SEMPERVIVUM (CRASULACEAE) IN SPAIN AND THE PYRENEES

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Resumen. Se ha realizado un estudio estadístico de 2926 plantas de *Sempervivum* recolectadas en 61 localidades, incluyendo 10 caracteres vegetativos de todas las plantas estudiadas y 15 caracteres florales para el 20% de las mismas. Se ha llegado a las siguientes conclusiones: En los Pirineos, se encuentran *S. arachnoideum* L., *S. montanum* L. y *S. tectorum* L., así como sus híbridos. En la Cordillera Cantábrica se encuentran *S. cantabricum* Huber y su híbrido con *S. arachnoideum* (*S. x giuseppii* Wale). En los Picos de Europa y sus proximidades se encuentran algunas plantas indistinguibles de *S. arachnoideum*. Los caracteres que presenta *S. nevadense* Wale, de Sierra Nevada, sugieren que debe ser de origen híbrido. Se describen como *S. cantabricum* subsp. *guadarramense* M. C. Smith, subsp. nov. las poblaciones de la Sierra de Guadarrama, y las procedentes de los Picos de Urbión como *S. cantabricum* subsp. *urbionense* M. C. Smith, subsp. nov. Se considera *S. andreanum* Wale, del Pirineo, como sinónimo de *S. tectorum*.

Summary. A statistical analysis of 2926 plants of *Sempervivum* collected at 61 localities has been made, covering 10 vegetative characters for the whole sample and 15 floral characters for 20% of the sample. The following conclusions have been reached: *S. arachnoideum* L., *S. montanum* L. and *S. tectorum* L. occur in the Pyrenees and frequently hybridise. *S. cantabricum* Huber and its hybrid with *S. arachnoideum* (*S. x giuseppii* Wale) occur in the Cantabrians. In and near the Picos de Europa a few plants morphologically indistinguishable from *S. arachnoideum* are found. *S. nevadense* Wale, from the Sierra Nevada, has characters suggesting it may have arisen from past hybridisation. Populations from the Sierra de Guadarrama are described as *S. cantabricum* subsp. *guadarramense* M. C. Smith, subsp. nov., and those from the Picos de Urbión as *S. cantabricum* subsp. *urbionense* M. C. Smith, subsp. nov. *S. andreanum* Wale, from the Pyrenees, is considered synonymous with *S. tectorum*.

INTRODUCTION

The aim of this study is the delimitation of taxa of *Sempervivum* occurring in Spain and the Pyrenees.

WILKOMM & LANGE (1874) reported only three species of *Sempervivum* from Spain: *S. arachnoideum* L., *S. montanum* L. and *S. tectorum* L. PRAEGER (1932) reported the same three species from the Pyrenees. HUBER (1934) described *S. cantabricum* from the Cantabrians. WALE (1941) described *S. andreanum, S. giuseppii* and *S. nevadense* from Spain. FAVARGER & ZÉSIGER (1964) accepted these seven species. At least 17 other specific names have been used on herbarium specimens or in the literature for the area, but many of these are names of the ill-defined species described from France by LAMOTTE (1864), JORDAN & FOURREAU (1866) and ROUY & CAMUS (1901), most of which were considered by PRAEGER (1. c.) to be synonymous with *S. tectorum*. The name *S. vicentei* Pau (PAU, 1906) has been used by several botanists for specimens collected in the Picos de Urbión.

Some species of *Sempervivum* resemble one another closely; hybrids are common; variation due to the environment is often great. Consequently the dividing lines between the species are difficult to determine. For these reasons I decided to base the study on statistical analysis of a large sample of plants, and to make all measurements on plants that had been cultivated under the same conditions.

MATERIAL AND METHODS

Sampling.

Sempervivums were collected in 1969 and 1970 from 21 localities in the Cantabrians, 7 in the Picos de Urbión, 21 in the Pyrenees, 7 in the Sierra Nevada and 4 in the Guadarrama. Most locality samples were of about 40-50 clones. I did not visit the Serranía de Cuenca, from which *S. tectorum* was recorded by WILKOMM & LANGE (1874) but not by later authors.

Random sampling was not practicable because of the rough terrain. To reduce bias, I collected portions of all plants found within increasing circuits of the first plant collected, with the proviso that adjacent clumps that looked as though they might have originated from the same clone were sampled only once. To reduce phenotypic variation all the plants collected were cultivated in one place at Bristol for 7-9 months before making measurements.

Characters.

10 vegetative characters were measured in 1970-1971 on all the plants collected. Only about 20% of the plants flowered and for these 15 floral characters were recorded (Table I). The small percentage which flowered was not due to the conditions of cultivation, for in the wild also only a small minority of rosettes flower in one year.

Vegetative: quantitative	Length of petals
Degree of incurving of rosettes leaves	Width of petals
Date of offset production	Percentage 'good' pollen
Marginal cilia thickness	Number of inflorescence branches
Marginal cilia length	Flowers per inflorescence
Apical cilia length	Height of inflorescence
Apical cilia number	
Length of apical colour patch	*Floral: qualitative*
Density of pubescence	Marginal colour of petals
Angle of leaf apex	Streaks of colour on petals
Rosette diameter	Petal ground colour
	Anther colour
Floral: quantitative	Extent of cauline leaf colour
Date of flowering	Cauline leaf hue
Number of petals	Pubescence of filaments

Table I.—Characters examined.

The measurements of vegetative characters were assigned to positions on scales having 16 intervals. Thus the statistical analysis was not based on conventional units but on the intervals of scales that had different units for each character. Some character scales had arithmetic intervals, others logarithmic ones. The intervals were chosen so as to disperse the variation observed in a character over a wide part of each scale. Eight of the floral characters were quantitative, assigned to 16 intervals: the others were qualitative, and were assigned to four states.

All measurements were made within April-June. Those concerning rosette diameter, degree of incurving of leaves, and colour of leaf apices (which are characters which change rapidly with the season) were made within a single week: for these characters, and for date of offset emergence and date of flowering, observations were made a week later in 1971 than in 1970 to compensate for the later spring.

Method of analysis.

The analysis of vegetative character data was made in three stages, separately for each of the five mountain ranges. In the first stage individual

plants were arranged on a scale between two extreme plants: locality samples drawn from populations containing more than one taxon could be distinguished by their frequency distribution along the scale. The second stage, comparison between locality samples leading to the grouping of samples into taxa, could therefore be restricted to samples from localities with only one taxon present. In the third stage individuals within the heterogeneous samples were compared with the taxa distinguished in stage 2, and were assigned to the taxa they most resembled.

Stage 1. Distinguishing between 'homogeneous' and 'heterogeneous' samples. The character data was put onto computer cards and run through a program which determined (a) the modal value for each character, (b) the individual (r_1) having a set of characters showing the greatest 'difference' from the modal set, and (c) the individual (r_2) that was the most 'different' from r_1. The 'difference', D_{jk}, between plants was defined as:

$$D_{jk} = \sum_{i=1}^{10} W_i \left| C_{ij} - C_{ik} \right|$$

where C_{ij}, C_{ik} are the ith character values of plants j, k: and W_i is the reciprocal of the standard deviation of the ith character.

r_1 was a small-growing clone of *S. arachnoideum* from locality 44 in the Pyrenees, with incurved rosette leaves, and very long cilia densely clustered at the leaf apices; the apices were blunt, with little colour, and offsets were produced early in Spring. r_2 was a large-growing clone of *S. tectorum* from locality 38 in the Pyrenees, with open rosettes, short, thick cilia, glabrous leaf surfaces, very acute apices with well-developed colouring and producing offsets late.

All individuals were then assigned positions on a scale (similar to the 'Hybrid Index' of ANDERSON, 1949) of which r_1 and r_2 were the extremes with values of 0 and 100 respectively. Thus if P_k is the position of plant k on the scale from r_1 to r_2 then:

$$P_k = \sum_{i=1}^{10} \left[(C_{i,r_1} - C_{i,k}) \frac{\left| C_{i,r_1} - C_{i,r_2} \right|}{(C_{i,r_1} - C_{j,r_2})} \right] \left(\frac{100}{D_{r1,r2}} \right)$$
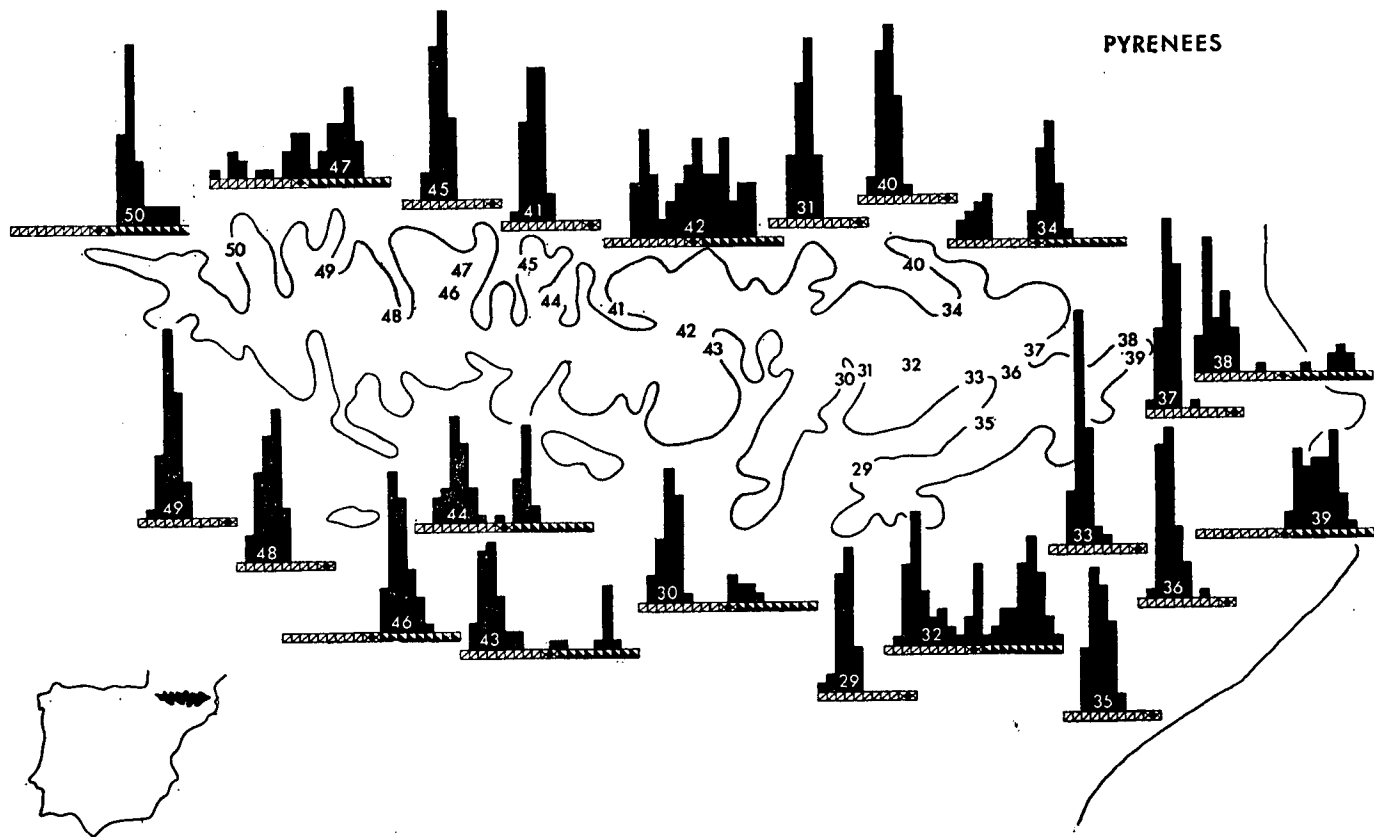
Fig. 1.—Frequency distributions along the r_1r_2 scale of locality samples from Pyrenees, showing unimodal, bimodal and trimodal examples. Scale is divided into 20 intervals between *'tectorum*-like' on left and *'arachnoideum*-like' on right, but to save space only the left-hand half of the scale is shown for some localities. (Left-hand half of scale indicated by white triangles on base line: right by black triangles). Land over 1.500 m. is outlined.
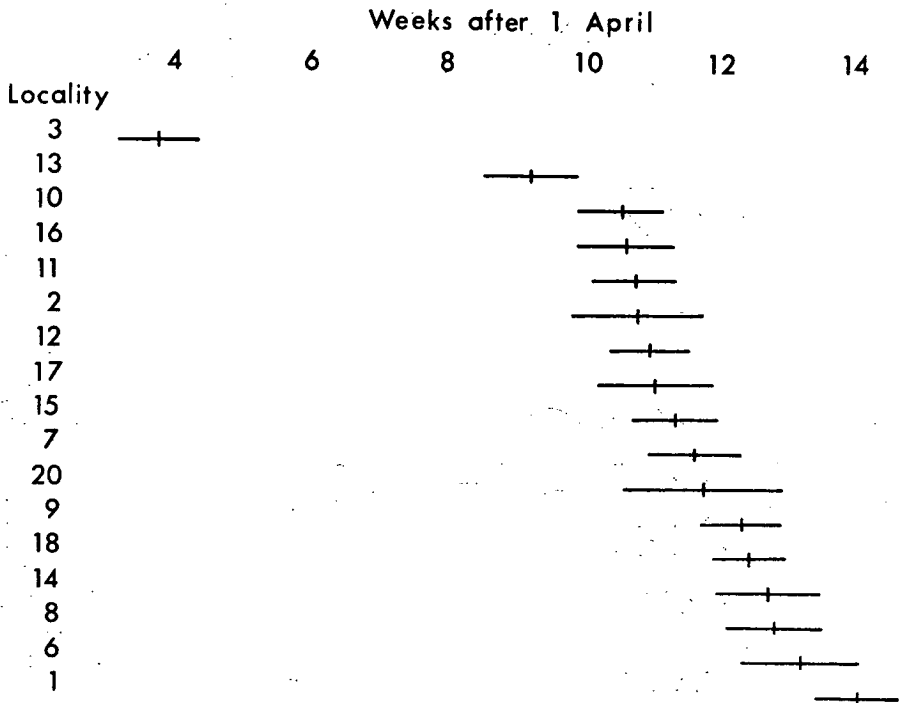
Fig. 2.—An example of a sequence of ascending character means; vertical bars indicate means: horizontal bars the range between the 5% confidence limits.

where $C_{i, k}$, $C_{i, r1}$, and $C_{i, r2}$ are, respectively, the ith character values of k, r_1 and r_2.

Histograms of the frequency with which the clones from each locality in the Pyrenees occurred in intervals 5 wide along the r_1 r_2 scale are shown in Fig. 1. Some of the histograms were clearly bimodal. The majority of locality samples had variances between 10 and 50, but a few (including all those for which the histograms appeared to be bimodal) had variances from 45 to 830. The value 45 was selected as the dividing line below which samples were provisionally treated as 'homogeneous' in stage 2. Com-

plete accuracy was not required for the method of assessing 'heterogeneity': it was sufficient if all but a few samples were allocated correctly. Later analysis revealed that the use of 45 as the dividing line led to the inclusion of two 'heterogeneous' samples among the 45 in the 'homogeneous' group and of one 'homogeneous' sample among the 16 in the 'heterogeneous' group.

Stage 2. Grouping of 'homogeneous' samples into taxa. In Fig. 2 are shown the means and 5% confidence limits for each 'homogeneous' locality sample from the Cantabrians, for a single character (date of emergence of offsets), arranged in ascending order of means.

Localities 3 and 13 differ significantly from the rest. Within the remaining group, there are significant differences between those at the top and bottom of the sequence, but there is no obvious point at which the group should be divided.

When tests are made of the internal homogeneity of many alternative subgroups formed from locality samples, the variance ratio cannot be regarded as significant whenever it exceeds the corresponding value of F. A larger statistic should be employed instead of F, to take into account the fact that many alternatives are being tested. A number of different methods have been used by various authors, as in Duncan's Multiple Range Test (STEELE, 1961), the S. N. K. Test (SOKAL & ROHLF, 1969), and Tukey's Method of Allowances (TUKEY, 1951). The method adopted here was proposed by GABRIEL (1964) and given the name 'Sums of Squares Simultaneous Test Procedure', or 'STP' for short.

In Gabriel's 'STP', the sums of squares, SS, of a subgroup, is computed from the formula

$$\sum_{p=1}^{N} \frac{\left(\sum_{k=1}^{n_p} C_{i,k} \right)^2}{n_p} - \frac{\left(\sum_{p=1}^{N} \sum_{k=1}^{n_p} C_{i,k} \right)^2}{\sum_{p=1}^{N} n_p}$$

where N is the number of localities in the subgroup, n_p is the number of plants in the pth locality sample of the subgroup, and $C_{i,k}$ the value of the ith character for the kth plant in a locality.

A 'critical' sum of squares, SS_{crit}, is also computed, from the formula

$$(a-1)MS_{within}\ F[0.05,\ a\text{-}1,\ a(g\text{-}1)]$$

where a is the total number of localities in all the subgroups, g is the grand total of plants, MS_{within} is the mean square within samples in the anova of all localities, and F is the variance ratio corresponding to (a-1) and a(g-1) degrees of freedom at a 5% level of significance.

A subgroup is treated as internally homogeneous if

$$SS < SS_{crit}$$

A computer program was written to calculate SS of every subgroup that can be formed from locality samples that are adjacent in the sequence of means. The program also selects that set of subgroups which (a) comprises the smallest number of subgroups that can be formed with all values of SS less than SS_{crit} and (b) has a sum of values of SS lower than any other set of subgroups having the same number of members.

From the data represented in Figure 2 one could form many sets of subgroups that are internally homogeneous; ie. with all subgroups having SS < 140, which is the value of SS_{crit} in this example. When a systematic search was made through all possible arrangements it was found that no arrangements with less than four subgroups had all values of SS < SS_{crit}, and that the arrangement with four subgroups which had the lowest total of SS was SS_1 (0), SS_2 (0), $SS_{3\text{-}11}$ (60), and $SS_{12\text{-}17}$ (95) with total SS of 155. This implied a division of the locality samples into subgroups comprising localities 3; 13; 10-20; and 9-1.

'STP' was carried out for each of the 10 vegetative characters on the 'homogeneous' locality samples from each mountain range in turn. Samples falling within one homogeneous subgroup were treated as having a 'similarity value' of 1 in respect of that character, and samples in different subgroups a 'similarity value' of 0. By summing the 'similarity values' for all characters total values from 0 to 10 might be obtained. A similarity matrix was drawn up in which each sample was compared with all the others from the same mountain range. The results of this comparison, for the Cantabrians, is shown in Fig. 3, in which 16 out of 17 of the 'homogeneous' locality samples are linked by similarity totals of 5 or more and are considered to fall into one taxon (referred to below as Ca_1), whereas one sample, from locality 3, has no similarity total greater than 3, and falls into another taxon (Ca_2).
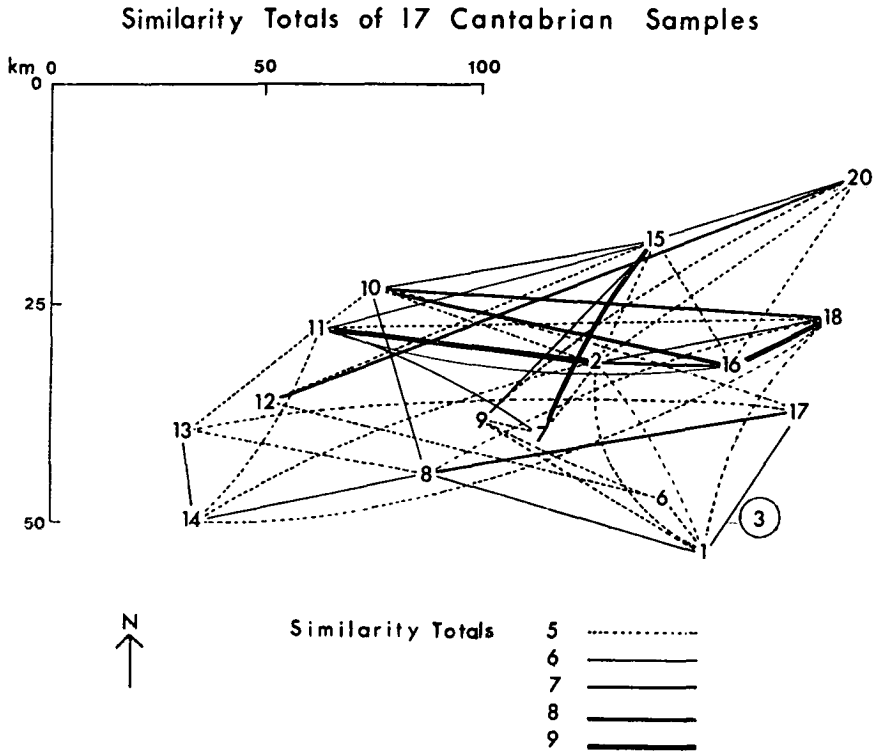
Fig. 3.—Similarity totals of 5 and over, drawn as lines linking locality samples, which are placed as on a map with a N-S scale twice as great as the E-W scale.

Stage 3. Division of 'heterogeneous' samples into constituent taxa. This stage of analysis will be illustrated using data from the Cantabrians. Of the 21 locality samples four had high variance and were designated as 'heterogeneous'. All but one of the low-variance samples (the exception being locality 3) were assigned in stage 2 to taxon Ca_1. Using a computer program 'Extraction', a comparison was made of each plant in the four 'heterogeneous' samples, and also in locality sample 3, with the 5% confidence limits of taxon Ca_1, for each character in turn. Some plants were found to fall outside the confidence limits of Ca_1 for 1, 2, 3 or 4 characters. A suitable criterion for plants to be treated as differing significantly from Ca_1 is that they should differ in respect of at least three characters, since the chance of this happening with a member of Ca_1 itself would be

$$1 - (0.95)^{10} - 10(0.95)^9 - 100(0.95)^8 = 0.019$$

16 members of sample 21 differed from Ca_1 in respect of 3 or more characters. The position of these 16 on the r_1r_2 scale had a unimodal distribution with a variance of only 11.8. Hence, those extracted formed a 'homogeneous' subsample representing a taxon different from Ca_1. Using program 'Extraction', the same procedure was applied to the other four locality samples being compared with Ca_1, with the result that two 'homogeneous' subsamples were formed (from localities 21 and 3). The plants extracted from the other three locality samples formed 'heterogeneous' subsamples.

Having allocated all but a minority of the plants to taxa the variation occurring in 'heterogeneous' locality samples was displayed on scatter diagrams of which the axes or corners were defined by the mean character values of the taxa that had been distinguished. The patterns of variation observed were compatible with some clones being hybrids, and analysis of floral characters, and in particular of the % good pollen, supported this view. Details of this stage of the analysis are given below separately for the Pyrenees and the Cantabrians.

Fisher's Linear Discriminant Analysis (FISHER, 1954) was used as a check on the consistency of the taxa distinguished. Some check was desirable because the allocation of plants to the earlier-distinguished taxa had been made without taking into account the characters of those distinguished later. Once the limits of the taxa had been defined provisionally it became possible to calculate a discriminant function for each plant in respect of each taxon: the plant was then placed in the taxon for which the discriminant function was highest.

Finally, a comparison was made of samples from different mountain ranges, for all localities that contained plants closely related to *S. tectorum*. A similarity matrix was derived, after using 'STP'. The similarity totals are displayed graphically in Fig. 4, which shows that discontinuities in the pattern of variation occur between regions, justifying the treatment of plants from each mountain range as separate taxa.

RESULTS

The Pyrenees.

S. tectorum, S. montanum and *S. arachnoideum.* 1171 plants were collected from 21 localities, at the places shown in Fig. 1. After statistical analysis it was found that only three distinct, non-hybrid, taxa were represented, corresponding to the Linnaean species *S. tectorum* (P_1), *S. montanum*
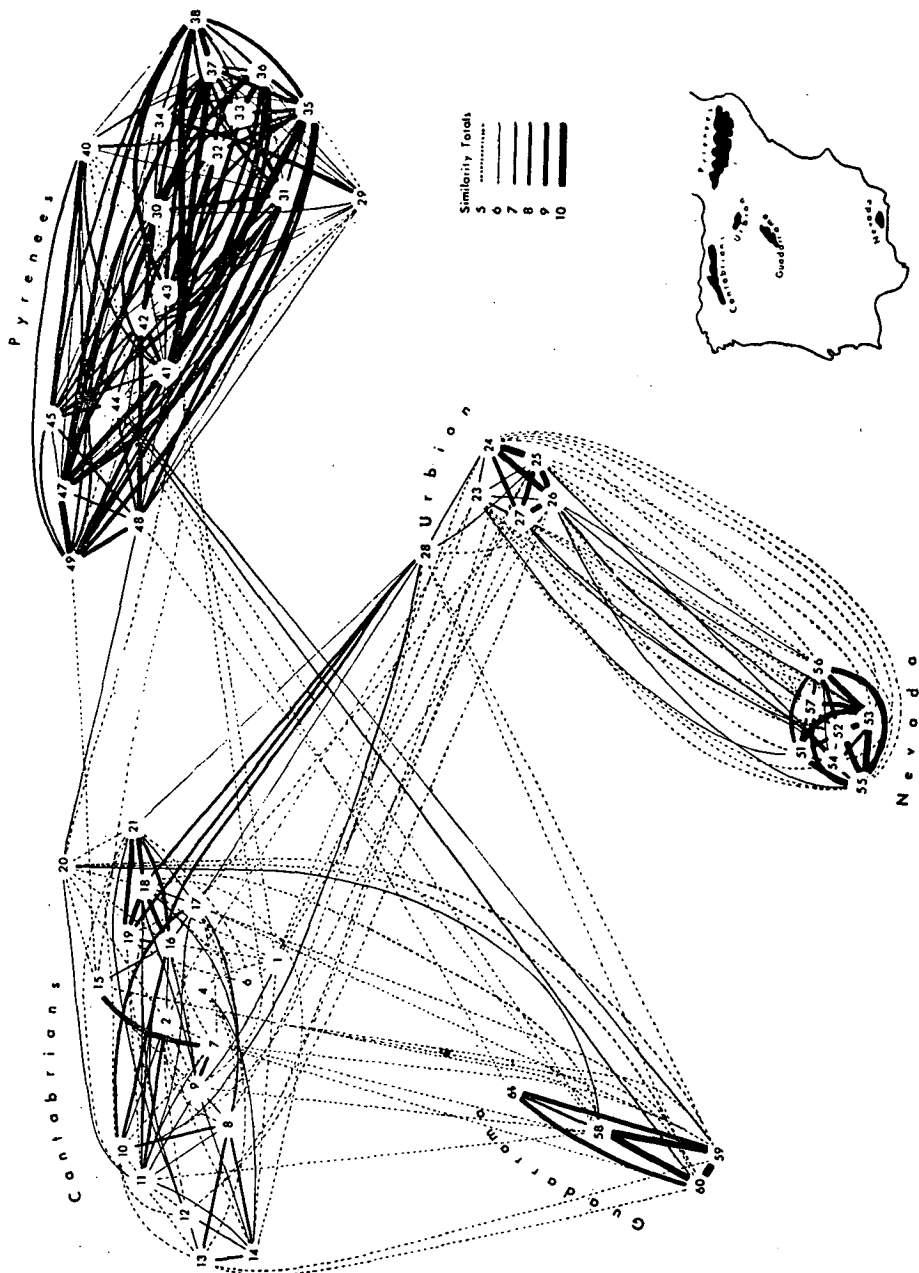
Fig. 4.—Diagram of similarity totals of 5 and over, for 55 samples containing *S. tecto-rum, S. cantabricum* and *S. nevadense*. Within each mountain range the localities have been placed in their relative geographical positions (but with the N-S scale exaggerated twofold). The distances between mountain ranges have been contracted. The true positions of the mountains are shown in the inset map of Spain.
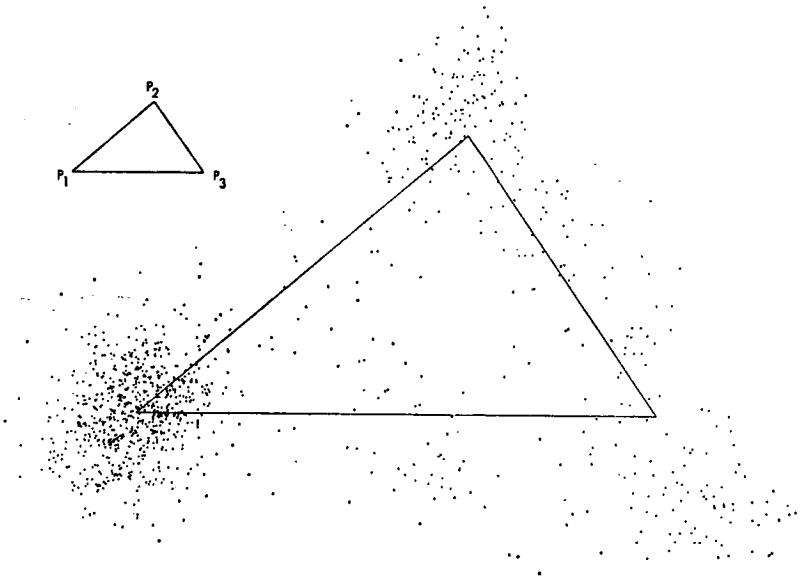
Fig. 5.—A projection of a 3-dimensional scatter diagram onto two dimensions, showing clusters of clones round the mean character sets for *S. tectorum* (P_1), *S. montanum* (P_2) and *S. arachnoideum* (P_3), with numerous intermediate clones.

(P_2) and *S. arachnoideum* (P_3). These three species are represented by the symbols P_1, P_2 and P_3 respectively in the triangular scatter diagram in Fig. 5. The corners of the triangle represent the mean values for 10 vegetative characters for each species, and the lengths of the sides are proportional to the taxonomic distances ($D_{P1,\ P2}$), etc., between mean character sets. The dots representing individuals would, in a 3-dimensional model, lie above the triangle at points having distances from the corners in proportion to the taxonomic distances between the individuals and the mean characters for the species. In Fig. 5, however, the 3-dimensional configuration has been projected onto the plane of the triangle.

It is clear from Fig. 5 that *S. tectorum* (P_1) was more abundant at the localities sampled than were the other species: it was found at 19 localities (in 10 of which it was the only species present), whereas *S. montanum* and *S. arachnoideum* each occurred at 8 places (in all of which there was more than one species). Fig. 5 shows many dots representing hybrid plants, intermediate between the three corner clusters. At the 11 localities where more than a single species grew, hybrids were found at all but two. Various different degrees of crossing were detectable at different localities, and some
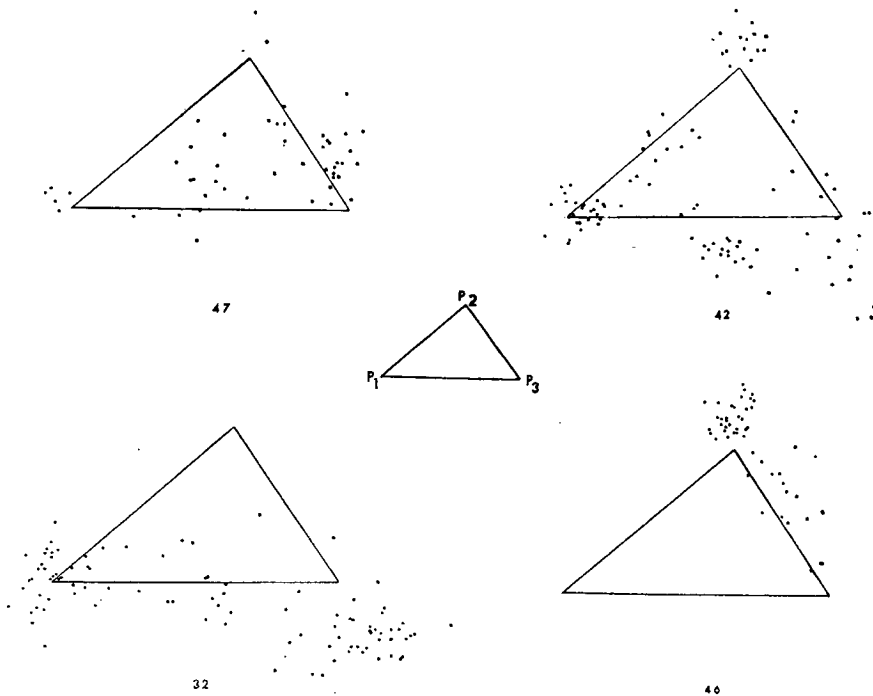
Fig. 6.—Scatter diagrams for four Pyrenean localities. The corners of the triangles represent mean character sets of *S. tectorum* (P₁), *S. montanum* (P₂) and *S. arachnoideum* (P₃). These locality samples illustrate formation of F₁ hybrids, and introgression, between two or three species.

examples of the patterns of hybridisation found are shown in the diagrams for four localities in Fig. 6.

At locality 32 (at Porté) *S. tectorum* and *S. arachnoideum* grew together; there were also many bybrids, most of which formed an intermediate cluster suggestive of formation of F₁'s with little backcrossing. A similar pattern, involving *S. arachnoideum* and *S. montanum* was found at locality 39 (Canigou), not illustrated here. At 50 (Col d'Aubisque, not illustrated), the sampled plants ranged from pure *S. arachnoideum* to pure *S. montanum*, but the centre of the cluster of the latter is shifted down the side of triangle towards the former, suggesting introgression of *S. arachnoideum* characters into *S. montanum*. At 46 (Cap du Long), pure *S. montanum* is present together with plants varying in the direction of *S. arachnoideum*, but pure *S. arachnoideum* is absent. This pattern suggests introgression between the two species with subsequent elimination of pure *S. arachnoi-*
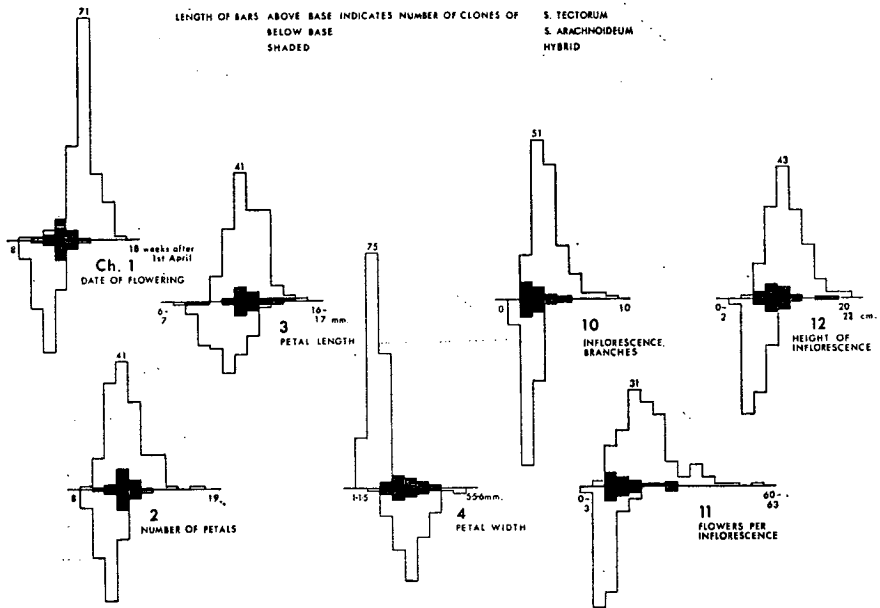
Fig. 7.—The Figure shows that clones of P₄ (hybrids) are intermediate between *S. tectorum* and *S. arachnoideum* in 6 out of 7 qualitative floral characters.

deum. At 42 (Bonaigua), all three species occur, as well as each primary hybrid. The hybrids, on the whole, form fairly distinct intermediate clusters, suggesting little back-crossing. At 47 (Cap du Long: lower site), all three species were present, with introgression between *S. arachnoideum* and *S. montanum*, and further introgression, giving triple hybrids, between their hybrids and *S. tectorum*.

For those plants which, on the basis of statistical analysis of vegetative characters, were assumed to be hybrids between *S. tectorum* and *S. arachnoideum*, measurements were also made in floral characters. A comparison between the two species and the hybrids, for seven floral characters, is shown in Fig. 7: it is based on all the plants of these taxa collected in the Pyrenees which flowered in cultivation in 1971-1972 namely 24 hybrids, 138 *S. tectorum* and 84 *S. arachnoideum*. The hybrids were intermediate between the parental species in 6 out of 7 floral characters.

In experimental crosses between the species occurring in the Pyrenees it was found that the % seed set in crosses was not significantly lower

than after pollination between clones of the same species. When the pollen of presumed hybrids between *S. tectorum* and *S. arachnoideum* was compared with that of members of the parental species it was found that only 13% of the hybrids had more than 95% good pollen, and that the average good pollen of hybrids was 50%. Of the *S. tectorum* and *S. arachnoideum* clones, 80% and 81% had more than 95% good pollen.

S. andreanum Wale. In most characters *S. andreanum* falls within the description of *S. tectorum* in PRAEGER (1932). *S. andreanum* differs in its smaller inflorescence (11 cm. v. 20 - 30 cm. tall) and smaller rosettes (1.5 - 3.0 cm. v. 3 - 20 cm. diameter), but its dimensions agree well with those that I found typical of *S. tectorum* throughout the Pyrenees. WALE's plant has very short offsets, whereas, according to PRAEGER (l. c.) *S. tectorum* has offsets about 4 cm. long. Although offsets were not measured in my sample of *S. tectorum*, their lengths were seen to vary from under 0.5 cm. upwards. Similarly, the *S. andreanum* character of very short, stout, strongly-curved cilia represents merely one extreme of the variation to be found in *S. tectorum*. *S. andreanum* is described as having yellow anthers, whereas in *S. tectorum*, according to PRAEGER (l. c), they are orange-red. Among 138 clones of *S. tectorum* in my sample that flowered, 91 had pink or red anthers, 28 buff-pink, 13 buff, and 6 yellow. Thus in this respect also *S. andreanum* represents one end of the range of variation found in *S. tectorum*. Finally, *S. andreanum* is stated to have the younger rosette leaves tightly adpressed in a conical bud: this attribute was noted to varying degrees in some of the plants from many localities in the Pyrenees. In short, plants showing some of ·the diagnostic characters of *S. andreanum* are to be found in many places growing alongside typical plants of *S. tectorum*. At locality 29, in the Sierra del Cadí, a few of the clones were like the description of *S. andreanum* in some particulars, but most were normal examples of *S. tectorum*. After growing the clone from which the description of *S. andreanum* was drawn up, and seeing it in flower, I consider that it falls inside the limits of variation of *S. tectorum*, and does not deserve even varietal rank.

The Cantabrians.

Sempervivums were collected at 21 localities, between Iján in the East and Puerto de Leitariegos in the West. I failed to find them further west, despite searching in five apparently-suitable places in the Sierra de Ancares, Candanosa and Piedras Apenadas. MERINO (1905), says that all the Sempervivums he had seen appeared to be escapes: he never saw any far from villages.

S. arachnoideum. At four localities the samples were 'heterogeneous'. After statistical analysis it was found that at three localities (3: Peña Espiguete; 5: Peña Prieta; and 19: Espinama), some clones did not differ significantly from Pyrenean examples of *S. arachnoideum.* Of four of these clones which flowered in cultivation three had 50-70% good pollen and one had 90-100% good. The % good pollen was less than for *S. arachnoideum* in the Pyrenees, from where out of 84 plants examined 80% had 90-100% good pollen. Whether these plants are pure *S. arachnoideum* will be clearer after chromosome counts, now being made by B. J. M. Zonneveld, have been completed. At 20 localities there were some plants corresponding fairly closely with the description of *S. cantabricum* Huber. At five localities there were plants intermediate between *S. cantabricum* and *S. arachnoideum*: these are presumed to be hybrids, and are discussed further below.

S. cantabricum. At the 17 localities where neither *S. arachnoideum* nor bybrids were present, the samples appeared to be 'homogeneous', and had low variance. These plants corresponded to *S. cantabricum* Huber, described by HUBER (1934) from a cultivated plant collected in 1910 in the Picos de Europa, except in three particulars which are noted in the amended diagnosis below. There were, however, fairly large differences between some of the localities sampled. This is displayed in Fig. 4, in which the similarity totals found between the Cantabrian samples were, on the whole, lower than those between samples of one taxon in other mountain ranges. Plants from localities at the eastern end of the Cantabrians have low similarity with those from the western end. There is, though, no apparent dividing line which can be used to separate the locality samples into clear-cut groups, so that it seems best to treat the plants from all 17 localities as falling within one variable species, *S. cantabricum.* The most aberrant sample was that collected on a smooth rock dome to the South of the road from Riaño to Puerto de Tarna, ½ km. NW of La Una: these plants have remained, in cultivation, at least twice the size of those from any other locality.

Hybrids. S. giuseppii. It was clear that plants intermediate between *S. cantabricum* and *S. arachnoideum* occurred with both parents at localities 5 and 19; that there were intermediates (hybrids) and *S. arachnoideum* (without *S. cantabricum*) at locality 3, and that at locality 21 (Iján) there were intermediates (hybrids) and *S. cantabricum* (without *S. arachnoideum*). The patterns of variation at each of these localities were compatible with most of the intermediates being F₁ hybrids, with some evidence for introgression towards *S. arachnoideum* at 5 and towards *S. cantabricum* at 19.

The % good pollen of the presumed hybrids was counted for 37 clones

which flowered in cultivation in 1970-1971: 34 clones had less than 50% good pollen, and only one had over 90% good.

Of 87 clones of *S. cantabricum*, 60 had more than 90% good pollen. Only four clones from the small sample of *S. arachnoideum* flowered: three had 50-70% good pollen and one had over 90% good.

The intermediate character and pollen sterility of some of the plants from localities 3, 5, 19 and 21 suggests that they are hybrids. They closely resemble the description of *S. giuseppii* given by WALE (1941), based on a plant collected at Peña Espiguete. This species, recognised by FAVARGER & ZÉSINGER (1964), should be regarded as a hybrid between *S. arachnoideum* and *S. cantabricum*.

Picos de Urbión.

This name will be used to refer to the mountain block which includes the Sierras de San Lorenzo, La Demanda, San Millán, Neila, Cebollera, Piqueras and Urbión. Sempervivums were collected at 7 localities.

With the exception of a single plant, forming part of a sample of 51 plants from a cliff 200 m. from the Monastery of Valvanera, all the locality samples from the Picos de Urbión were 'homogeneous'. The aberrant plant from Valvanera had glabrous leaves and other vegetative characters similar to *S. tectorum* var. *tectorum* (ie. the cultivated, roof-top variety, common through much of Europe). As this plant has not flowered I do not know whether it would exhibit the intermediates between carpels and stamens that occur in that variety, but I have tentatively assumed that the plant was an escape from cultivation.

S. vicentei (*). The other 340 plants collected in the Picos de Urbión had pubescent leaf surfaces. In this they all differed from the description of *S. vicentei* Pau, of which the type locality is the summit of Pico de Urbión. The brief descripton of it (PAU, 1906) differs in no particulars from the characters I have found common in *S. tectorum* in the Pyrenees. One of my localities was 100 m. from the summit of Pico de Urbión, and must have been close to the spot at which PAU's plant was collected. It has to be concluded either that PAU's plant was an anomalous specimen or that his

(*) This species, described by WALE (1941), is recognised by FAVARGER & ZÉSIGER (1964). In the original account, it is said to have been found (by Mrs. Andre Giuseppi) in the 'Sierra Cani', which, in a letter from Dr. P. L. Giuseppi to Dr. R. S. Wale (in the Kew Library), is given a latitude of 42°40' N. 'Sierra Cani' is not listed in gazeteers of Spain: it may be a misreading of 'Sierra del Cadí', and this view is taken in Flora Europaea, but a double error is implied since the Sierra del Cadi is 40' south of the latitude given in Giuseppi's letter.

description is in error as regards the pubescence of the leaves. These probabilities, together with the scantiness of PAU's description, suggest that the name *S. vicentei* is better disregarded. A descripition is drawn up below under the name *S. cantabricum* subsp. *urbionense*.

Sierras de Guadarrama and Gredos.

All plants collected at four localities between Peña Lobo in the Sierra de Ayllón and Peñalara in the Guadarrama, were similar in characters to *S. cantabricum,* but differed sufficiently to be treated as a subspecies, described below under the name *S. cantabricum* subsp. *guadarramense.*

Sempervivums also occur in the Sierra de Gredos, although I failed to find them during a short visit. A plant sent to me by Prof. Favarger, collected near Laguna Grande, is similar to the Guadarrama plants. There is a herbarium specimen collected by Rivas Mateos from the Gredos without precise locality (MAF) which resembles *S. arachnoideum*.

Sierra Nevada.

I made collections at seven points in the Sierra Nevada between Chulla in the East and Caballo in the West. A plant similar to those I found in the Sierra Nevada has been sent to me by B. E. Smythies, collected by him at the Collado de Santa Bárbara in the Sierra de Baza. Only one taxon was present in the seven localities, corresponding to *S. nevadense* Wale, except that WALE's plant had glabrous surfaces on the rosette leaves, whereas 90% of the clones in my samples of 345 plants had pubescent leaves. WALE (1941) was aware that plants from this area can be pubescent, for in his notes in the Kew Library there is an (unpublished) description of *S. nevadense* var. *hirtellum* with pubescent leaves.

IDENTIFICATION

S. tectorum, S. cantabricum and *S. nevadense* are a closely allied group of species. Since these species (and the separate subspecies of *S. cantabricum*) each occupy different mountain ranges, there is no difficulty in identification if the locality of origin is known. To determine how probable correct identification of individual clones would be, if the places of collection were not known, functions were calculated by Fisher's linear discriminant analysis, based on 10 vegetative characters for the entire sample of each taxon. This

permitted correct identification of 95% of the sample of *S. tectorum* (5% being misidentified as *S. cantabricum*), but only 77% correct identification of *S. nevadense* (the remainder being misidentified as either *S. cantabricum* or as hybrids of *S. arachnoideum*). Correct identification rates for the subspecies of *S. cantabricum* were 87% for subsp. *cantabricum*, 94% for subsp. *guadarramense* and 89% for subsp. *urbionense*, misidentification being mainly with the other subspecies. If instead of single clones a sample of five or more clones were available from the same locality, then the chance of misidentification of any of the taxa would be small.

In the Pyrenees and the Cantabrians the probability that hybrids will be encountered should be borne in mind when making identifications.

Identification Key (excluding hybrids)

(Mean values of measurements are given, with 5% confidence Limits in brackets. All measurements were made in April, on plants cultivated in England).

1. Long cilia at leaf apices (0.5 -) 2.5 (- 11.0) mm.; petals bright pink. **1. arachoideum.**
1. Apical cilia at leaf apices (0.1 -) 0.2 (- 0.8) mm.; petals whitish, pale or medium pink, or purplish pink. **2**

2. Hairs on leaf surfaces glandular; leaves viscid; petals purplish pink.
     2. montanum.
2. Hairs on leaf surfaces not, or only occasionally, glandular; leaves not viscid; petals pale or medium pink. **3**

3. Leaf hairs (excluding marginal cilia) usually absent; angle of leaf apex acute: (10° -) 31° (- 50°); rosette leaves not incurved, except during drought. **3. tectorum.**
3. Leaf hairs (excluding marginal cilia) usually present; leaf apex subacute: (22° -) 50° (- 75°); rosette leaves often incurved. **4**

4. Petals medium pink, usually without darker flecks; inflorescence (3 -) 7 (- 10) cm. long; apical cilia usually numerous. **5 nevadense.**
4. Petals pale pink or whitish, usually with darker flecks; inflorescence (7 -) 11 (- 15) cm. long, number of apical cilia usually scanty. **4. cantabricum.**

5. Apical colour patch on rosette leaves short or absent (0 - 1,6 mm.); rosette leaves usually strongly incurved. γ cantabricum subsp. **urbionense**
5. Apical colour patch usually long (0 - 5 mm.); usually slightly incurved. **6**

6. Leaf pubescence usually dense; cilia at leaf abundant.
     α cantabricum subsp. **cantabricum**
6. Leaf pubescence usually lax; cilia at leaf apex scanty.
     β cantabricum subsp. **guadarramense**

1. **S. arachnoideum** L., *Sp. Pl.* 465 (1753).

Widespread in the Pyrenees and occurs in a few localities in the Cantabrians.

Hybrids with *S. montanum* and *S. tectorum* occur at several localities in the Cantabrians.

S. x giuseppii Wale, *Quart. Bull. Alp. Gard. Soc.* 9: 115 (1941), hybrid of *S. arachnoideum* and *S. cantabricum* occurs in several localities in the Cantabrians. Its pollen is partly sterile.

2. **S. montanum** L., *Sp. Pl.* 465 (1753)

Widespread in the Pyrenees.

Hybrids with *S. arachnoideum* and *S. tectorum* are frequent.

3. **S. tectorum** L., *Sp. Pl.* 464 (1753).
   S. andreanum Wale, *Quart. Bull. Alp. Gard. Soc.* 9: 116 (1941)

This species is widespread in the Pyrenees and also occurs at several localities in Catalonia.

4. **S. cantabricum** J. A. Huber, *Feddes Repert.* 33: 364 (1934).

α   subsp. **cantabricum.**

Petals pale pink or whitish, with darker streaks, similar to *S. tectorum* L.; filaments usually pubescent; average diameter of mature rosettes 2.4 cm.

β   subsp. **guadarramense** M. C. Smith, **subsp. nov.**

Ab subsp. *cantabricum* folia rosulatum pubescentia et minores incurvata, apices foliorum ciliis paucis, filamenta saepe glabra, striae petalorum saepe deficientes differt.

Typus.   Puerto de Navafría, Segovia, 2.100 m. s. m., 19.IX.1970, *M. C. Smith*; in cultivation at Botanic Garden, University of Bristol.

Differs from subsp. *cantabricum* in sparser pubescence on surface rosette, leaves less incurved, fewer cilia at leaf apices, filaments often glabrous and streaks of dark colour on petals often absent.

γ subsp. **urbionensis** M. C. Smith, **subsp. nov.**
S. vicentei Pau, *Bull. Acad. Geogr. Bot.* 16: 76 (1906).

Ab subsp. *cantabricum* apices foliorum rosularum plerumque non brune-olae, foliis rosularum plus incurvata, diameter rosularum maturarum brevior (1.9 vel 2.4 cm.) filamenta plerumque glabra differt.

Typus.   Pico de Urbión, Soria, 2.300 m. s. m., 20.IX.1969, *M. C. Smith.* In cultivation at Botanic Garden, University of Bristol.

It differs from subsp. *cantabricum* in usually lacking brownish colour near apices of rosette leaves, rosette leaves more incurved, average diameter of mature rosettes smaller (1.9 to 2.4 cm.) and filaments usually glabrous.

5.   S. nevadense Wale, *Quart. Bull. Alp. Gard. Soc.* 9: 109 (1941).

It occurs in the Sierra Nevada and the Sierra de Baza. It differs from *S. tectorum* and *S. cantabricum* in its smaller size, earlier production of offsets, longer marginal and apical cilia, a denser cluster of cilia at the leaf apex, fewer and broader petals which are darker pink without streaks of colour, and shorter inflorescences with fewer branches. In all these respects *S. nevadense* differs in the direction of *S. arachnoideum*. I found a few plants with tufts of long cilia at the leaf apices as in *S. arachnoideum*, though less pronounced. I found no evidence that *S. nevadense* produces sterile pollen, but from its characters and from its high chromosome number (2n = 108, ZÉSIGER, 1961) I suggest it may have arisen by stabilisation through polyploidy of hybrids between *S. arachnoideum* and plants resembling *S. cantabricum* or *S. tectorum*.

COLLECTION LOCALITIES

Cantabrians.
 1. León, Montevieja, 1.600 m. s. m., 8.IX.1969, *Smith.*
 2. León, Puerto de Tarna, 1.500 m. s. m., 8.IX.1969, *Smith.*
 3. Palencia, Peña Espiguete, 2.300 m. s. m., 9.IX.1969, *Smith.*
 4. León, La Uña, 1.200 m. s. m., 8.IX.1969, *Smith.*
 5. Santander, Peña Prieta, 2.300 m. s. m., 10.IX.1969, *Smith.*
 6. León, Riaño, 1.300 m. s. m., 10.IX.1969, *Smith.*
 7. León, Puerto de Vegarada, 1.600 m. s. m., 11.IX.1969, *Smith.*
 8. León, Puerto de Pajares, 1.400 m. s. m., 11.IX.1969, *Smith.*
 9. León, Puerto de Piedrafita, 1.700 m. s. m., 12.IX.1969, *Smith.*
10. Oviedo, Puerto de Cienfuegos, 1.200 m. s. m., 13.IX.1969, *Smith.*
11. Oviedo, Puerto Ventana, 1.500 m. s. m., 13.IX.1969, *Smith.*

12. León, Puerto de Somiedo, 1.600 m. s. m., 14.IX.1969, *Smith*.
13. Oviedo, Puerto de Leitariegos, 1.800 m. s. m., 14.IX.1969, *Smith*.
14. León, Cuevas de Sil, 1.000 m. s. m., 15.IX.1969, *Smith*.
15. Oviedo, Lago Enol, 1.200 m. s. m., 15.IX.1969, *Smith*.
16. León, Puerto de Pandetrave, 1.500 m. s. m., 16.IX.1969, *Smith*.
17. Oviedo, Puerto de San Glorio, 1.500 m. s. m., 16.IX.1969, *Smith*.
18. Palencia, Puerto de Piedrasluengas, 1.500 m. s. m., 16.IX.1969, *Smith*.
19. Santander, Refugio de Aliva, 1.900 m. s. m., 17.IX.1969, *Smith*.
20. Santander, Ciceras, 1.200 m. s. m., 17.IX.1969, *Smith*.
21. Santander, Iján, 2.000 m. s. m., 18.IX.1969, *Smith*.

Picos de Urbión.
22. Logroño, Valvanera, 1.000 m. s. m., 19.IX.1969, *Smith*.
23. Logroño, Viniegra, 1.500 m. s. m., 19.IX.1969, *Smith*.
24. Soria, Puerto de Piqueras, 1.700 m. s. m., 19.IX.1969, *Smith*.
25. Logroño, La Ermita, Villoslada, 1.800 m. s. m., 20.IX.1969, *Smith*.
26. Soria, Laguna Negra, Urbión, 1.800 m. s. m., 20.IX.1969, *Smith*.
27. Soria, Pico de Urbión, 2.200 m. s. m., 20.IX.1969, *Smith*.
28. Soria, Pico de Gatón, 1.900 m. s. m., 21.IX.1969, *Smith*.

Pyrenees.
29. Lérida, 5 km. S. of Ges, 1.500 m. s. m., 22.IX.1969, *Smith*.
30. Andorra, Serrat, 2.000 m. s. m., 23.IX.1969, *Smith*.
31. Andorra, Soldeu, 1.500 m. s. m., 23.IX.1969, *Smith*.
32. Pyrenées Orientales, Porté, 1.600 m. s. m., 23.IX.1969, *Smith*.
33. Pyrenées Orientales, Targasonne, 1.500 m. s. m., 24.IX.1969, *Smith*.
34. Pyrenées Orientales, Lac des Boillouses, 2.100 m. s. m., 24.IX.1969, *Smith*.
35. Gerona, Tosa, 1.300 m. s. m., 25.IX.1969, *Smith*.
36. Pyrenées Orientales, La Perche, 1.500 m. s. m., 25.IX.1969, *Smith*.
37. Pyrenées Orientales, Fontpedrouse, 900 m. s. m., 25.IX.1969, *Smith*.
38. Pyrenées Orientales, Canigou (route forestière), 1.100 m s. m., 26.IX.1969, *Smith*.
39. Pyrenées Orientales, Pic Joffre, Canigou, 2.400 m. s. m., 26.IX.1969, *Smith*.
40. Ariège, Merens les Vals, 1.000 m. s. m., 27.IX.1969, *Smith*.
41. Lérida, Viella, 900 m. s. m., 27.IX.1969, *Smith*.
42. Lérida, Puerto de Bonaigua, 2.000 m. s. m., 28.IX.1969, *Smith*.
43. Lérida, Sorpé, 1.500 m. s. m., 28.IX.1969, *Smith*.
44. Haute Garonne, Superbagnères, 1.700 m. s. m., 28.IX.1969, *Smith*.
45. Haute Garonne, Col de Peyresourde, 1.500 m. s. m., 29.IX.1969, *Smith*.
46. Hautes Pyrenées, Lac du Cap de Long, 2.200 m. s. m., 29.IX.1969, *Smith*.
47. Hautes Pyrenées, Lac d'Oredon, 1.500 m. s. m., 29.IX.1969, *Smith*.
48. Hautes Pyrenées, Gavarnie, 1.500 m. s. m., 30.IX.1969, *Smith*.
49. Hautes Pyrenées, Pont d'Espagne, 1.600 m. s. m., 30.IX.1969, *Smith*.
50. Basses Pyrenées, Col d'Aubisque, 1.600 m. s. m., 1.X.1969, *Smith*.

Sierra Nevada.
51. Granada, Peñones de San Francisco, 2.500 m. s. m., 12.IX.1970, *Smith*.
52. Granada, Laguna de la Caldera, Mulhacén, 3.200 m. s. m., 12.IX.1970, *Smith*.
53. Granada, 3 km. S. E. of Pico de Mulhacén, 2.800 m. s. m., 12.IX.1970, *Smith*.
54. Granada, Laguna de las Yeguas, Veleta, 3.000 m. s. m., 13.IX.1970, *Smith*.

55. Granada, Laguna del Caballo, 2.700 m. s. m., 13.IX.1970, *Smith*.
56. Granada, Puerto de la Ragua, 2.300 m. s. m., 14.IX.1970, *Smith.*
57. Granada, Cerro Pellado, Trévelez, 2.600 m. s. m., 15.IX.1970, *Smith.*

Cordillera Central.
58. Segovia, Puerto de Navafría, 2.100 m. s. m., 19.IX.1970, *Smith.*
59: Madrid, Puerto de la Morcuera, 2.000 m. s. m., 20.IX.1970, *Smith.*
60. Madrid, Peñalara, 2.200 m. s. m., 22.IX.1970, *Smith.*
61. Segovia, Lobo, Sierra de Ayllón, 2.100 m. s. m., 22.IX.1970, *Smith.*

BIBLIOGRAPHY

ANDERSON, E. (1949) *Introgressive Hibridisation.* London & New York.

FAVARGER, C. & F. ZÉSIGER (1964) *Sepervivum,* in T. G. TUTIN & al. (eds.) *Flora Europaea* 1: 352-356. Cambridge.

FISHER, R. A. (1954) *Statistical methods for research workers,* ed. 12. Edinburgh.

GABRIEL, K. R. (1964) A procedure for testing the homogeneity of all sets of means in analysis of variance. *Biometrics* 20: 459-477.

HUBER, J. A. (1934) Sempervivum cantabricum. *Feddes Repert.* 33: 364.

JORDAN, A. & P. FOURREAU (1866) *Breviarum plantarum novarum* 1: 28-47.

LAMOTTE, M. (1864) *Etudes sur le genre Sempervivum* L. Clermont-Ferrand.

MERINO, B. (1905) *Flora descriptiva e ilustrada de Galicia* 1. Santiago de Compostela.

PAU, C. (1906) Sempervivum vicentei. *Bull. Acad. Geogr. Bot.* 16: 76.

PRAEGER, R. L. (1932) An account of the Sempervivum group. *Royal Hort. Soc. (London).*

ROUY, G. & E. G. CAMUS (1901) *Flore de France* 7. París.

SOKAL, R. R. & F. J. ROHLF (1969) *Biometry.* San Francisco.

STEEL, R. G. D. (1961) Some rank sum multiple comparison tests. *Biometrika* 17: 539-552.

TUKEY, J. W. (1951) Quick and dirty methods in statistics, part. II. *Proc. 5th Ann. Conv. Amer. Soc. Qual. Contr.*: 189-197.

WALE, R. S. (1941) Some new Spanish Semperviva. *Quart. Bull. Alp. Garden Soc.* 9: 109-119.

WILLKOMM, M. & J. LANGE (1874) *Prodromus florae Hispanicae* 3. Stuttgart.

ZÉSIGER, F. (1961) Recherches cytotaxinomiques sur les Joubarbes *Ber. Schweiz. Bot. Ges.* 71: 113-117.