Zeitschrift: Botanica Helvetica

Herausgeber: Schweizerische Botanische Gesellschaft

Band: 93 (1983)

Heft: 2

Artikel: Micro-endemism in Sedum (Crassulaceae) : the sibling species S. alsinefolium All. and S. fragrans spec. nov. from the French-Italian Alps

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DOI: https://doi.org/10.5169/seals-65252

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Micro-endemism in *Sedum* (Crassulaceae): the sibling species *S. alsinefolium* All. and *S. fragrans* spec. nov. from the French-Italian Alps

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Summary

't Hart H. (1983). Micro-endemism in *Sedum* (Crassulaceae): the sibling species *S. alsinefolium* All. and *S. fragrans* spec. nov. from the French-Italian Alps. Bot. Helv. *93:* 269–280. – *Sedum fragrans* sp. n. which is described here closely resembles *S. alsinefolium* All. The latter is a much branched annual, has large flowers with a corolla-tube 2–3 mm long and styles about 1 mm long. It has the chromosome number 2n = 26. *S. fragrans,* on the other hand, perennates through rooting non-flowering shoots with terminal rosettes. It usually has simple flowering shoots, smaller flowers with a corolla-tube about 1 mm long and styles about 0.7 mm long. It has the chromosome number 2n = 20. The hybrids between *S. alsinefolium* and *S. fragrans* have the chromosome number 2n = 23 and are completely sterile. Both species are endemic to the French-Italian Alps. *S. fragrans* occurs on limestone in the Maritime Alps and in Piemont. *S. alsinefolium* is calcifuge and restricted to Piemont. Although both species have many characters in common with the species of the series *Cepaea* (Koch) Fröd. they cannot be hybridized with any of these taxa. *S. alsinefolium* and *S. fragrans* are here classified in the series *Alsinefolia* Berger.

Introduction

Sedum alsinefolium All. is endemic to the French-Italian Alps, to Piemont and western Liguria in Italy and the dep. Alpes-Maritimes in France. It is a fragile plant that occurs between about 200 and 2000 m in shaded and humid places on steep cliffs, around the entrances to caves and in fissures and holes under projecting rocks (Allioni 1785, Rouy & Camus 1901, Fiori 1923, Coste 1937, Pignatti 1982). Opinions vary as to whether it is annual, biennial or perennial (l.c.). According to Allioni *S. alsinefolium* is biennial. Praeger (1921), Berger (1930) and Fröderström (1932) on the other hand described it as perennating through non-flowering rosulate off-shoots.

Travail dédié au professeur Claude Favarger, à l'occasion de son 70e anniversaire

S. alsinefolium has white petals and red anthers and belongs to the extremely heterogeneous group of white-flowered European *Sedum* species (t' Hart 1982a). De Candolle (1828) classified *S. alsinefolium* as a subspecies of *S. cepaea* L. This view has never been accepted and *S. alsinefolium* is generally regarded as a distinct species. Berger (1930) classified *S. alsinefolium* in the series *Alsinefolia* Berger of sect. *Sedum* (= sect. *Seda-genuina* Koch) together with *S. adenotrichum* Wall. and *S. rosulatum* Edgew. from the Himalayas. Fröderström (1932) classified it in the series *Hirsutum* Fröd. together with the European *S. candollei* Hamet, *S. hirsutum* All., *S. nebrodense* Gasp. ex Guss. and *S. winkleri* Wolley-Dod.

Hébert (1975) reported the chromosome number 2n = 20 for two plants of *S. alsinefolium* originating from Fontan (France, dep. Alpes-Maritimes) and Mt. Mongioié (Italy, prov. Cuneo), respectively.

Material and Methods

Living plants were collected in the wild and were cultivated in the experimental garden in Utrecht. They were grown in a somewhat shaded place in the temperate greenhouse and watered only once or twice a week. In addition specimens were examined from the following herbaria: G, K, LY and P (abbreviations according to Holmgren & Keuken, Index Herbariorum. I. ed. 6, 1968).

Chromosome numbers were determined in root-tip mitoses only ('t Hart 1982b). Vouchers of the cytologically investigated plants preserved in 70% alcohol have been deposited in the Botanical Institute in Utrecht (U). The anatomy of the flowers was studied in serial transverse sections of 20 microns stained with crystal-violet and erythrosine (Johansen 1940, Quimby 1971). Pollen fertility was determined using fresh pollen stained with aceto-carmine in glycerine. Seeds dried at 60 °C were examined and photographed with a Cambridge Stereoscan 600M.

Results

A. Natural habitat and habit.

The living plants were collected in six different localities; five in France in the dep. Alpes-Maritimes and one in Italy in Borgo in the province Cuneo (appendix, table 1). In France the plants grew in shaded places on steep cliffs, in fissures and in niches, under projecting rocks or around the entrances to caves. In all five localities in France they occurred on calcareous rocks only. In Borgo in Italy the plants occurred on schist. They grew in shaded and humid places, in fissures and niches as well as between rocks in steep roadsides and on drystone walls (muri a secco).

The plants in the Maritime Alps usually consisted of dense tufts of small rosettes many of which still bore the dried flowering shoots of the previous year. The plants in Borgo on the other hand were apparently all young plants. Most of them grew solitarily, or sometimes they were clumped together in fissures or niches. They were never rosulate, but were rather loose and usually much branched (fig. 1).

B. Cytology and hybridization

The plants from France all had the chromosome number 2n = 20. The two plants from Borgo had the chromosome number 2n = 26. Both cytotypes have symmetrical karyotypes consisting of small chromosomes about 2 microns long.

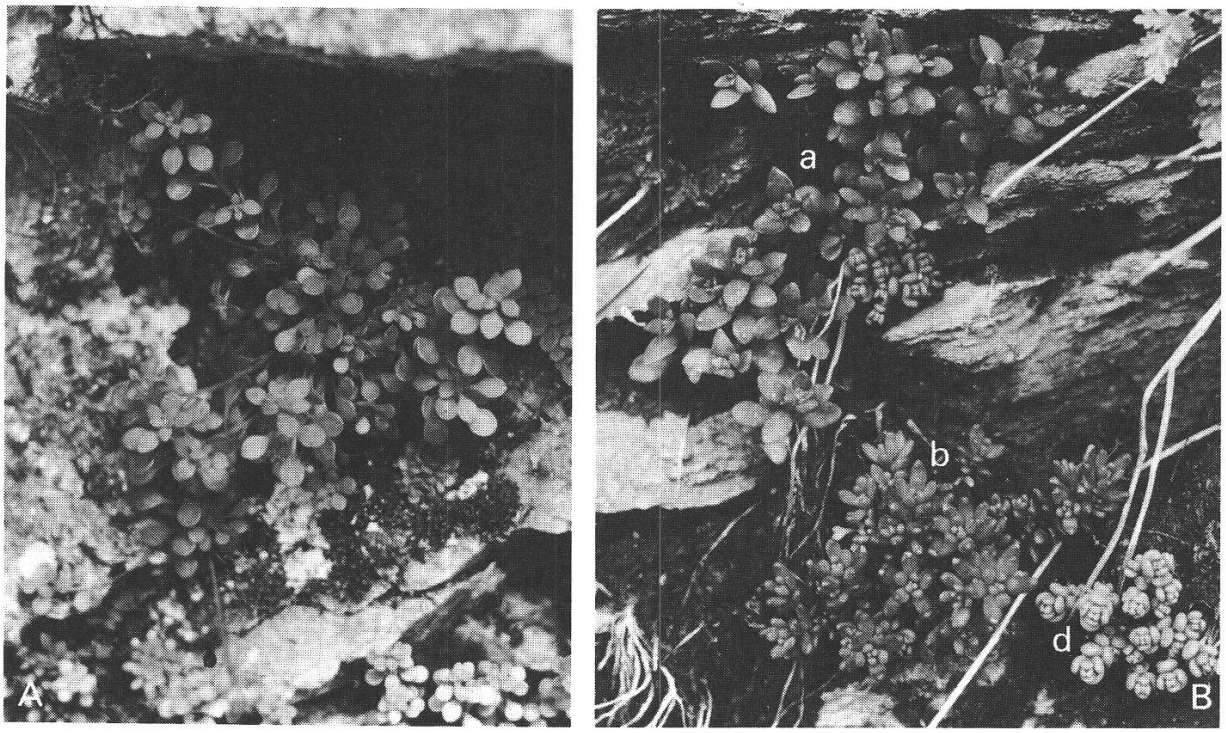


Fig. 1. *Sedum alsinefolium* and *S. fragrans* in their natural habitats. - A. *S. fragrans* on limestone rocks W of Tende, 850–900 m, 24.V.1980, no. 26010 (type). - B. *S. alsinefolium* (a), S. album (b) and S. dasyphyllum (d) on a drystone wall (schist) in Borgo, 1500 m, 29.V.1980, no. 26050.

The two cytotypes could be hybridized very easily. The 17 flowers pollinated in the 4 crosses produced an average of about 40 seeds per flower. The seeds germinated rapidly and the hybrid plants were vigorous. Thirty seven hybrid plants were examined cytologically; they all had the chromosome number 2n = 23. The hybrids flowered profusely but were completely sterile. Pollen stainability varied from 0% to 21%. However, 95% or more of the stainable pollen grains were abnormal, malformed large grains which usually had thin walls and an odd number of apertures. Selfing of the parental plants resulted in a vigorous offspring with the chromosome numbers 2n = 20 and 2n = 26. In the parental plants pollen stainability varied from 95% to 98%.

Both cytotypes were crossed with *S. cepaea* (2n = 22, 2n = 44), *S. creticum* Presl (2n = 22), *S. cyprium* Jackson & Turril (2n = 22), *S. hirsutum* (2n = 18, 2n = 20), *S. monregalense* Balbis (2n = 30) and *S. tristriatum* Boiss. (2n = 44). Of the 67 pollinated flowers used in these crosses not a single one produced seeds (fig. 2).

C. Morphology and anatomy

In addition to the abovementioned differences in ecological preference the two cytotypes also differ in a number of morphological characters.

The plants with the chromosome number 2n = 20 are perennial. They produce short stolons with dense rosettes at the tips from the axils of the basal leaves. These take root and after some time become independent plants. The rosettes are hapaxanthic. In spring they usually produce a single erect flowering shoot with a very lax terminal inflorescence. The flowering shoot is usually simple, but sometimes produces subsidiary inflorescences from the axils of the cauline leaves. The plants with the chromosome number 2n = 26 are monocarpic. The seeds germinate in autumn or spring. The young

plants are already much branched. Eventually all branches produce terminal inflorescences which are very lax and somewhat diffuse. Furthermore, subsidiary inflorescences develop from the axils of the cauline leaves.

The leaves of both cytotypes are succulent and flat, spatulate or pseudo-petiolate with a circular, broadly elliptical or oblong lamina. The leaves of the plants with the chromosome number 2n = 20 usually have a circular or broadly elliptical lamina, whereas the plants with the chromosome number 2n = 26 more often have an oblong or elliptical lamina (fig. 1).

The flowers of both cytotypes are long pedunculate and reflexed before anthesis. The peduncles continue to lengthen until the flowers have set seed. At the time of anthesis the peduncles of the flowers of the plants with the chromosome number 2n = 20 are on average 6 mm long, and the peduncles of the plants with the chromosome number 2n = 26 are about 9 mm long.

The two cytotypes differ most conspicuously in a number of floral characters (fig. 3). The diameter of the flowers of the plants with the chromosome number 2n = 20 is 6 (5–7) mm, of the plants with the chromosome number 2n = 26 7.5 (7–9) mm. Both cytotypes have narrowly elliptical, oblong or ovate sepals with acute or subacute tips. Variation in the length of the sepals is not correlated with the chromosome numbers. At their base the sepals are completely fused with the receptacle and their margins are only slightly connate (fig. 5). Both cytotypes have white petals which are distinctly connate at the base. The corolla-lobes are broadly ovate or cordate, long acuminate and spread

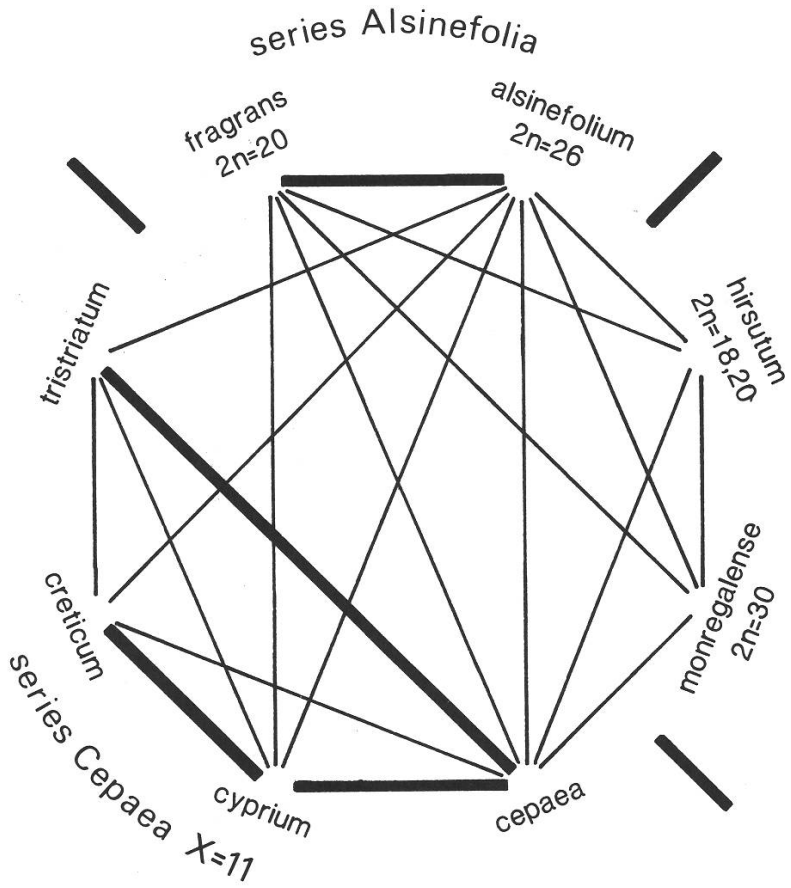


Fig. 2. Hybridization pattern of *Sedum hirsutum, S. monregalense* and the species of the series *Alsinefolia* and the series *Cepaea*. The heavy lines indicate the successful crosses, the thin lines the crosses which produced no seeds.

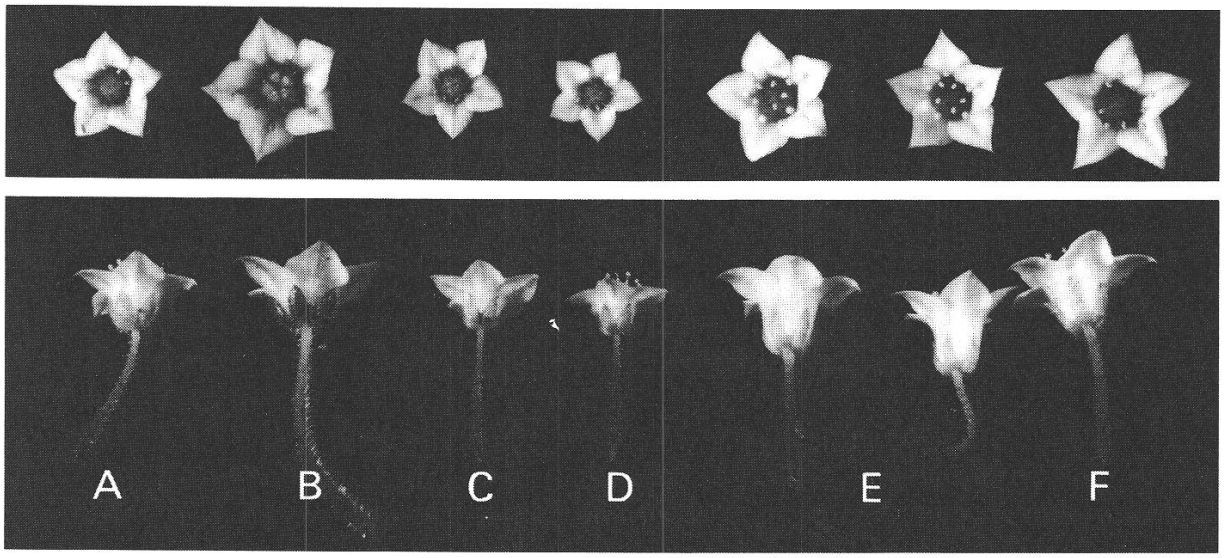
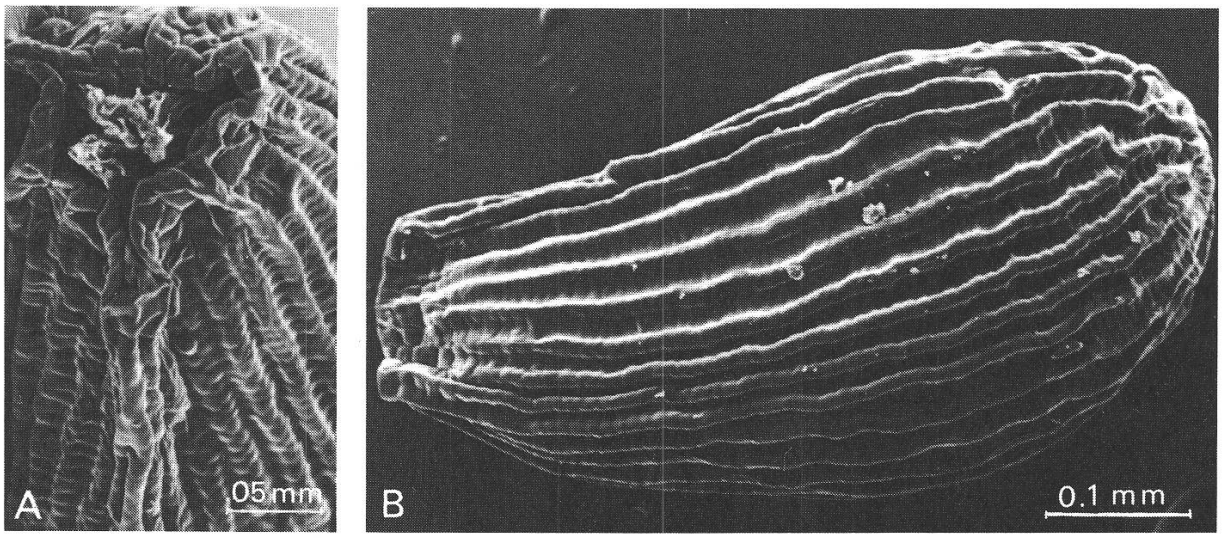


Fig. 3. The flowers of *Sedum alsinefolium* and *S. fragrans* from above and from aside. - *S. fragrans* from the Vallée de Cairos, no. 25987 (A), no. 25988 (B), and Tende, no. 26010 (C), no. 26011 (D). - *S. alsinefolium* from Borgo, no. 26047 (E) and no. 26050 (F).

Fig. 4. Seed of *Sedum fragrans* from the Vallée de Cairos (no. 25988). - A. Corona. - B. General view from aside.



during anthesis. The corolla-tube of the plants with the chromosome number 2n = 20 is 1 (0.8–1.4) mm long, the corolla-lobes are about 2.5 × 2 mm. The plants with the chromosome number 2n = 26 have larger corolla-tubes 2.5 (2–3) mm long and corolla-lobes about 3 × 2.5 mm. The filaments of the stamens of the plants with the chromosome number 2n = 20 are 2.5–3 mm long, those of the plants with the chromosome number 2n = 26 are 4 (3.5–4.5) mm long (measured from the base of the corolla-tube). The filaments are fused with the corolla-tube at the base, for 0.5–1 mm in the plants with the chromosome number 2n = 20 and for 1–1.5 mm in the plants with the chromosome number 2n = 26. The styles of the plants with the chromosome number 2n = 20 are 0.7 (0.5–0.9) mm long, those of the plants with the chromosome number 2n = 26 are 1 (0.9–1.1) mm long.

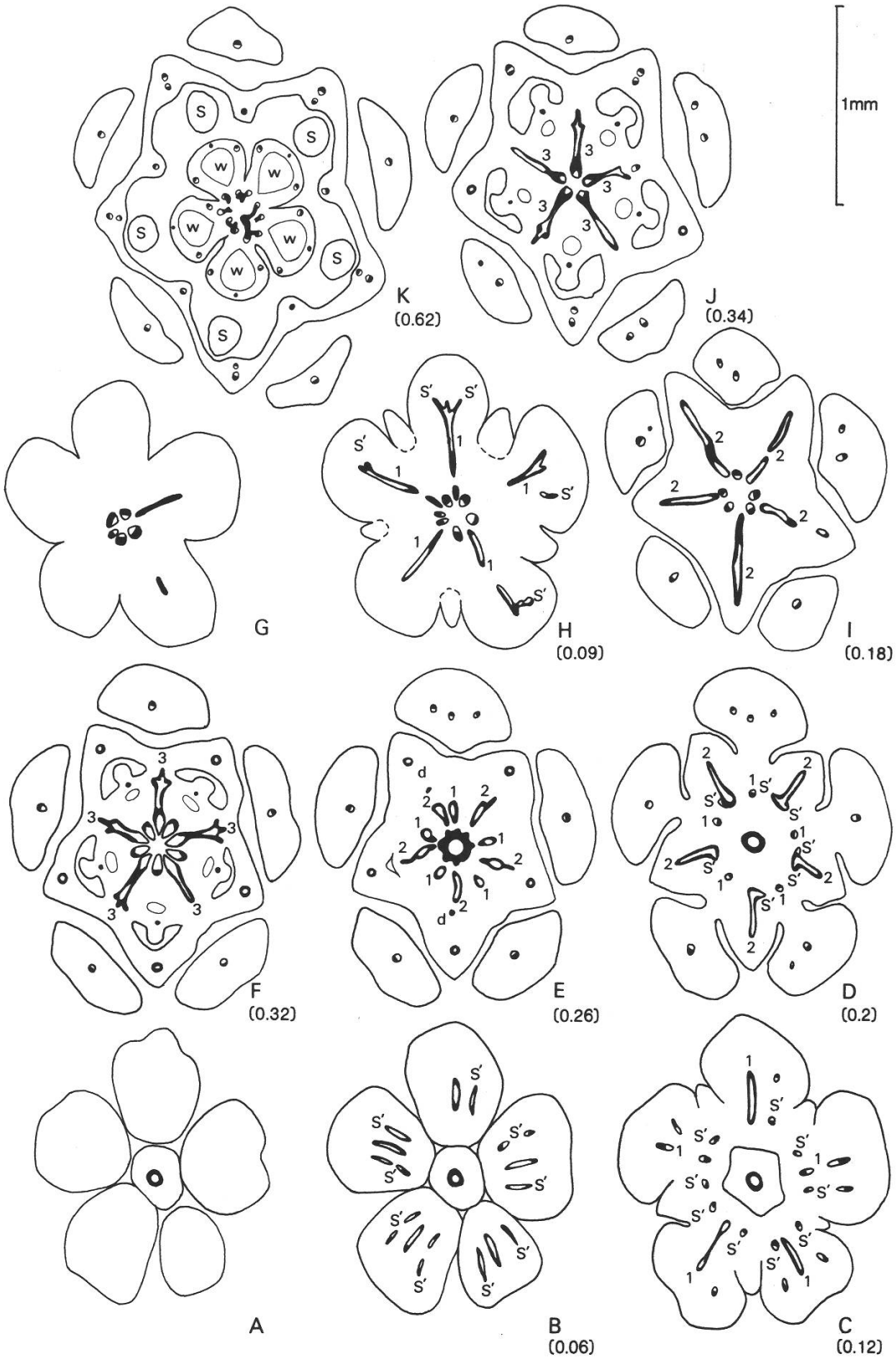


Fig. 5. Transverse sections through the flowers of *Sedum alsinefolium* (G–K) and *S. fragrans* (A–F). The numbers in brackets indicate the distance from each section to the first section of the flower (A and G). – Phloem black. – Xylem white. – The traces of whorl 1, 2 and 3 are indicated accordingly. – d, dorsal traces of the carpels. – s, squamae. – s', lateral traces of the sepals. – w, lumen of the carpels.

The number of ovules per carpel varies from 4 to 15 in both cytotypes. On average the plants with the chromosome number 2n = 20 have 7 ovules per carpel, whereas the plants with the chromosome number 2n = 26 have 10 ovules per carpel. The seeds of both cytotypes are shiny, black or dark brown, and have a laticostate testa and a narrow corona encircling the micropyle and funicle (fig. 4).

The vascular pattern of the flowers of both cytotypes agrees with group three of Quimby's system (Quimby 1971). In all flowers there are three independent whorls of traces departing from the stele (fig. 5), i.e.: Whorl 1; the traces to the sepals. Whorl 2; the combined traces to the petals, epipetalous stamens and the dorsal traces of the carpels. Whorl 3; the combined lateral traces of the carpels and the traces to the episepalous stamens. Whorl 4; the ventral traces of the carpels.

The flowers of the two cytotypes differ considerably in the shape of the receptacle and the courses of the traces of whorl 1 and whorl 2. The receptacle of the flowers of the plants with the chromosome number 2n = 20 is convex, its margin encircles the end of the petiole (fig. 5, E). The sepals are attached to the underside of the flowers and curve upwards abruptly (fig. 5, A–D). The receptacle of the plants with the chromosome number 2n = 26 is flat or disk-shaped and the sepals are attached laterally (fig. 5, G–H).

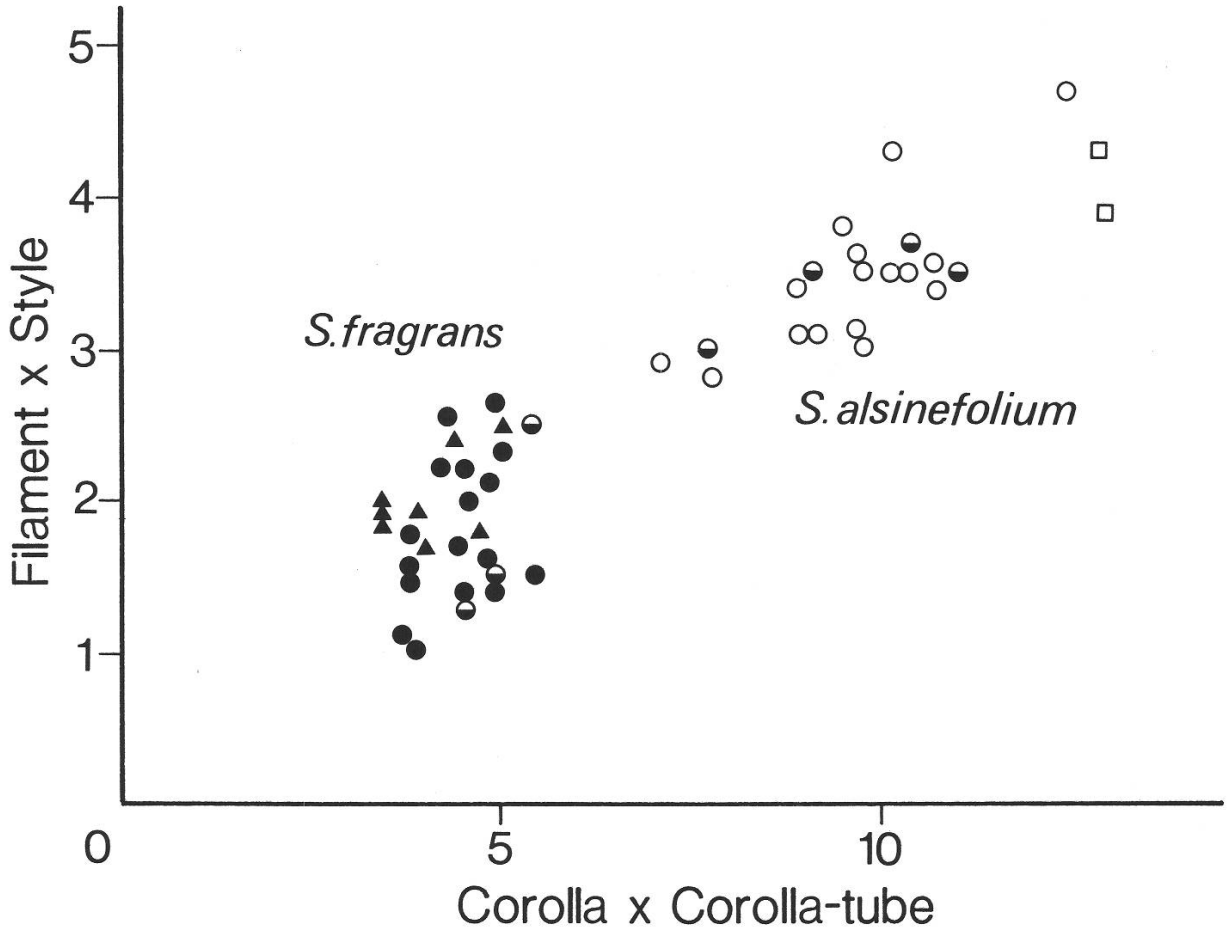


Fig. 6. Differences in the lengths of the corollas, corolla-tubes, filaments and styles (in mm) between the plants of *Sedum alsinefolium* and *S. fragrans* cited in the appendix (of each plant two flowers were measured). – □ *S. alsinefolium*, 2n = 26. – ▲ *S. fragrans*, 2n = 20. – ○ Herbarium specimens without non-flowering shoots. – ● Herbarium specimens with non-flowering shoots. – ◒ Incomplete specimen.

In the flowers of the plants with the chromosome number 2n = 20 the traces of whorl 1 and whorl 2 depart from the stele almost at the same level (fig. 5 E) and proceed downwards in the first part. The traces to the sepals (whorl 1) go downwards for about 200 microns (fig. 5 E–B) and then curve upwards within the sepals (fig. 5, B–F). The traces of whorl 2 go downwards for about 100 microns (fig. 5, E–D). The dorsal traces of the carpels (d) leave the traces of whorl 2 shortly after they depart from the stele (fig. 5, E). The laternal traces of the sepals (s') fuse with the combined traces of the petals and epipetalous stamens at the point where the latter enter into the petals and curve upwards (fig. 5, D). The traces of whorl 3 proceed almost horizontally up to the point where the lateral traces of the carpels and the traces to the episepalous stamens separate (fig. 5, F).

In the flowers of the plants with the chromosome number 2n = 26 the traces of whorl 1 and whorl 2 depart at different levels and they proceed almost horizontally in the first parts (fig. 5, G–J). The lateral traces of the sepals (s') sometimes combine with the traces of whorl 2 but more often with the traces of whorl 1 (fig. 5, H). The traces of whorl 3 also proceed horizontally to the point where the lateral traces of the carpels and the traces to the episepalous stamens separate (fig. 5, J). Only a short distance below the point where the carpels fuse the traces of whorl 4 leave the stele which at that point is sealed off by some anastomosing strands of phloem (fig. 5, K).

D. Geographical distribution

The herbarium specimens (app., tab. 2) could be divided into two distinct groups on the basis of the abovementioned four floral characters, i.e. the lengths of the corollas, corolla-tubes, filaments and styles (fig. 6). Each of these two groups is correlated with one of the two cytotypes. Except in the incomplete specimens, it could be observed that the plants with small flowers always had non-flowering shoots at the base (stolons with a terminal rosette), whereas the specimens with large flowers did not have non-flowering shoots.

The two groups have different distribution areas. The perennial plants with small flowers (chromosome number 2n = 20) occur in the Maritime Alps in France and adjacent Piemont in Italy. The annual plants with large flowers (chromosome number 2n = 26) are restricted to Piemont (prov. Cuneo and prov. Torino).

Discussion

The two taxa which were formerly included in *S. alsinefolium* differ in geographical distribution, ecological preference, habit, duration, a number of morphological characters, some aspects of the floral vasculature and chromosome number and moreover are reproductively isolated. Although the two taxa closely resemble each other they are classified here as distinct species.

Allioni (1785) described *S. alsinefolium* with the phrase «*Sedum* erectum ramosum foliis planis, floribus albis longe pedunculatis» and added that the species was biennial. The monocarpic, much branched plants of the cytotype with the chromosome number 2n = 26 from Piemont fully agree with this description. The rosulate, perennial plants with simple flowering shoots and smaller flowers of the cytotype with the chromosome number 2n = 20 thus represent the new species.

Sedum alsinefolium All., Fl. Pedem. 2: 119 (1785)

Fragile, much branched, erect, annual plants 8 to 15 cm high, glandular pubescent throughout. Leaves green or reddish-brown, succulent and flat, spatulate or pseudo-petiolate with an oblong or elliptic lamina, sometimes subsessile, to 15 (or 20) mm long and about 8 mm wide, with obtuse or rounded tips. Plants usually many-flowered, with very lax, diffusely cymose or cincinniform inflorescences. Flowers 5-merous, diplostemonous, about 7.5 (7–9) mm in diameter, reflexed before anthesis. Pedunculi about 9 (5–15) mm long. Sepals green, linear-oblong to elliptic or triangular-ovate, about 2×0.6 mm, acute. Petals white, glabrous at the inside, connate at the base; corolla-tube 2–3 mm long, diameter 2–2.5 mm; corolla-lobes broadly ovate to cordate, 2.5–3.5 mm long, 2.5–3 mm wide, long acuminate. Filaments glabrous, white, 3.5–4 mm long, united with the corolla-tube for about 1.5 mm. Anthers globose, red or pink, rarely yellowish. Squamae red, spatulate. Carpels pubescent, erect, 2–2.5 mm long, with about 10 (5–15) ovules. Styles about 1 (0.9–1.1) mm long. Follicles orthocarpic, whitish. Seeds shiny, black or dark brown, with a laticostate testa and a small corona. Chromosome number $2n = 26$. Endemic to Piemont (Italy: prov. Cuneo, prov. Torino). Calcifuge.

Sedum fragrans spec. nov.

Plantae perennes, fragiles, totae glanduloso-pubescentes, stolonibus basalibus radicantibus brevibus rosulis terminalibus. Folia viridia, plerumque rubella, succulenta et applanata, spathulata vel pseudopetiolata, laminis circularibus vel late ellipticis, ad 15 (vel 20) mm longa et 8 mm lata, apicibus rotundatis vel obtusis. Caules floriferi erecti, plerumque simplices, ad 20 cm longis, interdum inflorescentiis axillaribus subsidiaribus. Inflorescentiae terminales laxae et pauciflorae, cincinniformes, ramulis singulis vel binis. Flores 5-meri, diplostemoni, circa 6 (5–7) mm diametro, reflexi ante anthesin. Pedunculi circa 7 (4–9) mm longi. Sepala viridia, leviter inaequalia, lineari-oblonga, elliptica vel triangulari-ovata, 1.5 (1–2) mm longa, 0.5 (–1) mm lata. Petala alba, intra glabra, basibus connatis; tubus corollae 1 (0.8–1.4) mm longus circa 2 mm diametro, laciniae late ovatae vel cordatae, 2.5 (2–3.5) mm longae, 2.2 (1.7–3.5) mm latae, longe acuminatae. Filamenta alba, glabra, 2.7 (2–3) mm longa, basi tubo corollae adnata per circa 0.7 mm. Antherae rubrae, globosae. Squamae rubrae, spathulatae. Carpella pubescentia, erecta, circa 2 mm longa, basibus connatis, ovulis circa 7 (4–14). Styli 0.7 (0.5–0.9) mm longi. Folliculi albidi, orthocarpi. Semina nitida, nigra vel atro-brunnea, testis late costatis, coronis parvulis. Chromosomatum numerus $2n = 20$. – Hab. in rupibus calcareis alpinis Galliae meridionalis et Italiae septentrionalis.

Type: France (dep. Alpes-Maritimes), Tende, rocks W of the city, on limestone, 850–900 m, 't Hart 24.V.1980, no. 26010.

S. alsinefolium and *S. fragrans* closely resemble each other and presumably descend from a common ancestor. The larger corolla-tube and the annual habit of *S. alsinefolium* are advanced characters. The higher basic chromosome number of *S. alsinefolium* ($x = 13$) may also be regarded as derived. On the other hand the anatomy of the flowers of *S. fragrans* is more advanced. Since both species are partly sympatric and at the same time reproductively isolated they may be denoted as sibling species to indicate their evolutionary level.

In the classification of the European *Sedum* species the rank of series has been attributed to groups which form a comparium. Accordingly *S. alsinefolium* and *S. fragrans* are classified in the series *Alsinefolia*. *S. adenotrichum* and *S. rosulatum* from the

Himalayas have recently been classified in *Rosularia* Stapf (Jansson & Rechinger 1970, Ohba 1977, 1978, 1980) and are excluded from the series *Alsinefolia.*

Among the white-flowered European *Sedum* species, seeds with a laticostate testa and a corona also occur in the species of the series *Cepaea* (Koch) Fröd. ('t Hart & Berendsen 1980, 't Hart unpubl.). Although in *Sedum* the hybridization pattern of the species proved to be highly correlated with the ornamentation of the testa, the species of the series *Alsinefolia* and the series *Cepaea* could not be hybridized and apparently belong to different comparia.

However, in addition to the ornamentation of the testa, the species of the series *Cepaea* have many more characters in common with *S. alsinefolium* and *S. fragrans* which may indicate more remote relationships between these taxa. The annual and biennial species of the series *Cepaea* have basal rosettes. The perennial *S. tristriatum* closely resembles *S. fragrans* in habit; it also produces short, rooting stolons with a terminal rosette. The leaves of the species of the series *Cepaea* are succulent and flat, and more or less distinctly spatulate. The inflorescences of *S. cepaea, S. creticum* and *S. cyprium* are many-flowered and compact panicles concisting of large numbers of axial few-flowered cincinni. The inflorescences of *S. tristriatum* are usually small and cymose or cincinniform. The flowers of the species of the series *Cepaea* are pedunculate (1–5 mm), 5-merous and diplostemonous. They have oblong-ovate, acute sepals which are laterally attached to a narrow receptacle. Their petals are long acuminate and basally connate. The petals of *S. cyprium* are united for more than 1 mm. They have orthocarpic, many-seeded follicles. The vascular pattern of their flowers also agrees with Quimby's group three. The squamae of the species of the series *Cepaea* are broadly cuneate and dentate except for *S. cyprium,* which has very broad, low, quadrate squamae with an entire margin.

The species of the series *Cepaea* also resemble *S. alsinefolium* and *S. fragrans* in that they are entirely covered with multicellular glandular hairs. In *S. creticum* (including *S. hierapetrae* Rech.) the densely pubescent inflorescences have a distinct, rather strong resinous smell. The glandular hairs of *S. alsinefolium* and *S. fragrans* also emit a distinct odour. The sweet perfume given off by the flowering plants faintly resembles the smell of carnations or freesias and has an additional resinous element.

The new *Sedum* is named after this distinct character which is so peculiar in this genus of usually completely odourless plants.

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The author wishes to thank Dr. W. Berendsen of the Dept. Molecular Biology for the SEM-micrographs, Mr. Th. Heideman of Naarden International for his suggestions concerning the odour of *S. fragrans*, and Prof. Dr. K.U. Kramer who kindly corrected the latin description.

Appendix

Table 1. Chromosome number, origin and collection number of the plants studied.
Sedum alsinefolium All., 2n = 26
Italy: prov. Cuneo; Borgo W of Crissolo, on walls and in roadsides, on schist, 1500 m, 26047, 26050.
Sedum fragrans t' Hart, 2n = 20
France: dep. Alpes-Maritimes; Vallée de Cairos, 3 km S of St. Claire, cave near the bridge across the river, on limestone, 650 m, 25987, 25988; Vallée de Cairos, on rocks 1-2 km S of St. Claire, limestone, 800 m, 26000; Tende, on walls and rocks in the city, on limestone, 800-850 m, 26011, 26012; The cave named Trou du Diable W of St. Martin-Vesubie, on limestone, 1100 m, 26037, 26040.

Table 2. Herbarium specimens examined.
Sedum alsinefolium All.
Italy: Piemonte; prov. Cuneo; Bellino W of Casteldelfino, Boissier 1852 (G); Borgo W of Crissolo, Ferrari c.s. 1921, 2687 (G, K, P); Crissolo, Balbis s.d. (G), Boissier 1832 (G); prov. Torino; Col de la Croix, Saint-Lager s.d. (G); Bobbio Pellice, Reuter 1853 (P); Inverso Porte W of Pinerolo, Rostan 1853 (G); Perosa Argentina, Becherer 1936 (G); Perrero, Rostan s.d. (P); Pinerolo, Chevallier s.d. (G), Rostan s.d. (K, LY); Pra del Torno N of Torre Pellice, Boissier 1847 (G); San Germano NW of Pinerolo, Jordan 1873 (LY), Rostan 1851, 1854, 1880 (G, P); Val St. Martin, Rostan 1881 (G, LY); Villar Pellice W of Luserna, Alioth 1856 (G).

Sedum fragrans 't Hart
France: dep. Alpes-Maritimes; Beuil, Vidal 1894 (LY); Escragnolles, on Mt. Audibergue, Burnat c.s. 1896 (G); Fontan, Reverchon 1886, 165 (K, LY, P); Gourdon NE of Grasse, Consolat 1874 (LY, P); Roubion E of Beuil, Javras 1887 (G); Saorge, Gorges de la Bevera, Charpin 1977, 13901 (G); Saorge, Gorges de la Roja, Charpin 1973, 10356 (G); St. Martin-Vesubie, Burnat 1869, 1875 (LY, P), Thuret 1865 (G, P); Tende, Ardoino 1860 (P), Boissier 1852 (G), Burnat 1872 (LY), Hibon 1910 (P), Reuter 1843 (G, LY, P), Vetter 1879 (G); Vallée de Cairos, Micheli 1876 (G); Vignols near la Balma du Pin, Vidal 1901, 4726 (G, LY, P).
Italy: Piemonte; prov. Cuneo; Dronero, Ferrari 1906 (G); Stroppo, Allis s.d. (G); Valle d. Viale, near Roascia, Charpin 1973, 10333 (G); prov. Torino; Valle d. Germanasca, Rostan 1880 (K).