrakia); Mesti, 6km W of Avra along the road to Komotini, 150m, HRT-30220.
	Turkey (Konya); Aydos Dağı, foothills SE of Ereğli, rocky slopes at Eşeçoban near Madde, 3–4km S of Delimahmutlu along the road to Eğerkaya, greyish limestone pebbles, 1550m, HRT-31987 & 31989, ISTE 63264 & 63266.
	Turkey (Konya); Aydos Dağı, foothills SE of Ereğli, rocky slopes along the road to Eğerkaya, S of Delimahmutlu, limestone, 1650–1850m, HRT-31993, ISTE 63270.
	Turkey (Konya); Aydos Dağı, 19km SE of Ereğli, rocky slopes near Sinanlı along the road to village Delimahmutlu, near graveyard, limestone, 1350m, HRT-32001*, ISTE 63278 & 72678.
	Turkey (Niğde); Emli gorge, 9km E of Cukurbağlı, gravelly places at base of rocky

TABLE 1. (Continued).

*Sedum microcarpum* Smith*Sedum steudelii* Boiss.

limestone slopes, 1700m, HRT-31825, ISTE 62379.

Israel (Coastal Carmel); Atlit, HRT-31112\*.

Turkey (Van); N of Muradiye, valley of the river Bendimahi, 1800m, HRT-31249\*, ISTE 60911.



FIG. 1. Flowering and fruiting specimens of *Sedum ince* 't Hart & Alpinar from Aydos Dagi. On the left a plant cultivated at Utrecht (HRT-32001), on the right a wild-collected fruiting specimen (HRT-31987).

(Fröderström, 1936, 1960; 't Hart & van Ham, 1991). *Sedum ince* and *S. eriocarpum* subsp. *orientale* both have erect stems with linear-oblong, obtuse or rounded leaves, spatulate to oblong, sparsely dentate nectary scales and divergent or suberect follicles (Fig. 1). However, the latter differs significantly by having leaves in whorls of four (at least at the base of the stem), stouter stems, larger flowers with shorter pedicels (subsessile), often somewhat verrucose or mamillate follicles gradually tapering into the style, and ovoid, dark brown or almost black seeds. *Sedum ince* and *S. longibracteatum* resemble each other in the alternate, oblong leaves, pale brown follicles and oblong-ovoid, brown seeds. The leaves of *S. longibracteatum*, however, tend to be more elliptic and rather subacute than obtuse or rounded, and, most significantly, its has 6–7(–9-)merous flowers, with much larger, red-striped petals, cuneate, usually coarsely dentate scales and stellate patent follicles with very distinct lips along the ventral suture.

In contrast to the traditional view (Grisebach, 1843; Boissier, 1872; Berger, 1930; Fröderström, 1932; Chamberlain, 1972) *Sedum eriocarpum* and *S. hispanicum* are not closely related. Cytologically and morphologically the two species differ significantly and, moreover, they are separated by a strong reproductive barrier ('t Hart, 1991, 1996). Accordingly they have been classified in different infrageneric taxa, i.e. *Sedum eriocarpum* in *S. series Aithales* (Webb & Berth.) 't Hart and *S. hispanicum* in *S. series Glauco-rubens* Fröd., respectively. In addition to *S. eriocarpum*, *Sedum* series *Aithales* contains two more species, i.e. *S. pallidum* M. Bieb. and *S. rubens* L., whereas *S. series Glauco-rubens* also comprises *S. steudelii* Boiss. Because *S. ince* is quite distinct morphologically and by and large intermediate between *S. series Aithales* and *S. series Glauco-rubens* we have been unable to assign it unequivocally to either one of the two series. In order to learn more about the systematic position of *S. ince* we used the cultivated material in comparative cytological and molecular studies.

For our cytological studies we used root-tips which were fixed in Karpechenko's fixative and subsequently dehydrated, embedded in paraffin and sectioned at 15 $\mu\text{m}$  ('t Hart, 1985). The sections were stained according to Haidenhain's haematoxylin method and made permanent. *Sedum ince* has a chromosome number of  $2n=14$ . Its chromosomes are about 1 $\mu\text{m}$  long and the karyotype is rather symmetrical (Fig. 2a). The chromosome number  $2n=14$  is quite common in *Sedum* and has been reported for *S. eriocarpum* as well as *S. hispanicum* ('t Hart & Alpinar, 1991a; 't Hart 1996). In *S. hispanicum* there is a polyploid series based on  $x=7$ . The diploid cytotype ( $2n=14$ ) is most common and comprises the perennial as well as the strictly annual forms (including *S. longibracteatum*; 't Hart and van Ham, 1991). The basic chromosome number of *S. eriocarpum* is  $x=5$  or  $x=10$ , but dysploid cytotypes with chromosome numbers of  $2n=8$ ,  $2n=12$ ,  $2n=14$ , and  $2n=16$  have been reported from southern Anatolia and Israel ('t Hart and Alpinar, 1991b; 't Hart and van Ham, 1991; 't Hart, 1996). Although the chromosomes of *S. ince* are somewhat smaller than those of dysploid *S. eriocarpum* with a chromosome number of  $2n=14$  and somewhat larger than those of diploid *S. hispanicum* the karyotypes of these three species do not differ significantly (Fig. 2).

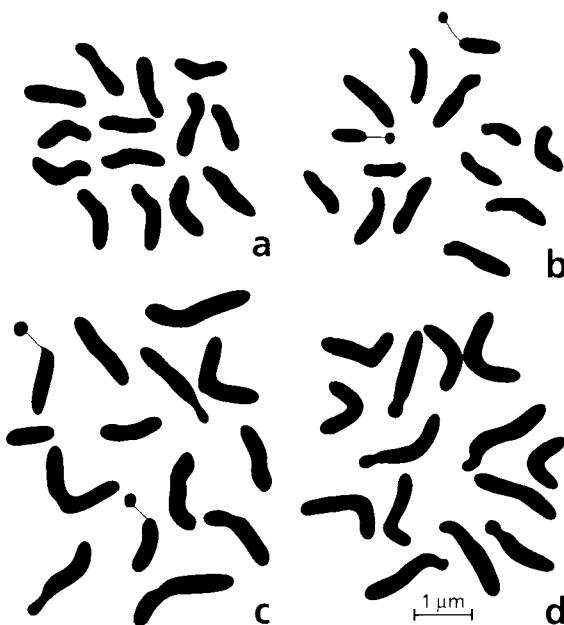


FIG. 2. Chromosome complements of Anatolian species of the *Leucosedum* lineage of *Sedum* with the diploid chromosome number of  $2n = 14$ : a. *Sedum ince* 't Hart & Alpinar, HRT-32001; b. *Sedum hispanicum* L., HRT-30220; c. *Sedum eriocarpum* Sibth. & Sm. subsp. *orientale* 't Hart, HRT-30294; d. *Prometheum aizoon* (Fenzl) 't Hart (after 't Hart & Eggli, 1989).

#### Molecular data

For a rapid assessment of the systematic position of *Sedum ince* we amplified and sequenced the chloroplast DNA *trnL*(UAA)-*trnF*(GAA) intergenic spacer (IGS; Taberlet *et al.*, 1991; van Ham *et al.*, 1994; Kim *et al.*, 1996) and compared the aligned sequence with our *Crassulaceae* database of this intergenic spacer which presently contains about 200, mainly Eurasian taxa. As we expected from our morphological studies (leaf shape, testa ornamentation and insertion of the sepals) parsimony analysis of a wide taxonomic sample from our molecular data-set (results not shown) included *S. ince* in the *Leucosedum* clade (van Ham & 't Hart, 1998) which is by and large identical to *S. subgenus Gormania* Clausen ('t Hart, 1995). Within this *Leucosedum* clade *S. ince* was included in a clade which also contained *S. hispanicum*, *S. microcarpum* (Smith) Schönland ( $\equiv$  *Telmissa microcarpa* (Smith) Boiss.), *S. steudelii*, and *Prometheum* (A. Berger) H. Ohba. The aligned *trnL-trnF* IGS sequences of a relevant subset of 12 taxa (including two outgroup species) is presented in Table 2. The results of a cladistic analysis of these 12 taxa is presented in Fig. 3.

In addition to the 20 phylogenetically informative base substitutions the aligned *trnL-trnF* IGS sequences contain several highly significant, large indels (4 bp or longer; van Ham *et al.*, 1994). A 5 bp insertion (position 7–11) which is unique for species of the *Leucosedum* clade (though secondarily lost in *Sedum microcarpum*).

TABLE 2. Aligned sequences of the chloroplast DNA *rnl*(UAA)-*trnf*(GAA) intergenic spacer of 12 *Solidoideae* (*Crassulaceae*). Spacer length

Species	Sequence	10	20	30	40	50
<i>Phedimus spurius</i>	AATCCC-----	-CTAA-----	-----TAAA	GGATTATTG	ATTACCTAAT	
<i>Sedum acre</i>	AATCCC-----	-CTAA-----	-----CAAA	GTAGCATTTG	ATTCCCTAAT	
<i>Sedum album</i>	AATCCCCTAA	TCTAA-----	-----TAAA	GTATCCTTT	TTTACCTAAT	
<i>Sedum eriocarpum</i> 2n = 14	AATCCCCTAA	TCTAA-----	-----TAAA	GTATCATTTG	ATTACCTAAT	
<i>Sedum eriocarpum</i> 2n = 20	AATCCCCTAA	TCTAA-----	-----TAAA	GTATTATTG	ATTACCTAAT	
<i>Rasularia sempervivum</i>	AATCCCCTAA	TCGAATCCTA	ATCTAAATAAA	GTATCATTG	ATTACCTAAT	
<i>Sedum microcarpum</i>	AAT-----	-----TAAA	-----TAAA	GTATCATTG	ATTACCTAAT	
<i>Sedum hispanicum</i>	AATCCCCTAA	TCTAA-----	-----TAAA	GTATCAGTTG	ATTACCTAAT	
<i>Sedum stedelii</i>	AATCCCCTAA	TCTAAAT-----	-TCTAATAAA	GTATCATTG	A-----CTAAT	
<i>Sedum ince</i>	AATCCCCTAA	TCTAA-----	-----TAAA	GTACCATTG	ATTACCTAAT	
<i>Promicraea aizoon</i>	AATCCCCTAA	TCTAA-----	-----TAAA	GTATCAATTG	ATTACCTAAT	
<i>Prometheum sempernoides</i>	AATCCCCTAA	-----TAAA	-----TAAA	GTATCAATTG	ATTACCTAAT	
		60	70	80	90	100
<i>Phedimus spurius</i>	ACTTTTTCCTC	CATACTCCCG	TTTCTTTT--	-----CATT		AGTGGTTICA
<i>Sedum acre</i>	TCTTTTTCCTC	-ATACTCTCG	TTTCTTGG--	-----CAT-		AGTATTTICA
<i>Sedum album</i>	TCTTTTTCCTC	-ATATTCCTCG	TTTCTTTT--	-----CAT-		AGTAGTTICA
<i>Sedum eriocarpum</i> 2n = 14	TCTTTTTCCTC	-ATATTCCTCG	TTTCTTTT--	-----CAT-		-----
<i>Sedum eriocarpum</i> 2n = 20	TCTTTTTCCTC	-ATATTCCTCG	TTTCTTTT--	-----CAT-		-----

TABLE 2. (*Continued*).

Species	Sequence	60	70	80	90	100
<i>Rosularia sempervirenum</i>	TCTTGTGTC	-ATATTCTCG	TTTCCTTTT-	CAT-	AGTAGTTCC	
<i>Sedum microcarpum</i>	TCTTTTTTTC	-ATATTCTCG	TTTCCTTTT-	---CAG-	AGTAGT-CA	
<i>Sedum hispanicum</i>	-TPTC	-CTATTCCGG	TTTCCTTTCT	TCCTTTCAT-	AGTAGTTCA	
<i>Sedum stenellii</i>	TCTTTTTTTC	-ATATTCTCG	TTCCTTT-	-----CAT-	AGTAGTTCA	
<i>Sedum ince</i>	TCTTTTTTCTC	-ATATTCTCG	TTCCTTT-	-----CAT-	AGTAGTTCA	
<i>Prometheum atoon</i>	TCTTTTTTCTC	-ATATTCTCG	TTCCTTT-	-----CAT-	AGTAGTTCA	
<i>Prometheum sempervirens</i>	TCTTTTTTCTC	-ATATTCTCG	TTCCTTT-	-----CAT-	AGTAGTTAA	
<i>Phedimus spurius</i>	110	120	130	140	150	
<i>Sedum acre</i>	AGCTTGTTAT	CTTCTCTATT	CACCTATT-	-----AG	TTTACAAAG-	
<i>Sedum album</i>	AGCTTGTTAT	GTTTCTCAT	CAACCTATT	TATCTVACTT	TTTACAAAG-	
<i>Sedum eriocarpum</i> 2n = 14	AGCTTGTTAT	GTTTGCATT	CGACCAATT	T-----TT	TTTACAAAA-	
<i>Sedum eriocarpum</i> 2n = 20	-	-	-	-	-	
<i>Rosularia sempervirenum</i>	AGCTTGTTAT	GTTTCTCAT	CAACCTATT-	-----TT	TTTGTAAAAA	
<i>Sedum microcarpum</i>	AGCTTGTTAT	GTTTGCATT	CAATCCATT-	-----TT	TTTACAAAG-	
<i>Sedum hispanicum</i>	AGCTTGTTAT	GTATCTCAT	CAATCTATT-	-----TT	TTTA?AAA-	
<i>Sedum stenellii</i>	AGCTTGTTAT	GTTTCCATT	CAATTCTTT-	-----TT	TTTACAAAA-	
<i>Sedum ince</i>	AGCTTGTTAT	GTTTCTTATT	CAATCTATT-	-----TT	TTTACAAAA-	
<i>Prometheum atoon</i>	AGCTTGTTAT	GTTTCTTATT	CAATCTATT-	-----TT	TTTACAAAA-	
<i>Prometheum sempervirens</i>	AGCTTGTTAT	GTTTCTTATT	CAATCTATT-	-----TT	TTTACAAAA-	

TABLE 2. (continued).

Species	Sequence		
<i>Phedimus spurius</i>	-AGATCCTAT	160	170
	-AAATCCTAG		180
<i>Sedum acre</i>	-AAATCCTAA		190
<i>Sedum album</i>	-AAATCCTAA		200
<i>Sedum eriocarpum</i> 2n=14	ATAAA-TTGG	ATTCCTCTTT	GAAAGTCTAG
<i>Sedum eriocarpum</i> 2n=20	ATAAA-TTGG	ATTCCTCTTAT	GAAAGTCTAG
<i>Rosularia sempervivum</i>	ATAAA-TTGG	ATTCCTATTT	GAAAGTCTAG
<i>Sedum microcarpum</i>	AAAAA-TTGG	ATTCCTATTT	GAAAGTCTAG
<i>Sedum hispanicum</i>	AAAAAATGGG	ATTCCTATCT	GAAAGTCCCG
<i>Sedum stenodii</i>	AAAAAAATTGG	ATTCGATTAT	GAAAGTCITG
<i>Sedum ince</i>	AAAAAAATTGG	ATTCCTATTT	GAAAGTCTAA
<i>Prometheum azoon</i>	AAAAAATTGG	ATTCCTATTT	GAAAGTATAG
<i>Prometheum sempervivoides</i>	AAAAAATTGG	ATTCCTATTT	GAAAGTCTAG
		210	220
<i>Phedimus spurius</i>	GGACTGTATA	AGACTTTAA-	240
<i>Sedum acre</i>	GGGCTGTATA	AGACTTTAAAT	-----TAAT
<i>Sedum album</i>	GGACTGTATA	CGATTTAA-	TTGAATAAAAT
<i>Sedum eriocarpum</i> 2n=14	GGACTGCATA	AGACTTTAA-	-----TAAT
<i>Sedum eriocarpum</i> 2n=20	GGACTPGCATA	AGACTTTAA-	TTTA?TAAT
			TTTTAATAAAAT

TABLE 2. (Continued).

Species	Sequence	210	220	230	240	250
<i>Rosularia sempervivum</i>	GCACTGTTATA	AGA-----	-----	-----	-----	ACCCTTTCGTT
<i>Sedum microcarpum</i>	GGGTGTTATA	AGACTTTPAA-	-----	-----	-----	ACCCTTTCAT
<i>Sedum hispanicum</i>	GCACTGTTATA	AGACTGTTAA-	-----	-----	-----	AGCCTTGCAT
<i>Sedum sieboldii</i>	GGCGGGTATA	AGACTTTAA-	-----	-----	-----	AGCCTTTCGTT
<i>Sedum inc'e</i>	GGACTGTTATA	AGACTTTAAC-	-----	-----	-----	ACCCTTTGAT
<i>Prometheum alizoon</i>	GGAATGTTCTA	AGACTTTAA-	-----	-----	-----	ACCCTTTCAT
<i>Prometheum sempervirens</i>	GGACTGTTCTA	AGACTTTAA-	-----	-----	-----	ACCCTTTCAT
<i>Pheidimus spurius</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T-AAT	-----	-----	-----	-----	-----
<i>Sedum acre</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> TAT	TGACATAGCC	TGACATAGCC	TCAAGTCATA	TAGTAATAATT	AGACTGATACT
<i>Sedum album</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> TAT	TGACATAGCC	TGACATAGCC	TCAAGTCATA	TCGTAATAATT	AAAGTGATACT
<i>Sedum eriocarpum</i> 2n = 14	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> TAT	TGACATAGCC	TGACATAGCC	TCAAGTCATA	TCGTAATAATT	AGACTGATACT
<i>Sedum eriocarpum</i> 2n = 20	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> TAT	TGACATAGCC	TGACATAGCC	TCAAGTCATA	TCGTAATAATT	AGACTGATACT
<i>Rosularia sempervivum</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> TAT	TGACATAGCC	TGACATAGCC	TCAAGTCATA	TCGTAATAATT	AGACTGATACT
<i>Sedum microcarpum</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> -AT	TGACATAGCC	TGACATAGCC	TCAAGTCATA	TCGTAATAATT	AGACTGATACT
<i>Sedum hispanicum</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> TAT	TGACATAGCC	TGACATAGCC	TCAAA?CATA	TCGTAATAATT	AGAC?GATAC
<i>Sedum sieboldii</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> TAT	TGACATAGCC	TGACATAGCC	TCAAGTCATC	TCGTAATAATT	AGACTGATACT
<i>Sedum inc'e</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> TAT	TGACATAGCC	TGACATAGCC	TCAAGTCATA	TCGTAATAATT	AGACTGATACT
<i>Prometheum alizoon</i>	TTCCTTTTTT-AT	-----	-----	-----	-----	AGACTGATACT
<i>Prometheum sempervirens</i>	T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> T <sup>n</sup> -AT	-----	-----	-----	-----	AGACTGATACT

TABLE 2. (Continued).

Species	Sequence	
<i>Phedimus spurius</i>		310
<i>Sedum acre</i>	GGAGAGGATG [257 bp]	
<i>Sedum album</i>	GCAAAGGATG [281 bp]	
<i>Sedum eriocarpum</i> 2n = 14	GAAAGGATA [261 bp]	
<i>Sedum eriocarpum</i> 2n = 20	GCAAAGGATG [179 bp]	
<i>Rosularia sempervivum</i>	GGAAAGGATG [180 bp]	
<i>Sedum microcarpum</i>	GGGAAGGATG [263 bp]	
<i>Sedum hispanicum</i>	AGAAAGGCTG [249 bp]	
<i>Sedum stenophyllum</i>	GGAAAGGATG [259 bp]	
<i>Sedum ince</i>	GGAAAGGAGG [260 bp]	
<i>Prometheum atroon</i>	GGAAAGGATG [264 bp]	
<i>Prometheum sempervivoides</i>	GGAAAGGATG [261 bp]	
	GGAAAGGATG [261 bp]	

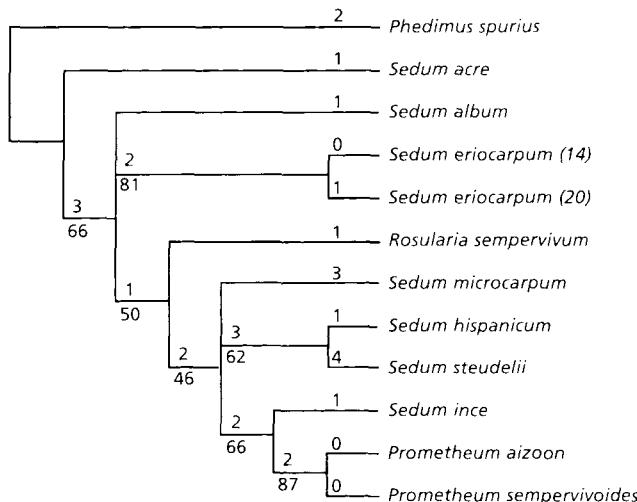


FIG. 3. Strict consensus of the six most parsimonious Wagner trees (PAUP version 3.1.1. Branch and Bound option; Swofford, 1993) of the sequences presented in Table 2, using *Phedimus spurius* as outgroup. The tree has a length of 30 steps and a consistency index of 0.700 (including autapomorphies). Branch lengths (base substitutions) are indicated above the branches and the figures below the branches indicate bootstrap values (100 replicates).

also occurs in *S. ince* and strongly supports its inclusion in *S.* subgenus *Gormania*. The unique position of *S. ince* relative to the species of *S.* series *Aithales* and *S.* series *Glauco-rubens* is supported by four unique indels which separate it from *S. eriocarpum* and *S. hispanicum*, respectively. The two cytotypes of *S. eriocarpum* stand apart from all other taxa in this sample by a shared, large 107 bp deletion (position 78–184), whereas *S. hispanicum* is characterized by two unique indels, a 9 bp deletion (position 48–56) and an 8 bp insertion (position 79–86), respectively. Finally, *S. ince* contains a unique, small 4 bp deletion (position 42–45).

## CONCLUSIONS

The chloroplast DNA analysis indicates *Sedum ince* as the sister of a clade comprising *Prometheum aizoon* (Fenzl) A. Berger (= *Rosularia aizoon* (Fenzl) A. Berger) and *P. sempervivoideis* (M. Bieb.) H. Ohba (= *Sedum sempervivoideis* M. Bieb.). This clade represents the monophyletic genus *Prometheum* (A. Berger) H. Ohba which comprises about eight, perennial or hapaxanth (biennial), densely rosulate species with white, pink, red or yellow flowers (Ohba, 1978; 't Hart, 1995). Basal to *S. ince* are *S. microcarpum* and a clade comprising the two species of *S.* series *Glauco-rubens*, *S. hispanicum* and *S. steudelii*. The two cytotypes of *S. eriocarpum*, with  $2n=14$  and  $2n=20$ , respectively, form a monophyletic clade that appears to be only distantly related to *S. ince* and *S.* series *Glauco-rubens*.

Cytologically the clade comprising *Sedum ince*, *S. microcarpum*, *S.* series *Glauco-*

*rubens*, and *Prometheum* is surprisingly uniform considering the enormous cytological variation (particularly chromosome numbers) which is so characteristic for *Sedum* and related genera (Uhl, 1963; 't Hart, 1991). The basic chromosome number  $x=7$  occurs in 10 out of the 12 species of this lineage and the other two species, *Prometheum pilosum* (M. Bieb.) H. Ohba (= *Sedum pilosum* M. Bieb.) and *Sedum steudelii*, both have a basic number of  $x=6$  as a result of two independent, descending dysploid changes (Moran, 1972; 't Hart, 1985; 't Hart & Eggli, 1989; 't Hart & Alpinar, 1991a). On the other hand, this clade is extremely diverse morphologically. The rosulate, slightly sympetalous species of *Prometheum* form a distinct group and so do *S. hispanicum* and *S. steudelii* which form a comparium ('t Hart, 1991), whereas *S. microcarpum* is a highly specialized annual with 4-merous, haplostemonous flowers and 1- to 2-seeded carpels. Because *S. ince* is not clearly affiliated with any of these taxa we classify it in a new, monotypic series, *S. series Elegans*.

#### ***Sedum* series *Elegans* 't Hart & Alpinar, *series nova***

Plantae glanduloso-pubescentes. Folia alterna, oblonga vel linearia, obtusa. Flores 5-meri. Sepala basin receptaculo adnata. Petala alba. Folliculi suberecti vel patentes. Semina apice acuta, testa costata.

Type species: *Sedum ince* 't Hart & Alpinar.

#### ACKNOWLEDGEMENTS

The authors wish to thank Dr Jan F. Veldkamp (Leiden) for correcting the Latin diagnosis and Herman van der Klis for technical assistance with the cytological and molecular studies.

#### REFERENCES

- BERGER, A. (1930). Crassulaceae. In: ENGLER, A. & PRANTL, K. (eds) *Die Natürlichen Pflanzenfamilien*, 2nd edn, 18a: 352–483. Leipzig: Verlag Wilhelm Engelmann.
- BOISSIER, E. (1872). *Flora Orientalis*, 2. Geneva and Basel: H. Georg.
- BÖTTCHER, W. & JÄGER, E. J. (1984). Zur Interpretation der Verbreitung der Gattung *Sedum* L. (Crassulaceae) und ihrer Wuchsformtypen. *Wiss. Z. Univ. Halle* 33: 127–141.
- CHAMBERLAIN, D. F. (1972). *Sedum* L. In: DAVIS, P. H. (ed.) *Flora of Turkey and the East Aegean Islands*, 4, pp. 224–243. Edinburgh: Edinburgh University Press.
- FRÖDERSTRÖM, H. (1932). The genus *Sedum* L., 3. *Acta Horti Gotob.* 7, app.: 1–125.
- FRÖDERSTRÖM, H. (1936). The genus *Sedum* L., 4. *Acta Horti Gotob.* 10, app.: 1–262.
- FRÖDERSTRÖM, H. (1960). *Sedum longibracteatum*. In: RECHINGER, K. H. Zur Flora von Syrien, Libanon und den angrenzenden türkischen Gebieten. *Arkiv Bot.* 5: 189–190.
- GRISEBACH, A. (1843). *Spicilegium Florae Rumelicae et Bithinicae*, 1. Braunschweig.
- KIM, J. H., 'T HART, H. & MES, T. H. M. (1996). The phylogenetic position of

- East Asian *Sedum* species (Crassulaceae) based on chloroplast DNA *trnL*(UAA-*trnF*(GAA) intergenic spacer sequences. *Acta Bot. Neerl.* 45: 309–321.
- MORAN, R. (1972). The genus *Meterostachys* Nakai (Crassulaceae). *Cat. Succ. J.* 44: 262–273.
- OHBA, H. (1978). Generic and infrageneric classification of the Old World Sedoideae (Crassulaceae). *J. Fac. Sci., Univ. Tokyo*, sect. 3, 12: 139–198.
- RECHINGER, K. H. fil. (1943). Flora Aegaea. Flora der Inseln und Halbinseln des ägäischen Meeres. *Akad. Wiss. Math.-Naturwiss. Kl. Denkschr.* 105: 1–924.
- SWOFFORD, D. L. (1993). *Phylogenetic Analysis Using Parsimony (PAUP)*. Version 3.1.1. Champaign, Illinois: Illinois Natural History Survey.
- 'T HART, H. (1985). Chromosome numbers in *Sedum* (Crassulaceae) from Greece. *Willdenowia* 15: 115–135.
- 'T HART, H. (1991). Evolution and classification of the European *Sedum* species (Crassulaceae). *Flora Medit.* 1: 31–61.
- 'T HART, H. (1995). Infrafamilial and generic classification of the Crassulaceae. In: 'T HART, H. & EGGLI, U. (eds) *Evolution and Systematics of the Crassulaceae*, pp. 159–173. Leiden: Backhuys Publishers.
- 'T HART, H. (1996). Variation in *Sedum litoreum* and the *S. rubens* complex (Crassulaceae); new names and combinations. *Ot Sistematič Botanik Dergisi* 2 (1995): 1–10.
- 'T HART, H. & ALPINAR, K. (1991a). Biosystematic studies in *Sedum* (Crassulaceae) of Turkey. I. Notes on four hitherto little known species collected in the western part of Anatolia. *Willdenowia* 21: 143–156.
- 'T HART, H. & ALPINAR, K. (1991b). Biosystematic studies in *Sedum* (Crassulaceae) of Turkey: Morphological and cytological variation in *S. pallidum* and *S. rubens*. *Bot. Chronika* 10: 641–649.
- 'T HART, H. & EGGLI, U. (1989). Cytotaxonomic studies in *Rosularia* (Crassulaceae). *Bot. Helv.* 98: 223–234.
- 'T HART, H. & VAN HAM, R. C. H. J. (1991). Cytotaxonomic notes on *Sedum* (Crassulaceae) species of Israel. *Israel J. Bot.* 40: 323–329.
- TABERLET, P., GIELLY, L., PAUTOU, G. & BOUVET, J. (1991). Universal primers for amplification of three noncoding regions of chloroplast DNA. *Plant Mol. Biol.* 17: 1105–1109.
- UHL, C. H. (1963). Chromosomes and phylogeny of the Crassulaceae. *Cact. Succ. J. Amer.* 35: 80–84.
- VAN HAM, R. C. H. J. & 'T HART, H. (1998). Phylogenetic relationships in the Crassulaceae inferred from chloroplast DNA restriction site variation. *Amer. J. Bot.* 85: 123–134.
- VAN HAM, R. C. H. J., 'T HART, H., MES, T. H. M. & SANDBRINK, J. M. (1994). Molecular evolution of noncoding regions of the chloroplast genome in the Crassulaceae and related species. *Curr. Genet.* 25: 558–566.

*Received 18 August 1998; accepted with revision 12 February 1999*