ALEXANDER

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EXPERIMENTAL TAXONOMY IN SOME ANNUAL SPECIES OF *SENECIO* FROM THE MEDITERRANEAN AREA

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DECLARATION

The composition of this thesis and the research reported in it, unless otherwise attributed, are declared to be the work of the undersigned candidate.

[redacted]

'Why botany, a potentially fascinating subject ..... should have been from the beginning reduced to a dull taxonomy, an endless Latin dirge, in which progress is measured more by the number of corpses catalogued than by the numbers of blossoms cherished, is perhaps the greatest mystery in the study of plant life'.

Tompkins, P. & Bird, C. (1973) The Secret Life of Plants

Taxonomy ..... is an essential foundation for the understanding of plant group relationships and evolution. Some of the data may seem dull to gather, analyze, and read about, but in their relation to evolutionary thought they furnish character and plot to one of the most exciting and elegant stories ever told.

Galston, A.W. (1974), reviewing Tompkins and Bird.

ACKNOWLEDGEMENTS

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ABSTRACT

Problems have long been encountered in identifying many of the annual and related perennial species of Senecio L. comprising the Sections Obaejaceae DC., Obaejacoideae DC. and Jacobaea (Cass.) Dumort. from the Mediterranean area. The formidable synonymy in the group indicates the difficulties experienced in setting satisfactory species limits.

The research reported in this thesis falls into two main sections. The first part is concerned with a formal and descriptive approach. Details of the taxonomic history of the group are given and the taxonomic value of characters from morphological, geographical and ecological studies is discussed. The range of form found in various organs is described. Among the species which are taxonomically difficult, floral morphology is very uniform and emphasis has often been placed on vegetative characters, which are shown to be very variable in several species. Morphological studies were made from herbarium and living specimens. Sixty-four figures including maps and tables are included.

Cultivated accessions from S. Europe, N. Africa and S.W. Asia were used for the experimental work which is reported in the second part of the thesis. Somatic chromosome numbers were counted for all accessions cultivated, four counts being made for taxa whose chromosome numbers have not been previously recorded.

Nine accessions were used in experiments to investigate phenotypic plasticity, which showed that the morphology of some species is very susceptible to environmental modification. The experimental approach was confined largely to breeding experiments which involved determining the breeding systems of the plants used, and performing a series of intra- and inter-specific crosses. Difficulties in emasculating and isolating experimental material are discussed and methods of overcoming them described. Correlation was found between breeding system, ray-length and ploidy-level. Outbreeders tend to have long rays and be diploid, whereas inbreeders are either rayless or shortrayed and tetraploid or hexaploid. About 140 crosses were made. The resulting seed was sown and a study made of the morphology and pollen fertility of the viable hybrids. The interfertility of the taxa investigated is discussed, bearing in mind the rather small sample involved. In general interspecific fertility is high, even between morphologically dissimilar species.

In the final section of the thesis a formal taxonomic treatment is given which includes species which are peripheral, geographically or morphologically, to the group investigated. This is preceded by discussions on the conflict between the biological and morphological species concepts, and on the species concept adopted in this work. It is concluded that binomials should be reserved for morphological entities which are recognisable in the field or as herbarium specimens. A key is provided to 27 species followed by formal descriptions and diagnoses. The new taxa *S. riffensis* and *S. leucanthemifolius* var. *casablancensis* are described and several infra-specific combinations are made. The neglected names *S. glaucus* L. and *S. trilobus* L. are resurrected. In conclusion some evolutionary speculations are presented, the evidence suggesting that the population structure of the taxonomically difficult species is conducive to rapid evolution.

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PART I

INTRODUCTION AND DESCRIPTIVE WORK

CHAPTER 1. INTRODUCTION AND PROCEDURE

1.1 RATIONALE AND AIMS

This research began as a short formal taxonomic investigation undertaken as part of a course in plant taxonomy formerly run jointly by the University and the Royal Botanic Garden, Edinburgh. A revision was attempted of some annual species of Senecio L., (Compositae), native to S. Europe, N. Africa and S.W. Asia. The wide range of morphological variation in many species and the difficulty in deciding upon species limits made it very difficult to construct a workable classification, and it was felt that data derived from experimental techniques might be useful.

No comprehensive treatment of Senecio as a whole has been attempted since that of de Candolle (1838) and the sectional limits of the genus, apart from being illegitimate under Article 5 in the International Code of Botanical Nomenclature (see 2.2), are very unsatisfactory in geographical as well as morphological terms. The species considered in this thesis come from three of de Candolle's Sections, Obaejacae, Obaejacoideae and Jacobaea, which are comprised of annuals, biennials and short-lived perennials, most of which show some form of pinnate division of the leaf.

Annual species of Senecio, from the areas mentioned above, have not received much attention from experimental taxonomists. Walters (1964) writes "The species of two Sections (Obaejacae and Obejacoideae) make excellent experimental material, and it is obvious that the taxonomic problems can usefully be tackled by cultivation and crossing experiments".

Some experimental hybridisation has been done using British species of Senecio. Gibbs (1971) crossed the tetraploids S. viscosus and S. vulgaris, and Walters (in litt.) reports spontaneous hybridisation in the greenhouse between S. squalidus and S. rodriguezii from the Balearic Islands. However, no experimental work involving the Mediterranean species has previously been attempted.

1.2 PROCEDURE

A project was planned involving both formal and experimental work. Herbarium material was borrowed from Israel, Italy, France and Morocco as well as Britain. Requests for seed were sent to important areas, and further material and seed were collected in the field. A disadvantage of having to plan an experimental programme before a detailed study has been made of herbarium material is that the significance of some taxa may not be appreciated until it is too late to obtain seed of them.

The experimental work consisted of four main approaches; determination of breeding systems, hybridisation, cultivation of accessions in standard conditions to assess morphological differences, and experiments on phenotypic plasticity. In addition, a brief examination of leaf flavonoid patterns was made using paper chromatography. This was soon abandoned as very few interspecific differences were found.

The non-experimental work involved the usual procedures for the study of herbarium material; supplemented by scanning electron microscope studies of pollen grains and leaf surfaces,which are described in the experimental part of the thesis.

Finally, an attempt was made to combine the data resulting from the different approaches to produce a formal taxonomic treatment of the species concerned. This raised many problems involving the conflict between data from morphological and experimental work.

1.3 EXPERIMENTAL CATEGORIES

From the time that experimental techniques became common in taxonomy, the number of terms used by taxonomists to describe the groups of plants they were working with has increased rapidly. Groups defined in terms of reproductive isolation as revealed by experimental work could not share the same terminology as those defined by the morpho-geographical type-concept of formal taxonomy. When the research reported in this thesis was started, it was planned to use the 'deme' terminology of Gilmour and Gregor (1939) to describe the different groups of plants investigated. The essence of this system lies in the fact that the terms used, e.g. genodeme, phenodeme, carry no implications other than those conveyed by the prefix chosen. Other systems of experimental categories such as the ecotype concept of Turesson (1922 and 1929) attempted to combine morphological and genetic information into single terms. In practice, however, the deme terminology is rather cumbersome to use and it is often easier to describe the situation in a few words rather than employ one of these terms. In addition there are several other more well known terms in general use such as biotype (= genodeme), which are more widely understood. It is clearer to talk about "a series of local biotypes" than "a series of genotopodemes". Had it proved impossible to construct a formal classification from the data obtained, the deme terminology would have been a useful way of giving an informal description of the variation encountered. In practice however, it seemed essential to achieve a system based on formal categories and the plan to use the deme terminology was dropped. Some reasons for the failure of the deme terminology to gain wider popularity are discussed in 9.1.1.

1.4 CRITICAL HINDSIGHT

When planning an experimental programme of the type described in Chs. 5, 6 and 7, there is a temptation to spread the net too wide and attempt to cover too much ground. In this case, it might have been better to have concentrated on a smaller part of the problem, e.g. the relationships of S. leucanthemifolius, S. vernalis and the related perennials, and replicate the crosses several times to give reliable results, rather than try to cover the group as a whole in less detail. However, it has been very useful to have been able to make some quite wide-ranging crosses, and although the results of a smaller and more detailed investigation might have been statistically significant, they would have been less significant as far as the taxonomy of the group as a whole is concerned.

As discussed in 2.3, the name changes resulting from this research are not incorporated into the text of parts I and II. This decision was taken because it was found much easier to refer to local groups of plants by names, even if they were later abandoned. It was realised that this might cause a few problems when the new names are used in part III, especially when reference is being made back to parts I and II. However, the name changes are few and they are explained in the text of part III and in Fig. 2.

1.5 NUMBERING OF ACCESSIONS

A list of accessions cultivated and used in the experimental work reported in part II of this thesis is given in Appendix I. When reference is being made to these accessions in Ch. 3 and in part II, the accession number is given in brackets after the specific name. These numbers should not be confused with the numbers given to species described and diagnosed in the taxonomic treatment, 9.2.3.

CHAPTER 2 TAXONOMIC HISTORY

2.1 SPECIES LEVEL AND BELOW

The post-Linnean taxonomic history of this group can be divided into two periods. The first period, lasting for about 140 years, began with the publication of Species Plantarum by Linnaeus (1753). He described eleven species of which nine still stand today, though two of the nine names, S. glaucus and S. trilobus, have been largely neglected ever since (see 9.2.3) Linnaeus did not make any infra-specific taxa. From Linnaeus' time until about 1890, nearly all names published were at specific rank, though a few infra-specific names were published by de Candolle (1838) and Boissier (1875). The latter sometimes grouped species together under a single binomial without actually assigning them to a definite rank. For instance he comments that S. humilis, S. vernus and possibly S. crassifolius should probably be considered under S. leucanthemifolius. Admittedly, the main area of distribution of these four species is outside the area covered by Flora Orientalis, and both he and de Candolle made infra-specific taxa in quite a number of species. Other writers such as Desfontaines (1799) and Pomel (1874) concerned themselves with describing new species rather than attempting to 'fit' newly collected specimens into existing binomials. This was presumably because of ideas then current about the 'fixity of species'. A specific name was not expected to embrace the degree of variation that exists within this group and thus many species were described which cannot be accepted today.

With the publication of Flore de l'Algérie by Battendier & Trabut in 1889 began a proliferation of infra-specific categories which lasted for about 60 years. The varieties described in Flore de l'Algérie were mostly formed by combining previously described local species as varieties of more widespread species. It was accepted that local environmental conditions could cause plants from different parts of a species' range to look very different from each other. Following this began what might be described as a feverish hunt for minor variants which were described at the level of variety and form. In some cases the situation was clarified by the increasing use of the subspecies, originally employed simply as a category intermediate between species and variety and later with geographical connotations,* but several works were produced which included rather daunting lists of varieties under most of the specific names e.g. Fiori & Paoletti (1903), in Europe and Jahandiez & Maire (1934) in N.W. Africa.

Fig. 1. shows in tabular form the history of some names applied to species of Senecio in Morocco and Algeria. The change in approach that took place at the end of the 19th century is striking. This change is partly due to the fact that many earlier works such as de Candolle's Prodromus and Boissier's Flora Orientalis covered wide areas (in de Candolle's case, the whole world), and authors, faced with the task of describing enormous numbers of species, had little time to become involved in infra-specific categories.

Floras for this area published since Jahandiez & Maire, such as Quézel & Santa (1963), show a marked tendency to decrease the number of varieties recognised. For instance under S. leucanthemifolius subsp. poiretianus, Quézel & Santa say "includes S. humilis, S. fradini and S. atlanticus" without describing them as varieties. The implication presumably is that they do not warrant varietal rank, as some varieties are described within other species.

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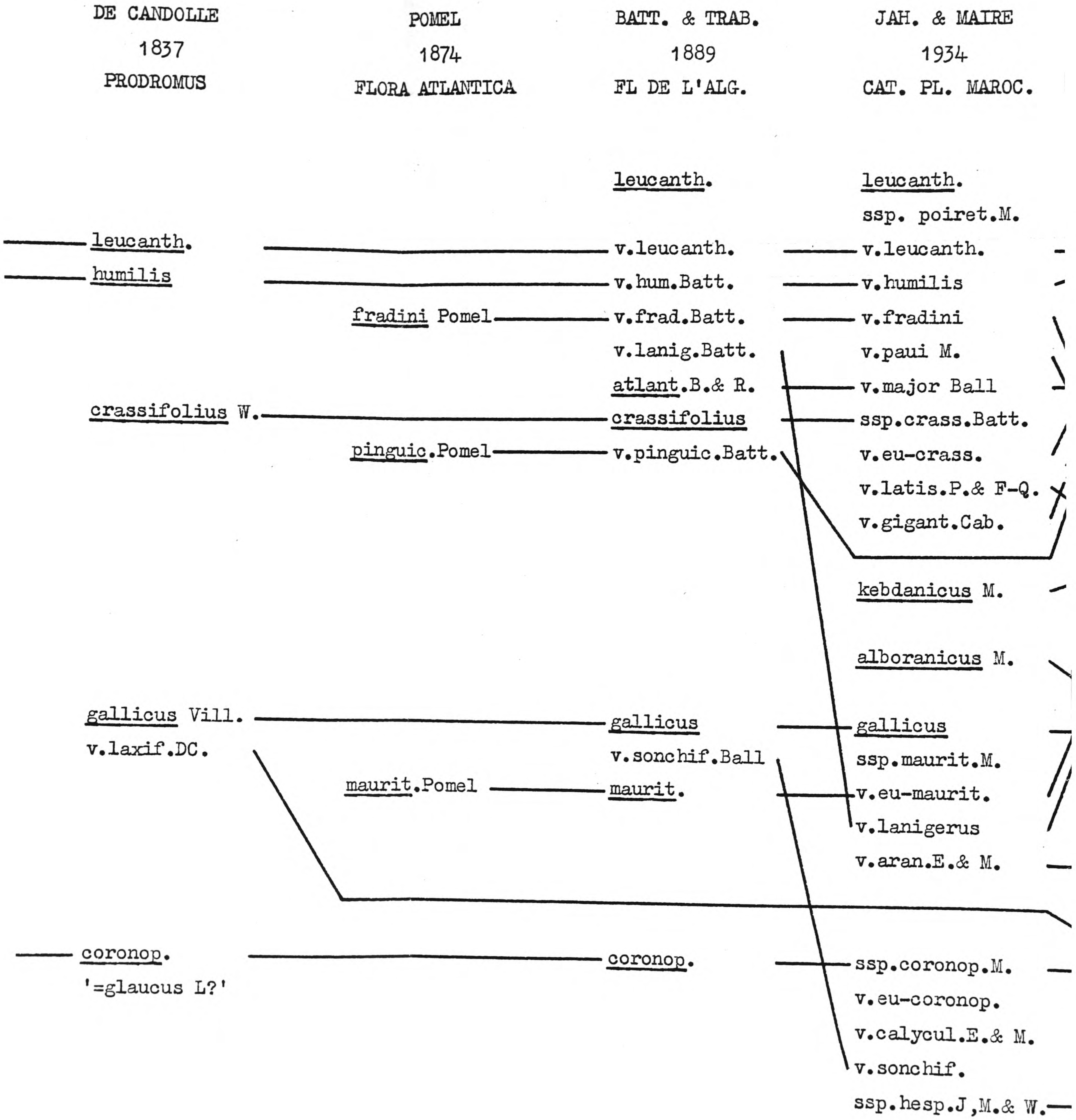
* Consistent use of the subspecies is made difficult by Art. 26 in the International Code of Botanical Nomenclature which makes erection of a type subspecies automatic (autonym) when any subspecies are described (see remarks under S. leucanthemifolius, 9.2.3).



DE CANDOLLE 1837 PRODROMUS	POMEL 1874 FLORA ATLANTICA	BATT. & TRAB. 1889 FL DE L'ALG.	JAH. & MAIRE 1934 CAT. PL. MAROC.
		leucanth.	leucanth.
			ssp. poiret.M.
leucanth.		v.leucanth.	v.leucanth.
humilis		v.hum.Batt.	v.humilis
	fradini Pomel	v.frad.Batt.	v.fradini
		v.lanig.Batt.	v.paui M.
		atlant.B.& R.	v.major Ball
crassifolius W.		crassifolius	ssp.crass.Batt.
	pinguic.Pomel	v.pinguic.Batt.	v.eu-crass.
			v.latis.P.& F-Q.
			v.gigant.Cab.
			kebdanicus M.
			alboranicus M.
gallicus Vill.		gallicus	gallicus
v.laxif.DC.		v.sonchif.Ball	ssp.maurit.M.
	maurit.Pomel	maurit.	v.eu-maurit.
			v.lanigerus
			v.aran.E.& M.
coronop.		coronop.	ssp.coronop.M.
'=glaucus L?'			v.eu-coronop.
			v.calycul.E.& M.
			v.sonchif.
			ssp.hesp.J,M.& W.

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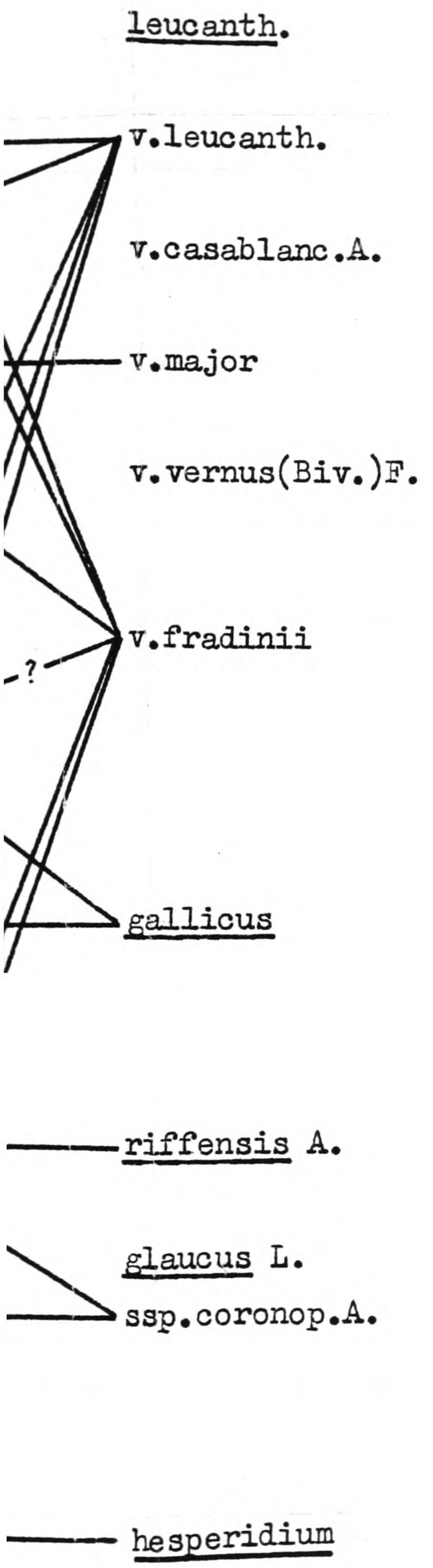

FIG. 1 TABLE SHOWING THE HISTORY OF VARIOUS NAMES AMONG THE ANNUAL SPECIES OF SENECIO FROM MOROCCO AND ALGERIA

Synonymy is indicated by lines joining names together. Species names are underlined. Lines attached to subspecies imply that all varieties within that subspecies have been treated together. Where a subspecies has no lines attached then varieties within it are connected individually. In a few cases, names described after the work cited at the top of each column are included. Authorities are only given the first time each name is mentioned; where status is changed only the newer authority is given. Abbreviations of authorities can be checked in the index. Other abbreviations are as follows:-

araneosus
atlanticus
calyculatus
coronopifolius
crassifolius
casablancensis
fradini
giganteus
hesperidium
hispanicus
humilis
lanigerus
latisectus
laxiflorus
leucanthemifolius
mauritanicus
pinguiculus
poiretianus
sonchifolius

DESFONTAINES 1799 FLORA ATLANTICA	DE CANDOLLE 1837 PRODROMUS	POMEL 1874 FLORA ATLANTICA	BATT. & TRA 1889 FL DE L'ALG.
			leucanth.
leucanth.Poir.	leucanth.		v.leucanth.
humilis Desf.	humilis		v.hum.Batt.
		fradini Pomel	v.frad.Batt.
			v.lanig.Batt
			atlant.B.& R
	crassifolius W.		crassifolius
		pinguic.Pomel	v.pinguic.Ba
	gallicus Vill.		gallicus
	v.laxif.DC.		v.sonchif.Ba
		maurit.Pomel	maurit.
coronop.Desf.	coronop. '=glaucus L?'		coronop.

2.2 ABOVE SPECIES LEVEL

At series and sectional level, very few changes have beenmade since de Candolle (1838), who used series as a category above section in the taxonomic hierarchy, making them illegitimate according to Article 5 in the International Code of Botanical Nomenclature (1972). Nevertheless, most authors still use de Candolle's sections, and merely drop his series names. This means that "section" may be being used at a rather lower level than in some genera whose sectional classification has been reworked since de Candolle's time. However it would not be correct merely to transpose his series with his sections, as the former were defined purely in geographical terms; an understandable response when faced with the task of dividing up an enormous cosmopolitan genus. In a footnote he remarks that series Caucasici, which covers Europe, N. Africa, the Orient and Siberia, is defined by the area inhabited by Caucasian man. He divided this 'series' into ten Sections, which are delimited on morphological characters. The species involved in the investigation reported here come from three of these sections:- 1. Obaejacae, rayless or very short-rayed annuals; 2. Obaejacoideae, long-rayed annuals; 3. Jacobaeae, perennials with pinnately lobed leaves. Sect. Obaejacae had previously been split by Cassini into Sect. Senecio, discoid species, and Sect. Obaejaca, very short rayed species. Boissier (1875) combined de Candolle's Sect. Obaejacoideae into Sect. Obaejacae. With the adoption of the rule that sections containing the type species of a genus must bear the generic name, Sect. Obaejacae (sensu Boissier) became Sect. Senecio. The distinction between Sects. Senecio and Jacobaea is discussed further in 9.2.1.

2.3 NAME CHANGES IN THIS THESIS

One of the results of the research reported here was the abandonment of several specific names, which did not seem to warrant that status. These names were found to be very useful when referring to the local population or infra-specific group concerned, e.g. it was much easier and clearer to refer to

'S. pinguiculus' than to the Algerian phenotopodeme of S.leucanthemifolius. Thus it was decided to use the unchanged names in the bulk of the thesis, i.e. parts I and II, and then use the new names in part III once all the data supporting the changes had been reported and discussed. This has its drawbacks, e.g. when referring from part III back to figures in the earlier part of the thesis. To avoid confusion, the names used in parts I and II are added in brackets after the new name in part III when reference is being made to earlier chapters. The major nomenclatural changes effected in this thesis are shown in Fig. 2 which is duplicated as Fig. 35 in Ch. 9 to avoid confusion.

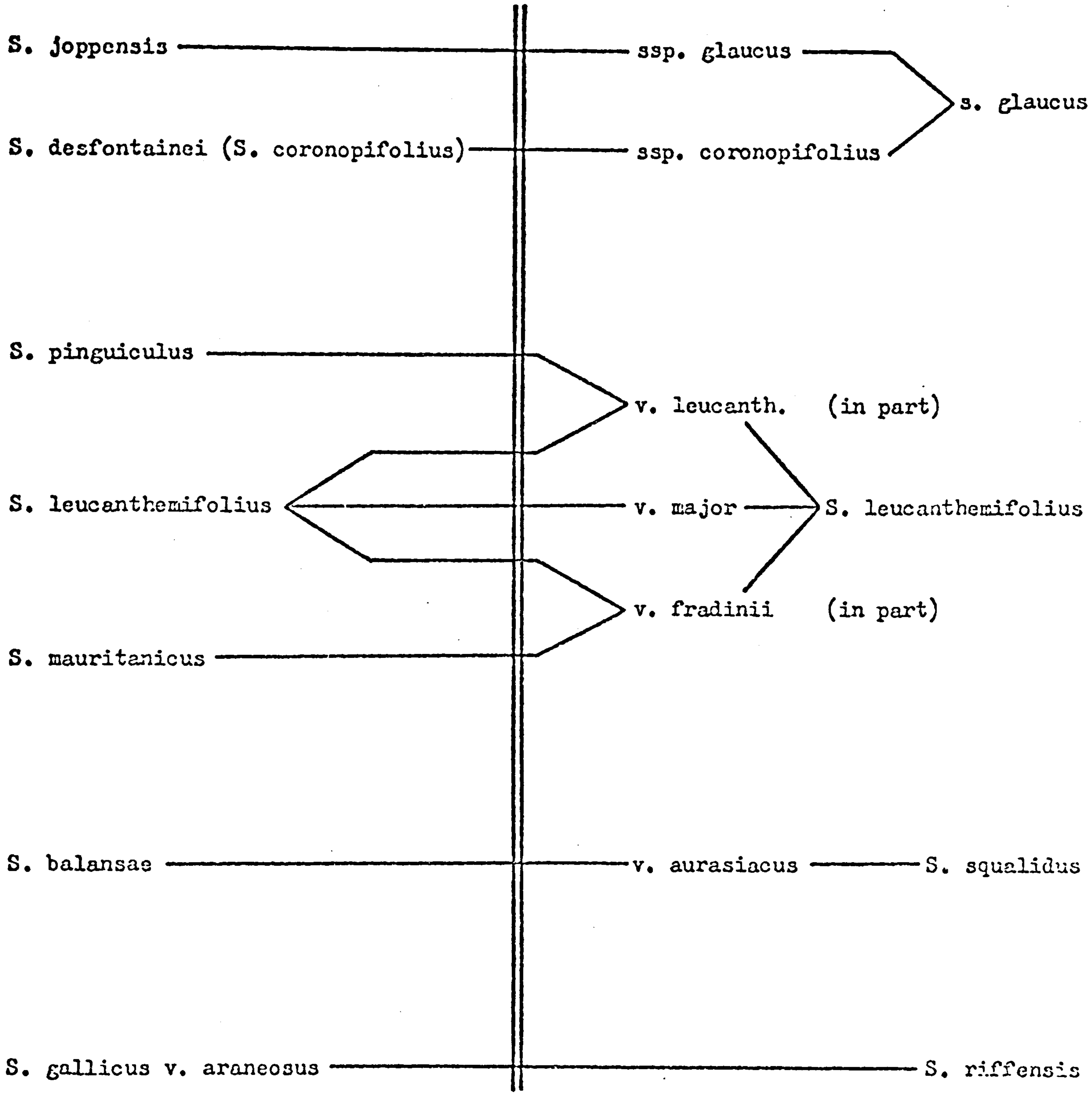

Fig. 2. MAJOR NOMENCLATURAL CHANGES IN THIS THESIS.
Names on the left are used in parts I and II, those on the right in part III. Other names are constant.

CHAPTER 3 MORPHOLOGICAL CHARACTERS

3.1 INTRODUCTION

Although there is a considerable range of floral and vegetative morphology within the group, about one third of the species recognised are difficult to identify over all or part of their range. The problems lie mainly among the annual diploids, where floral morphology is relatively uniform. Emphasis has therefore been placed on vegetative characters, especially leaf shape, which is difficult to describe and has been shown in some species to be highly plastic (see Ch. 6). The situation is further complicated by marked inter-population variation, which has resulted in the description of large numbers of infra-specific taxa. In addition, examination of mass gatherings shows that, in some cases, intra-population variation occurs as well. This could be due to plasticity showing up small scale environmental differences such as shade and moisture availability. In this chapter the usefulness of morphological characters in the taxonomy of this group is discussed.

3.2 LIFE FORM AND HABIT

The group consists of annuals and short-lived perennials, sometimes described as perennants, which, in cultivation, come into flower during their first year, though they remain vegetative for a longer time than the annuals do. Most of them develop a thickened stem base which enables them to survive summer drought or winter cold. They live for at least two years; a few in cultivation at Edinburgh survived to flower for a third season. Most of the aerial parts are lost during the resting phase and subsequent new growth takes place from lateral shoots near the original stem base. S. squalidus is often described as being perennial, biennial or annual (Flora Europaea in press), though Section Jacobaea (Cass.) Dumort. in which it is placed is described as perennial, rarely biennial. The inadequacy of life-form as a taxonomic criterion in this group is also suggested by the high inter-fertility of some annual and perennial populations. This is further discussed in 7.4.2.

Most species have an erect main stem. In cultivation, the annuals mostly grow without branching until flowering has been initiated when a few lateral branches develop in the upper half of the main stem. Later, branches are produced lower down. Some coastal and inland populations of S. leucanthemifolius show vigorous production of branches when the plant is still quite small giving the plant a pyramidal profile. These lateral branches may be procumbent. While the easily recognised species may have a very characteristic habit, there is much local and environmental variation in the more difficult species.

The stature of most species is extremely variable. Mature plants of most of the annuals range from 10-50 cm in height. S. vulcanicus, a montane species, rarely exceeds 10 cm. Some of the perennials, e.g. S. balansae, may reach 100 cm.

3.3 ROOTS AND STEMS

The form and extent of the root system seems to depend very much on environment. Species growing on loamy soils as weeds of cultivated and fallow fields usually have an unspecialised fibrous root system. The same species growing in drier habitats produce a well developed tap-root which carries the root system to a greater depth. Plants of maritime and desert sands, e.g. S. flavus and S. joppensis, also develop a strong tap-root, which may be more or less unbranched for several centimetres below soil level, producing a cluster of fibrous roots at the bottom. Montane species such as S. hoggariensis and S. chalureaui also have this type of root system. The perennials mostly have a well developed tap-root which may grow more or less horizontally a little below soil level, from which fibrous roots arise all along its length, e.g. S. squalidus and S. gallicus v. araneosus.

The stems of all species examined are terete and usually finely ridged, the ridges being continuous with the main veins of the cauline leaves. Most stems are dull yellowish green, often tinged with red towards the base. The perennials may develop stems with a basal diameter of 5-10 mm, which can become quite woody in the plant's second year. Some of the annuals, e.g. S. aegyptius, also produce thick lignified stems.

3.4 LEAVES

A considerable variety of leaf shape is found in the annuals and related perennials. Leaf silhouettes of most of the accessions cultivated and used in the experimental work, are shown in Figs. 46-64 (Appendix II) in the form of 'leaf spectra' (see 5.2). Silhouettes of cotyledons and seedling leaves are shown in Fig. 3.

All leaf spectra and silhouettes are taken from cultivated specimens which come from more mesic conditions than gatherings of wild plants do. Descriptions of leaves and other organs are intended to cover wild and cultivated specimens.

The terms used to describe pinnately divided leaves have often been applied in a confusing and inconsistent manner. In this account, leaves divided to about one third of the lamina width are described as pinnatifid; deeper lobing almost to the main vein is termed deeply pinnatifid or pinnatipartite and leaves divided right down to the main vein are called pinnatisect.

Apart from S. flavus (Fig. 58) most species show some sort of pinnate

FIG. 3 COTYLEDONS AND SEEDLING LEAVES

1. S. desfontainei (3), 2. S. joppensis (2), 3. S. gallicus (29), 4. S. leucanthemifolius (30), 5. S. mauritanicus (22), 6. S. mauritanicus (13), 7. S. pinguiculus (10), 8. S. vernalis (44), 9. S. hesperidium (71), 10. S. vulgaris (43), 11. S. massaicus (66), 12. S. aegyptius (34), 13. S. hoggariensis (45), 14. S. gallicus v. araneosus (79), 15. S. squalidus (31). All x 1.


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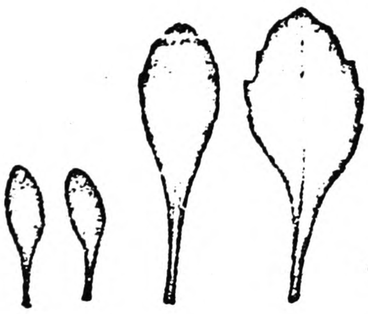
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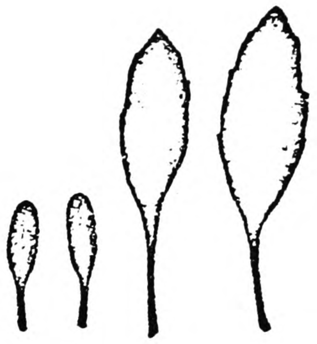
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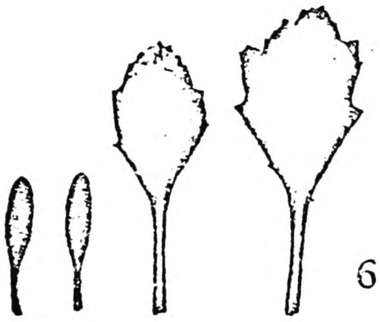
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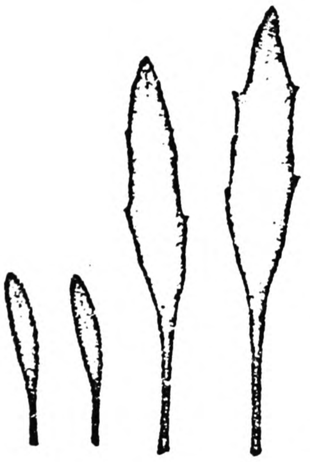
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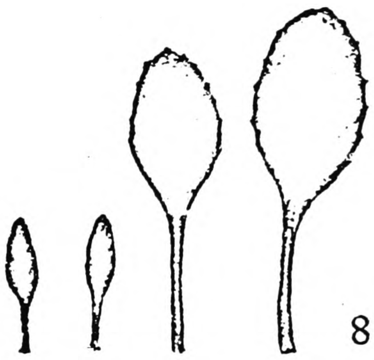
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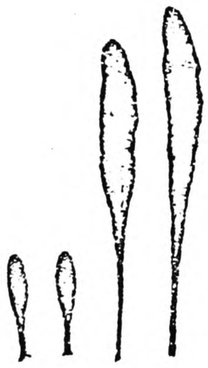
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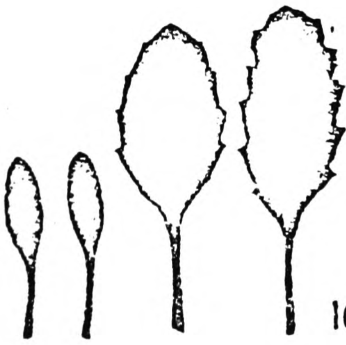
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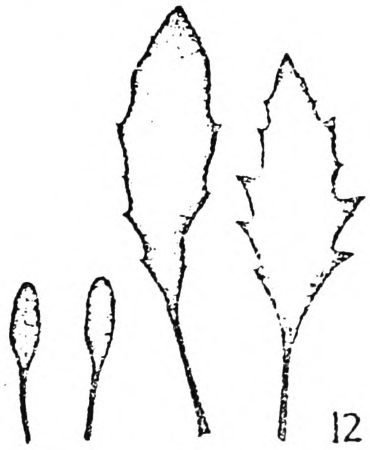
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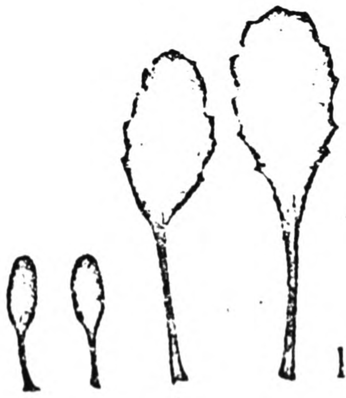
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division when grown in mesic conditions. Some populations of S. leucanthemifolius may produce mostly ovate or spathulate leaves, but the pinnatifid tendency is usually noticeable in leaves produced once flowering has been initiated (Figs.53 & 54). In other populations, the leaves are well divided from an early stage (Fig. 52). Cases in which coastal species, e.g. S. pinguiculus and S. massaicus, enter the reproductive phase while still producing more or less entire leaves might easily be attributed to neoteny, or more correctly paedogenesis (Davis & Heywood, 1963, p. 157). However, leaf spectra taken from specimens of these species under cultivation show a much greater degree of lobing than do wild specimens. Thus the absence of lobing is due to environmental conditions and is not under genetic control as true neotenous development would be. In coastal habitats there is presumably considerable pressure to complete the life-cycle as quickly as possible, which may also account for plants flowering while still having juvenile foliage. However, short life-span does not always exclude the development of mature leaf shapes. One of the most ephemeral of all flowering plants, S. vulgaris, produces mature pinnatifid leaves within about 30 days of germination.

Of the other widespread annual diploids, S. desfontainei (Fig. 3:1, Figs. 46-49) is most easily identified. The fully grown cotyledon leaves are linear, being at least fifteen times longer than broad. The middle cauline leaves are deeply pinnatifid with distant linear lobes. S. joppensis (Fig. 3:2, Figs. 46 and 47) is very similar but is larger and fleshier in all its parts. S. hesperidium (Fig. 3:9 and Fig. 49), a fleshy coastal plant from W. Morocco, was originally described as a subspecies of S. gallicus, which included S. desfontainei. Although S. hesperidium has broader cotyledons and basal leaves, in manner of leaf lobing it is similar to Moroccan S. desfontainei, and some populations intergrade. S. gallicus (Fig. 3:3 and Fig. 50), commonly considered conspecific with S. desfontainei, has shorter and broader cotyledons which are five to eight times as long as broad. The pinnatifid mid-cauline leaves have broader patent lobes which are usually denticulate. Intermediates between *S. gallicus* and *S. desfontainei* are found. On seedling morphology, *S. gallicus* seems closer to the *leucanthemifolius* group.

Taxa within the *leucanthemifolius* group are difficult to separate both as seedlings and as mature plants. As mentioned above, the name *S. leucanthemifolius* has been applied in S. Europe to plants with more or less obovate-spathulate leaves (Figs. 53 and 54) and also to plants with more pronounced division (Fig. 52). In N. Africa such plants with pinnatifid leaves have been refered to *S. mauritanicus* (Figs. 52 and 55). At subspecific rank this name has been moved backwards and forwards between *S. gallicus* and *S. leucanthemifolius* (see Fig. 1). On morphological grounds it belongs clearly to the *leucanthemifolius* group. Coastal forms of *S. leucanthemifolius* have been referred to *S. crassifolius* and *S. humilis*. The type description of the former describes the leaves as linear-lanceolate, though the name has frequently been applied to fleshy plants with obovate or spathulate leaves. The name *S. humilis* also appears to have been widely misused. The leaves are described as spathulate, decurrent and unequally toothed or lobed.

It is often difficult to distinguish *S. vernalis* (Fig. 3:8, Figs. 56 and 57) from *S. mauritanicus* and pinnatifid *S. leucanthemifolius* (Fig. 3:4-6, Figs. 52 and 55). *S. vernalis* usually has narrower, less distant lobes, the leaf margins being finely denticulate. While typical forms are easily identified, there are no constantly reliable criteria for separating *S. vernalis* from *S. leucanthemifolius* s.l. There are particular problems in S.E. Europe where both species are said to occur. *S. gallicus*, (Fig. 50), also has finely denticulate leaves with narrow lobes, though the lobes are more distant than in *S. vernalis*. In *S. gallicus* the basal leaves are usually at least six times longer than broad, those of *S. vernalis* being less than five times their breadth. *S. pinguiculus*, (Fig. 3:7, Fig. 57), a glaucous coastal species from Algeria, has narrow lanceolate leaves with acute forward-pointing lobes. Though morphologically distinct from S. leucanthemifolius s.l. it is often treated as a variety of S. crassifolius.

The perennials considered in this investigation are close to the leucanthemifolius group in leaf shape. S. gallicus v. araneosus (Fig. 3:14, Fig. 59) has broader cotyledons and seedling leaves than true S. gallicus. Its mature leaves are lobed more in the manner of S. mauritanicus, (see 3.2 and 7.4.2). In S. Europe, S. squalidus (Fig. 3:15, and Fig. 60) is sometimes hard to distinguish from S. leucanthemifolius, especially when the former is in its first year. However, typical S. squalidus has deeply dissected mature leaves with narrow, dentate forward-pointing lobes, less distant than usually found in S. leucanthemifolius. S. balansae (Fig. 61) has less deeply divided leaves than S. squalidus, with rounder denticulate lobes; the upper cauline leaves are usually auriculate.

The polyploid species are more constant morphologically than the diploids. The two accessions of S. vulgaris (Fig. 62) from Scotland and Morocco are very similar in leaf shape. The broad cotyledons and seedling leaves suggest affinity with the leucanthemifolius group. S. aegyptius (Fig. 3:12 and Fig. 63) has deeply dissected leaves similar to S. squalidus (Fig. 60), though the lobes are broader, less finely denticulate and often overlapping. S. massaicus (Fig. 3:11 and Fig. 64) has narrow leaves with short, distant, forward-pointing lobes. The hexaploid S. hoggariensis (Fig. 3:13 and Fig. 64) has long narrow cotyledons and seedling leaves. In mature leaf shape it is similar to S. gallicus (Fig. 50) though less denticulate.

There is noticeable correlation between breeding system and inter-population variability in leaf shape. The outbreeders tend to be much more variable than the inbreeders. The greater inter-population variation seen in outbreeders could be a consequence of a deeper gene pool allowing more marked plasticity in response to minor habitat differences. This explanation is plausible only if variation in leaf shape is largely due to phenotypic plasticity. In more stable phenotypes one might expect greater differences between inbreeding lines of autogamous species than between populations of outbreeders, as the inbreeding lines are genetically more isolated.

3.5 INDUMENTUM

There are few qualitative differences in indumentum between the taxa investigated. Most species are sparsely villous to arachnoid, the hairs being concentrated in the axils and on the veins of the leaves. The hairs are thin, simple and straggling. A few coastal and desert forms, e.g. S. joppensis and S. flavus are practically glabrous, though a few scattered hairs can almost always be found. In S. gallicus var. araneosus and S. chalureaui there is a denser lanate indumentum, especially in the younger parts of the plant. S. mauritanicus var. lanigerus is similar though the indumentum is less dense. Populations of these last three taxa are found which are only very sparsely villous. Some species are characterised by the possession of glandular hairs. A combination of glandular and simple hairs is found in several species, e.g. S. nebrodensis, S. lividus, S. sylvaticus and S. viscosus. The last has a compound indumentum, being very viscid and also possessing the usual straggling hairs together with some shorter stiffer ones. Indumentum characters are of little help in the taxonomically difficult species: S. leucanthemifolius, S. mauritanicus, S. vernalis and S. squalidus all being sparsely villous to arachnoid.

3.6 INFLORESCENCES AND CAPITULA

3.6.1 ARRANGEMENT AND SHAPE OF CAPITULA

Most species bear large numbers of capitula in corymbs which may be dense and more or less flat-topped, as in S. aegyptius and S. massaicus, or more loosely

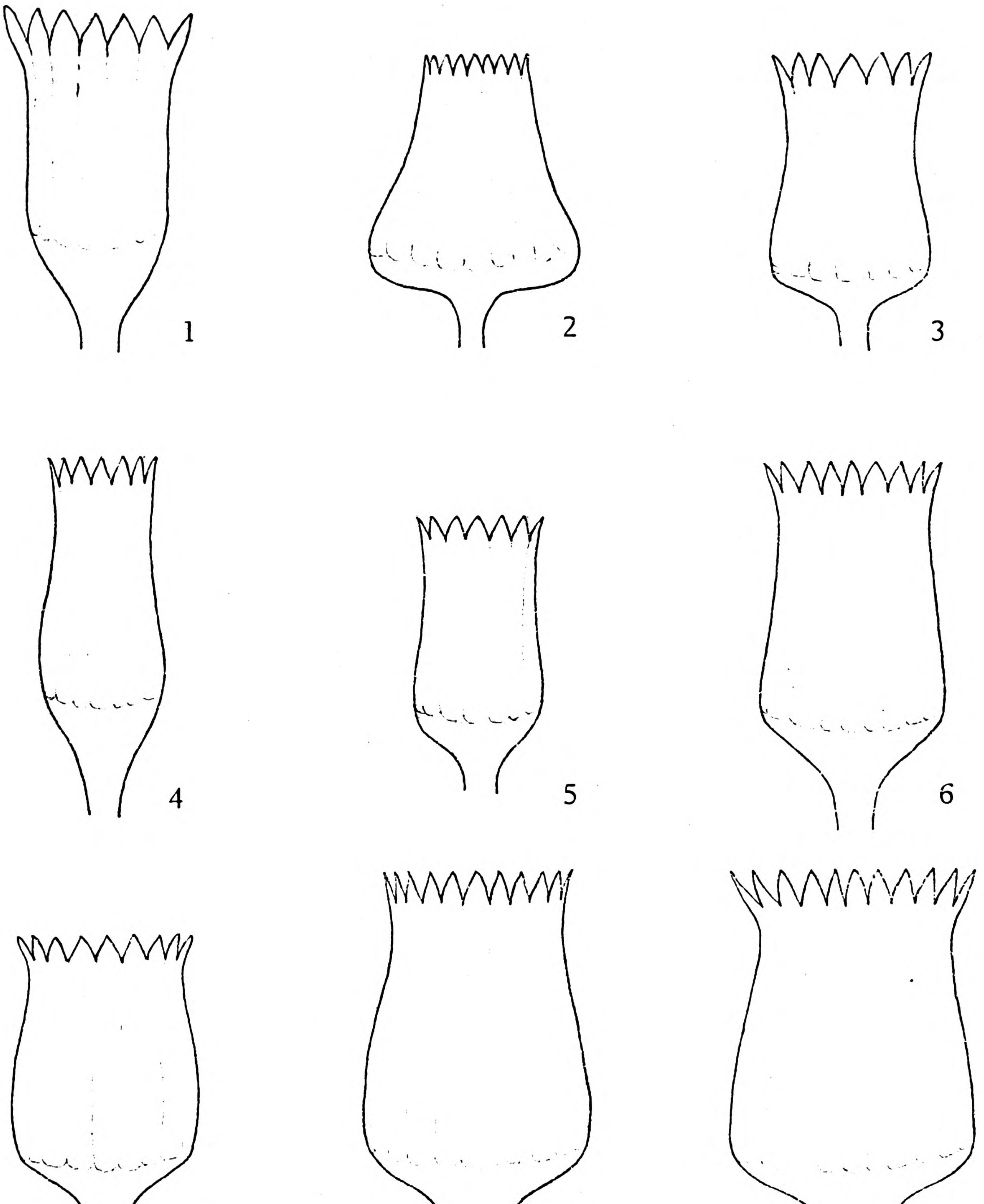


FIG. 4. DIAGRAMS OF CAPITULUM SHAPE

1. *S. vulgaris* (43), 2. *S. aegyptius* (34), 3. *S. massaicus* (66), 4. *S. flavus* (7), 5. *S. hoggariensis* (45), 6. *S. mauritanicus* (22), 7. *S. gallicus* (29), 8. *S. joppensis* (4), 9. *S. squalidus* (31). All x 7.

arranged, e.g. *S. desfontainei* and *S. vernalis*. Once flowering has been initiated such species continue to produce capitula until drought or cold causes them to stop. In cultivation, a single plant of *S. hoggariensis* may produce over 100 capitula. Species of smaller stature such as *S. minutus*, *S. rodriguezii* and *S. vulcanicus* produce much fewer capitula arranged basically in the same manner. However, reduction of the main axis, as in *S. rodriguezii*, may give the impression of several flowering stems each bearing one or two capitula. Sometimes there is only one capitulum per plant.

A range of involucre size and shape is found in the group. Examples are shown in Fig. 4 with ray flowers and calyculus bracts omitted. Most species have capitula which are basically cylindrical to campanulate in profile. When considering involucre shape it is important to compare capitula at the same stage of development as there is a considerable change. Young unopened capitula are more or less globose, gradually becoming campanulate when the ray or outer disc flowers open. Once the central disc flowers are open, the involucre is cylindrical in profile. Finally, when the fruits ripen, the phyllaries become completely reflexed liberating the achenes. One exception is *S. aegyptius* (Fig. 4:2) in which the capitula are strongly urceolate, the achenes being retained by the phyllaries even when ripe. Fig. 4 illustrates capitula at the stage when the ray flowers or marginal disc flowers have just opened. Some differences are found in the sharpness of the angle at which the capitulum narrows under the receptacle. In *S. vulgaris* and *S. hoggariensis* (Fig. 4:1 and 5) the capitulum tapers gradually into the stem, while most other species, notably *S. aegyptius* (Fig. 4:2), show a more sudden transition.

When pressed during the preparation of herbarium specimens, the phyllaries usually become more spread out giving cylindrical and campanulate capitula a more cup-shaped profile.

3.6.2 CALYCULUS

Descriptions of the genus Senecio usually state that there is only one series of involucral bracts or phyllaries, and then add that a group of smaller supplementary bracts, the calyculus, may also be present at the base of the capitulum. Of the species investigated here, S. petraeus and S. minutus are the only ones which were never seen to have a calyculus. Most species usually have a noticeable calyculus of one to twenty bracts, though most populations of S. gallicus are lacking. Other species often found without a calyculus are S. flavus, S. desfontainei, S. pedunculatus and S. erraticus. In many cases the calyculus merges imperceptibly with the peduncular bracts making it very difficult to say exactly how many bracts comprise the calyculus. I have used the term only to include those bracts which originate on the swollen part of the receptacle immediately below the base of the phyllaries, and I have excluded any bracts, however long, whose base is on the unswollen stem.

There is a considerable range in shape and dimensions of calyculus bracts, even on the same capitulum, illustrated in Fig. 6: 1-8. S. trilobus is unique in having lacerate calyculus bracts, those of all other species being entire (Fig. 5).

FIG. 5

CALYCULUS BRACTS OF S. TRILOBUS x 20

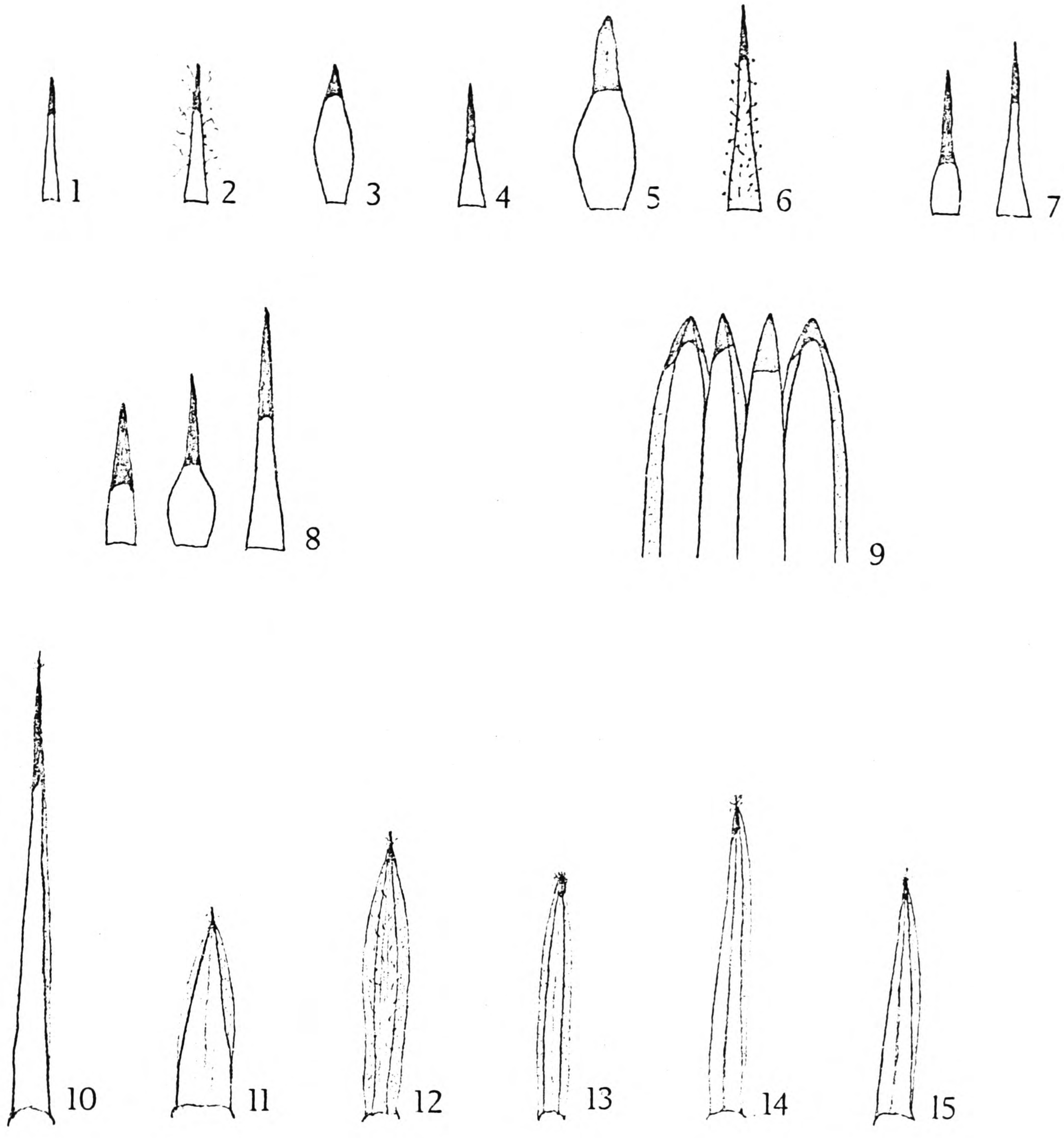


FIG. 6. DIAGRAMS OF CALYCULUS BRACTS AND PHYLLARIES.

Calyculus bracts x 10:- 1. S. desfontainei (3), 2. S. leucanthemifolius (74), 3. S. pinguiculus (10), 4. S. vernalis (6), 5. S. squalidus (31), 6. S. lividus (51), 7. S. mauritanicus (19), 8. S. mauritanicus (21). Phyllaries x 10:- 9. S. mauritanicus (21) showing arrangement of hyaline margins. Phyllaries x 7:- 10. S. lividus (40), 11. S. erraticus (D.50792), 12. S. delphinifolius (D.54330), 13. S. aegyptius (34), 14. S. joppensis (4), 15. S. mauritanicus (22). Hyaline margins are shown stippled.

Usually the bracts are glabrous, but a few populations of S. leucanthemifolius (Fig. 6:2) have villous or arachnoid bracts. The glandular species such as S. lividus (Fig. 6:6) may or may not have a glandular calyculus. Calyculus bracts are usually black-tipped, the black area sometimes being as much as half the bract length.

3.6.3 PHYLLARIES

The phyllaries are much more regularly positioned than the calyculus bracts. They are borne in a single whorl, overlapping each other. In any capitulum there are three types of phyllary:- those with two hyaline margins, those with only one hyaline margin, and those with no hyaline margin. They are positioned in such a way that no two hyaline margins are adjacent (see Fig. 6:9 and Fig. 7).

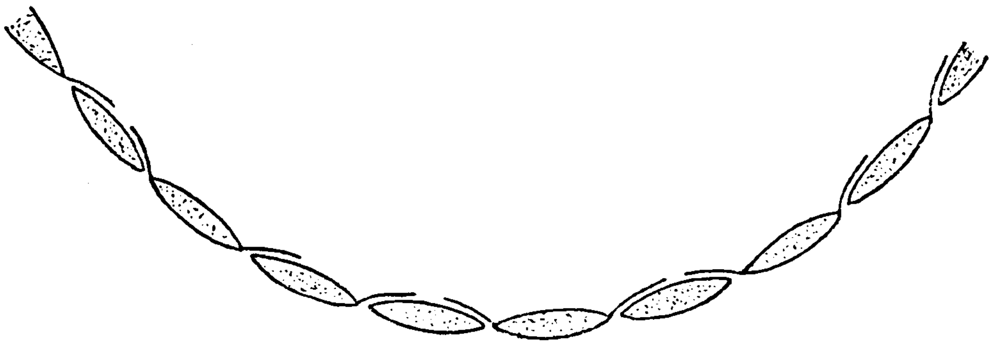


FIG. 7
T.S. INVOLUCRE SHOWING ARRANGEMENT OF PHYLLARIES

This arrangement and other points of capitulum structure are described by Berton (1947). Of the 21 phyllaries in a typical capitulum of S. mauritanicus, eight will be double-flanged, five will be single-flanged and eight will have no flange, though much variation is found even in one plant. In other species the proportions are usually similar, though proportions such as 10:3:10, 7:1:7 and 8:6:8 can be found.

Phyllary length ranges from three or four mm in species with small capitula, such as S. aegyptius and S. vulcanicus, to nine or ten mm in S. flavus and S. lividus which have very long capitula. Some variation in proportions is found between species.

Long narrow phyllaries are found in *S. lividus* (Fig. 6:10) and *S. joppensis* (Fig. 6:14). *S. erraticus* has much shorter broader phyllaries (Fig. 6:11). In most species, the phyllaries are glabrous, but *S. minutus* and *S. delphinifolius* (Fig. 6:12) both have strigulose phyllaries. They are usually considered to constitute a separate section *Delphinifolius* Reichenb.

3.7 FLOWERS

3.7.1 RAY FLOWERS

A variety of size and shape of ray flowers is found in the group (see Fig. 8:1-10). The ligule length ranges from 1.5 mm in the ligulate variety of *S. flavus* (Fig. 8:13) to over 15 mm in *S. gallicus* var. *araneosus* (Fig. 8:10) and other perennials. The ray flowered species can be fairly satisfactorily divided into those having ligules of 5 mm or less, and those with ligules longer than 5 mm. This division also separates the self pollinated inbreeders from the cross-pollinated outbreeders. The correlation between ligule length, chromosome number and breeding system is discussed in 5.3.2 and 7.3.3. The situation is complicated by the occurrence of short-rayed forms of long-rayed species, e.g. *S. leucanthemifolius* var. *caroli-malyi* with 1.5 mm ligules.

There seems to be some confusion in the literature over descriptions of ligule length. Some accounts use the phrase "ligules equal to or barely exceeding the involucre" for species such as *S. lividus* with very short ligules which can just be seen above the tops of the phyllaries. Other authors use this or similar phrases to describe ligules which are equal in length to the phyllaries and are therefore long and plainly visible.

In cultivation the length of the ligules produced becomes progressively shorter as the flowering season progresses. In one cultivated accession of *S. gallicus* the average ligule length dropped from 8.0 mm to 5.3 mm during the first month of

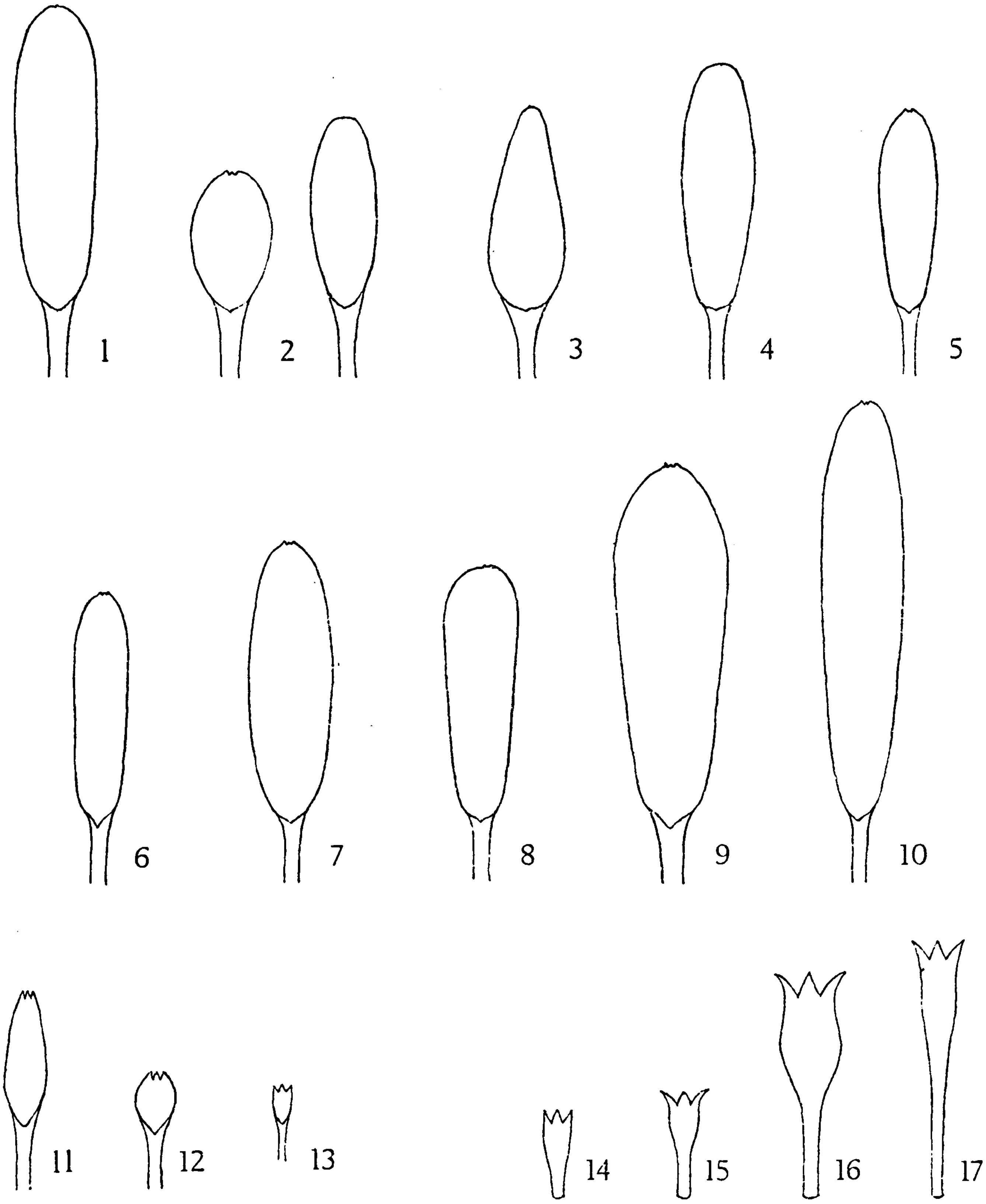


FIG. 8. DIAGRAMS OF FLOWERS

Ray flowers x 4:- 1. *S. mauritanicus* (22), 2. *S. leucanthemifolius* (30),
3. *S. mauritanicus* (14), 4. *S. pinguiculus* (10), 5. *S. vernalis* (6)
6. *S. desfontainei* (3), 7. *S. joppensis* (4), 8. *S. gallicus* (24), 9. *S. hesperidium* (52),
10. *S. gallicus v. araneosus* (79), 11. *S. hoggariensis* (45), 12. *S. lividus* (40),
13. *S. flavus* (7). Disc flowers x 4:- 14. *S. aegyptius* (34), 15. *S. massaicus* (66),
16. *S. petraeus* (41), 17. *S. lividus* (64).

flowering. Specific diagnoses based on small differences in ligule length are not to be relied upon. Similarly the numbers of ray-flowers produced per capitulum also decrease with the age of the plant. Although most species show a clustering of ray-flower numbers which centres around a certain level in the Fibonacci series, e.g. 5 8 13 21 (Church, 1902 pp. 83-89), depauperate or old plants produce capitula with lower numbers of rays.

In most cases three vestigial corolla lobes are visible at the distal end of the ligule. The veins alternate with the corolla lobes, dividing to form an arch in each lobe. The ligule colour of the long-rayed species is a fairly constant sulphur yellow, though paler forms are recorded in the literature, e.g. the forma pallescens Maire (Maire, 1934) of S. leucanthemifolius var. humilis. Most of the short-rayed species also have sulphur yellow ligules, though notable exceptions are S. hoggariensis with purple rays and S. rodriguezii with very pale lilac rays. Radiate populations of S. flavus have pale yellow rays with distinct red veins.

There is considerable variation in ligule shape, but there are as many differences within species or even within populations as there are between species (Fig. 8:2).

There is probably a certain amount of decrease in ligule length during drying of herbarium specimens. The measurements given in 9.2.3 include both living and herbarium specimens.

The length of the tube of the ray-flowers is correlated with the height of the capitulum, which is usually expressed by measurements of phyllary length. It has not therefore been considered as a separate character.

Ray flowers are always female, having narrow divergent style branches. Occasionally a vestigial anther tube is present, which may be quite pronounced in hybrids between rayed and rayless species (see 7.5).

3.7.2 DISC FLOWERS

The flowers of the disc are highly uniform from species to species, except for expected differences in length which correlate with phyllary length in the same way as the tubes of the ray flowers discussed above. There are also some differences in profile as shown in Fig. 8:14-17 some species having tube flowers which are broader than others in proportion to their length. However, differences in profile can also be found between disc flowers from the same capitulum. Throughout this section of the genus, the disc flowers are uniformly five-toothed, though other numbers occur, especially in hybrids (see 7.5).

S. rodriguezii is unique among the annuals from Europe, N. Africa and S.W. Asia in having purple disc flowers. Disc flowers of all other species examined are yellow.

Some interspecific differences are found in number of disc flowers per capitulum, when early opening capitula are compared. However, counts made repeatedly from single plants in cultivation show that there is a gradual decrease in disc flower number throughout the flowering season. Thus the character is probably of limited value for identifying field or herbarium material. It is not known whether this falling off in flower numbers is caused by decreasing nutrient level in potted plants or is purely time-dependent.

In this group, the disc flowers are all hermaphrodite, each having a pistil and a ring of epipetalous stamens. They are strongly protandrous, the pollen being presented on the tips of the unopened arms of the stigma as the style grows up through the anther tube (see Fig. 25). About 48 hours later, the branches of the style open out and the flower enters the female phase.

Venation in the tube-flowers is similar to that of the ray-flowers in that the conducting strands alternate with the corolla lobes and divide to form an arch in each lobe.

3.7.3 STAMENS AND POLLEN

The anther tube is supported by five filaments which are borne on the wall of each tube flower at the point where it first broadens out. Apical and basal appendages are developed from the sterile tissue of each anther, a selection of which is illustrated in Fig. 9:1-6. A considerable range of length and shape of apical appendages was found (Fig. 9:1-5). The basal appendages seem more uniform (Fig. 9:1, 2 and 6). In all cases examined, pronounced 'knees' were seen on the filament just below the anther. Whether this is part of the filament or originates as a downgrowth of the anther connective is not clear. In some cases the 'knees' are truncate basally (Fig. 9:2) and in others truncate apically (Fig. 9:6).

Only a very superficial survey of anther characters was made. A more detailed investigation would be necessary to determine how constant and reliable they are.

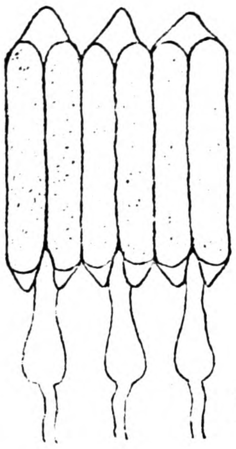
The pollen morphology of several accessions was examined by scanning electron microscopy. Micrographs of pollen grains are shown in Figs. 33 and 34 and a description of the type of grain found in the group is given in 8.2.4. Average measurements of the meridional diameter of the pollen grains of six diploid and three tetraploid accessions show no appreciable differences. The diploids have an average diameter of 28.2μ and the tetraploids 27.7μ. The hexaploid *S. hoggariensis* (45) is distinctly larger with a diameter of 35.7μ.

3.7.4 PISTILS

The pistil, present in both ray and disc flowers, consists of a long filamentous style which is bifid at the apex. The tips of the style branches of disc-flowers end in a truncate tuft of hairs which is important in the pollen presentation mechanism mentioned in 3.7.2 (see Fig. 9:7). Those from ray-flowers are usually more slender and devoid of terminal hairs (Fig. 9:8). In both cases the stigmatic area is on the inner surface of the style branches and is protected from pollination until the branches diverge after the style has elongated.

FIG. 9 STAMENS, STIGMAS, ACHENES AND PAPPUS HAIRS

Stamens x 20:- 1. *S. joppensis* (4), 2. *S. leucanthemifolius* (30), Apical appendages of stamens x 25:- 3. *S. gallicus* v. *araneosus* (9), 4. *S. vulgaris* (59), 5. *S. squalidus* (31), 6. Basal appendages and filaments of *S. massaicus* (66). Stigmas x 40:- 7. from disc flower of S. *leucanthemifolius* (63), 8. from ray flower of *S. hoggariensis* (45). Achenes x 15:- 9. *S. mauritanicus* (22), 10. *S. vulcanicus* (Bornmüller 7478), 11. *S. delphinifolius* (D.51952). Pappus hairs x 100:- 12. Toothed hair of *S. mauritanicus* (22), 13. Fluked hair of *S. vulgaris* (D.54030), 14. Fluked hair of *S. desfontainei* (D.53502).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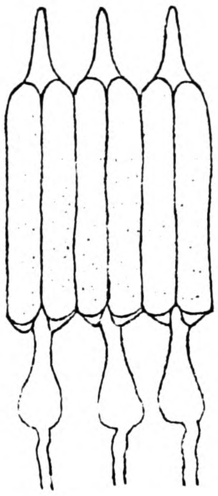
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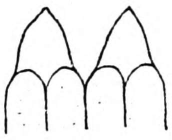
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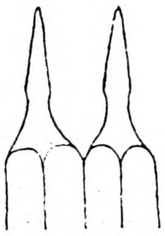
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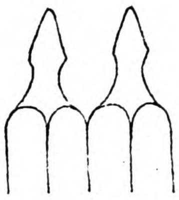
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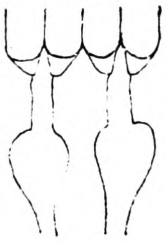
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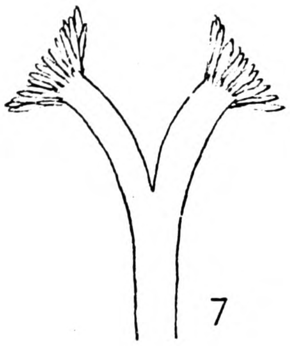
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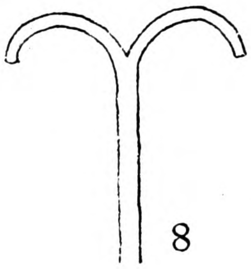
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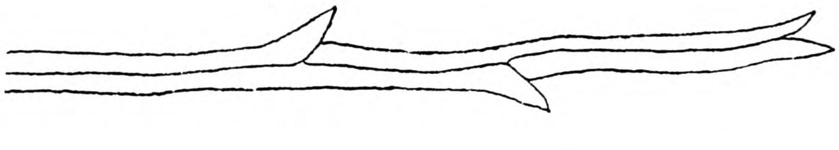
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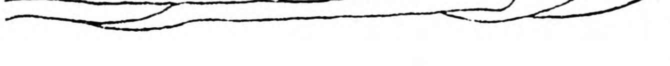
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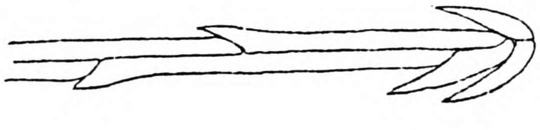
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3.7.5 ACHENES AND PAPPUS

The achenes (strictly called cypselas) of most species are subcylindrical and usually slightly compressed and angular, due to being packed tightly into the capitulum during development. Achene length ranges from 1.5 mm in S. aegyptius and some coastal varieties of S. leucanthemifolius (S. pygmaeus) to 4.0 mm in S. lividus and S. viscosus. This character, like ray-flower tube and disc-flower length, is often correlated with phyllary length. The achenes of most species are covered with short appressed hairs which originate on a series of longitudinal ridges (Fig. 9:9). However, a few species, e.g. S. viscosus and S. vulcanicus have glabrous achenes (Fig. 9:10). The achenes of S. flavus are canescent with adpressed pubescent hairs.

If dry ripe achenes of the species with short achenial hairs are placed in water, the hairs immediately stand out away from the achene. After a few seconds a sudden discharge of mucilaginous threads takes place from the distal end of the hairs, two threads being produced from each hair. The function of the mucilage is presumably to prevent the achene drying out once imbibition of water has started.

The pappus hairs of Senecio are often described as 'simple', though microscopic examination shown them to be more complex. Apart from species such as S. delphinifolius and S. minutus which can be excluded from the group on other grounds, all species have pappus hairs of the type shown in Fig. 9:12 with small forward pointing teeth all along the length of the hair and which end in a slightly diverging tip. In addition most species examined have in each pappus a very few hairs of one of the types shown in Fig. 9:13 and 14. These hairs which are weaker and more straggling than the normal hairs have backward-pointing teeth or cells at their apices and are called 'fluked' hairs by Drury and Watson (1966). As there are only a few of these hairs on each fruit, and because they are restricted to one small area in the outer pappus whorl of each achene, they are easily overlooked even if a deliberate search is being made. I suspect that most of the annuals and related perennials possess them. On the grounds that presence of fluked hairs coincides with other characters such as ovarian crystal structure, achene hair type and anatomical features, Drury and Watson suggest that these hairs may be useful in sectional delimitation and castigate past taxonomists for failing to find such an "obvious" character. This seems a bit harsh as it is a truly microscopic character.

CHAPTER 4 GEOGRAPHY AND ECOLOGY

4.1 DISTRIBUTION OF THE GROUP

There are considerable difficulties in setting geographical limits to an investigation such as this. Nevertheless there is a distinct group of species either restricted to, or having their centre of distribution around, the Mediterranean basin, e.g. S. gallicus, S. leucanthemifolius and S. squalidus; setting aside local endemics such as S. massaicus and S. petraeus. There are also species in the Mediterranean area whose range extends well outside it, e.g. S. desfontainei which occurs as far East as W. Pakistan. Species of very similar morphology occur in adjoining areas. Some of the S. African annuals should probably be included in Sect. Senecio. A survey of sectional limits in this genus is long overdue. As discussed in 2.2 the sections in current use are still subdivisions of de Candolle's geographically based series which, for instance, separate Ser. Capenses from Ser. Caucasici. Looking eastwards from the Mediterranean area more similarities are found, e.g. between S. desfontainei and S. krascheninnikovii in W. Pakistan, which transgress de Candolle's series limits.

Many widespread annuals and perennials seem relatively unspecialised ecologically, occurring in a variety of open or disturbed habitats. Conversely species which are more particular in their ecological requirements tend to be less widespread, e.g. the calcicoles S. petraeus, and S. trilobus. Presumably their short dispersal range prevents them from spreading, even though suitable habitats may abound beyond it.

A few species are very restricted in their distribution, being endemic to very small areas. S. hesperidium, an annual, is only recorded from sandy shores near Sidi Moussa in S.W. Morocco. It is probably a local derivative of S. desfontainei. Local endemics are also found among the perennials, e.g. S. nebrodensis which is restricted to calcareous mountains in S. Spain.

The distribution of each individual species is given in Ch. 9, where distribution maps are included for species central to this investigation.

4.2 ECOLOGICAL OBSERVATIONS

From field observations made in Morocco and this country, and from collectors notes, most species seem unable to compete in closed communities preferring open and disturbed habitats. One species, S. mauritanicus, was found growing in the more or less closed sward of mountain pastures in N. Africa, and S. vernalis, which is closely related (see 9.2.3), is recorded from similar habitats in Turkey and E. Europe. Senecio species appear to have colonised most open habitats, being represented in all six habitat categories defined by Stebbins (1972).

Among the annual species, a few are often found as agricultural weeds, e.g. S. vulgaris, S. vernalis and S. mauritanicus, though no clear distinction can be made between agrestals such as these, and ruderals such as S. desfontainei, S. flavus and S. hoggariensis. Several species are common in both types of habitat. Many of the annuals are associated with desert or maritime sand. S. gallicus is commonly found in Pinus forest on fixed dunes, and the closely related S. desfontainei is a widespread desert species which has probably given rise to the localised maritime species S. joppensis and S. hesperidium, mentioned above. Maritime populations of S. leucanthemifolius are almost always found on sandy shores, though the related S. rodriguezii occurs on maritime rocks. The annuals seem less common in calcareous habitats than the perennials, though exceptions are S. trilobus and S. petraeus, both local species from limestone hills. A few annuals are found exclusively in montane habitats, e.g. S. vulcanicus and S. krascheninnikovii.

The perennials, though some of them are capable of flowering in their first year are not associated with arable land, as their rates of growth are considerably slower than the annuals, and thus their life-cycle is more vulnerable to interruption.

Many of the perennials favour montane disturbed conditions such as volcanic screes, cliffs, and boulder fields, e.g. *S. aethnensis*, *S. balansae*, *S. chalureaui* and *S. nebrodensis*. *S. gallicus* var. *araneosus* are usually associated with marly and shaly banks at lower altitudes though it is not recorded from below about 1000 m. Of the perennials considered in this investigation, only *S. squalidus* is widespread in lowland conditions, though these lowland plants, now common in Britain, **have a narrow range of variation**, being descended from plants which escaped from the Oxford Botanic Garden at the end of the 18th century. The more typical upland and montane aspect of this species is shown in its main area of distribution in Central and S. Europe. *S. chrysanthemifolius*, endemic to lowland Sicily, is often considered to be a subspecies of *S. squalidus*.

~~If, as seems likely, the annuals are derived from the perennials, then they probably inherited a weedy tendency from them, shown by their preference for open habitats, which the perennials, being slower growing, could not exploit~~.

Habitat notes are given with the species descriptions in 9.2.3. Fig. 10 shows in tabular form the habitat preferences of several species, some names being duplicated in different habitats.

MARITIME SAND

desfontainei
gallicus
hesperidium
joppensis
leucanthemifolius
vernalis

DESERT SAND & ROCK

desfontainei
flavus

INLAND MESIC SAND

chrysanthemifolius
delphinifolius
gallicus

CALCAREOUS

balansae
chalureaui
leucanthemifolius
nebrodensis
petraeus
trilobus

MONTANE

aethnensis
chalureaui
gallicus v.araneosus
hoggariensis
krascheninnikovii
nebrodensis
vulcanicus

PASTURE

mauritanicus
vernalis

DAMP HABITATS

aegyptius
minutus

WOODLAND

sylvaticus
viscosus

SALTMARSH

massaicus

FIG.10. HABITAT PREFERENCES OF SOME ANNUAL AND PERENNIAL *SENECIO* SPECIES

PART II

EXPERIMENTAL WORK

CHAPTER 5 INTRODUCTION TO EXPERIMENTAL WORK, AND CYTOLOGY

5.1 PROPAGATION AND CULTIVATION DETAILS

A total of some 80 accessions of seed was made or collected from Europe, North Africa and South West Asia, the majority being from North Africa. Shortage of greenhouse space made it impossible to cultivate more than about half of these. Selection of which to grow was made on the basis of geographical distribution and morphology of voucher specimens where available. A complete list of accessions is given in Appendix I. Ten achenes of each accession chosen for cultivation were sown in John Innes no. 1 potting compost in 4 in. clay pots; where possible, all ten achenes were taken from one capitulum. When the seedlings were about 15 days old, they were thinned to leave four strong seedlings in each pot. This was usually 20 to 30 days after sowing. As the plants came into flower, two more were thinned from each pot. All the accessions came into flower between 28 and 111 days after sowing. In general, weedy forms such as *S. vulgaris* and certain populations of *S. vernalis* came into flower early, while short lived perennials such as *S. squalidus* took much longer. Repeated sowing made it comparatively easy to have flowering material of most accessions available when needed. At each stage the thinnings were kept and either pressed intact or used to make leaf spectra (see 5.2). Thus each accession cultivated provided material for breeding experiments, study of microscopic and gross morphology, and flavonoid chromatography. The plants were grown in an unshaded temperate greenhouse under a 16 hour daylength using natural daylight supplemented when necessary with artificial light in the morning and evening. At monthly intervals, the plants were fed nitrogen, phosphorus and potassium in solution. Infestations of leaf-miner, white-fly and green-fly were kept down by spraying with 'Metasystox' and by fumigation. Unfortunately some young plants were severely affected by fumigation especially if the foliage was at all moist. On one occasion several dozen plants were lost. Some accessions were susceptible to fungal attack at the base of the stem, which was especially difficult to detect in plants with short internodes and a rosette habit. Treatment of lesions with sulphur powder, followed by spraying with 'Benlate' coped with most cases but there were some fatalities.

Apart from these problems, this group makes good experimental material, being fast growing and relatively easy to germinate. In some cases there was a short dormancy period of up to two or three months. Achenes of S. hoggariensis germinated freely within a fortnight of being released from the capitulum. The viability of achenes stored on herbarium sheets does not usually extend beyond four or five years though one six year old specimen of S. mauritanicus gave 90% germination. The optimum age for germination is probably about one year.

In addition to these plants cultivated in standard conditions, the phenotypic plasticity of nine accessions was investigated by cultivation in two extreme environments. Details of this experiment are given in Ch. 6. The breeding experiments are described in Ch. 7. Scanning electron microscopy and flavonoid chromatography are discussed in Ch. 8.

5.2 PREPARATION OF LEAF SPECTRA

Description of leaf shapes in this group presents considerable problems. Differences in lobing which are easily appreciated visually are almost impossible to describe in words. Conversely, the identity of plants described in the literature is not always clear. During the present investigation, I have found it convenient to illustrate leaf shapes by 'xerox' copying pressed leaves. The full range of leaf morphology from cotyledon to youngest leaf can be shown in the form of a leaf spectrum (Melville, 1953). Leaf spectra of all the cultivated accessions are shown in appendix II, The usefulness of leaf shape in classifying this group is discussed in Ch. 3.

5.3 CHROMOSOME NUMBERS

5.3.1 THE BASE NUMBER IN SENECIO

There is some disagreement in the literature about the base chromosome number in Senecio. Afzelius (1949) concludes that the base number for the tribe Senecioneae is five, and remarks that up to that time S. discifolius was the only member of the tribe recorded as having the base number. However, in a previous paper, he recorded counts of n=5 for two species of Emilia (Afzelius, 1924), and he certainly regarded Emilia as a member of the Senecioneae. Emilia is distinguished by having triangular or acuminate tips to its style branches while those in Senecio are truncate. Hoffmann (1894) in Die Naturlichen Pflanzenfamilien 4(5): 297 treats Emilia as a sub-genus of Senecio. As in many of the other splits made in Senecio, the morphological boundary between Emilia and Senecio is rather vague. Since then a further three species of Senecio and four species of Emilia have been recorded as n=5 (Fedorov, 1969). The absence of any species of Senecio with haploid numbers which are multiples of 5 rather than 10 is cited by Ornduff et al (1963) as evidence for a base number of ten in the genus (see Fig. 11). They suggest that the single species of Senecio then recorded as n=5 must have undergone aneuploid loss, though no counts have yet been recorded between n=5 and n=9. They do, however, believe five to be the base number of Emilia which as mentioned above is morphologically very close to Senecio Palmblad (1965) in a paper giving chromosome counts for thirteen previously uncounted species says that his data agree with those of Ornduff et al (1963) that all New World Senecioneae so far investigated are at least tetraploid with n=20. While they do agree on chromosome number, Ornduff et al.regard 2n=20 as the diploid level. Turner and Lewis (1965) record two new counts of n=5 for species of Senecio from East and Central Africa, making a base number of 10 rather unlikely. They account for the absence of species having n=25, 35 etc. by pointing out that

2n	10	18	20	38	40	42	44	46	48	60	76	80	90	100	104	130	180
No. of species	4	1	36	1	106	1	2	18	8	23	1	5	2	1	1	1	1

FIG. 11. TABLE OF SOMATIC CHROMOSOME NUMBERS IN SENECIO AFTER FEDOROV (1969), WITH ADDITIONS

formation of these complements would involve uneven numbers in the initial gametic combinations and this would lead to irregularities at meiosis. However, examination of the frequency of different chromosome numbers in other large Composite genera shows that species do occur on odd multiples of the base number in genera where apomixis has not been recorded. Chrysanthemum, for instance, with a base number of 9, has species with n=27 and n=45.

On the available data it seems likely that 5 is the base number for Senecio. The absence of species with odd multiples of 5 suggests that fairly early in the history of the genus, the mechanisms of chromosome repatterning caused a diploidisation of the existing tetraploids. Structural changes could have caused two identical sets of five chromosomes to become one set of 10 different chromosomes. Since then, species with n=5 do not appear to have been involved in the evolution of the group. N=10 is here regarded as the secondary basic number. In this account such species are referred to as diploids.

5.3.2 NEW COUNTS FOR SENECIO

The chromosome numbers of all accessions cultivated were counted from root tip squashes stained with lactopropionic orcein (Dyer, 1963). The tips were pre-treated in paradichlorobenzene for two hours at 4°C and fixed in acetic alcohol. Before squashing they were hydrolysed in IN hydrochloric acid to aid spreading. Fig. 12 gives the somatic numbers counted, together with counts recorded in the Index to Plant Chromosome Numbers (Cave, 1959-65; Moore, 1973) and by Fedorov (1969). Photographs of the somatic chromosomes of S. desfontainei (73), S. balansae (18) and S. hoggariensis (45) are shown in Fig. 13.

Among the annuals there is a marked correlation between ploidy and breeding system. The tetraploids (2n=40) and hexaploid (2n=60) have a strong inbreeding tendency, associated with shortness or absence of ligules (see 7.3.3). Grant (1958) remarks that in annuals, allopolyploidy occurs more frequently in autogamous species than in their cross-fertilised relatives. Polyploidy is probably a way in which inbreeders can preserve heterozygosity (Stebbins, 1957). There are two points of disagreement in Fig. 12 between counts recorded in Moore (1973) and those which I have counted. In both cases, S. desfontainei and S. vernalis, the Index to Plant Chromosome Numbers gives 2n=40; my counts are both 2n=20. Since both species as represented in my collection are outbreeders with long ligules, I think that they are basically diploids which may have some tetraploid populations. The count for S. desfontainei (Mehra and Remanandan, 1969) comes from the Western Himalayas where S. pendunculosus Edgw. also occurs. The later is very similar to S. desfontainei in leaf shape but has short ligules and could be polyploid. It is possible that their count is really for this species. Two other counts of 2n=20 for S. vernalis have been published (Afzelius, 1924; Tischler, 1934). The count of 2n=40 was given by Majovsky et al (1970) from Czechoslovakian material. Misidentification is rife in this complex, and provenance cannot always be relied upon.

		I.P.C.N. 1959-1973	FEDOROV (ed.) 1969	ALEXANDER 1975
	aegyptius		40	40
P	balansae			20, 20
	desfontainei	40		20, 20
	flavus	20		20
	gallicus	20	20	20,20
P	gallicus v. araneosus			20
	hesperidium			20
	hoggariensis	60	60	60
	joppensis			20, 20
	leucanthemifolius	20, 20	20	20, 20
	massaicus		40	40
	mauritanicus			20, 20, 20
	petraeus			20
	pinguiculus			20
	rodriguezii	20		
P	squalidus	20	20	20, 20
	vernalis	40	20, 20	20, 20
	vulgaris	40 (many)	38, 40 (many)	40

FIG. 12. TABLE OF SOMATIC CHROMOSOME NUMBERS FOR SPECIES OF SENECIO CULTIVATED DURING THIS INVESTIGATION

I.P.C.N. = Index to plant chromosome numbers edited by Cave and later by Moore. Where counts in Fedorov are from the same source as the I.P.C.N. counts, they are not repeated. Each figure represents a different report. In each case, the original references have been consulted. Perennials are marked P. All the rest are annuals.

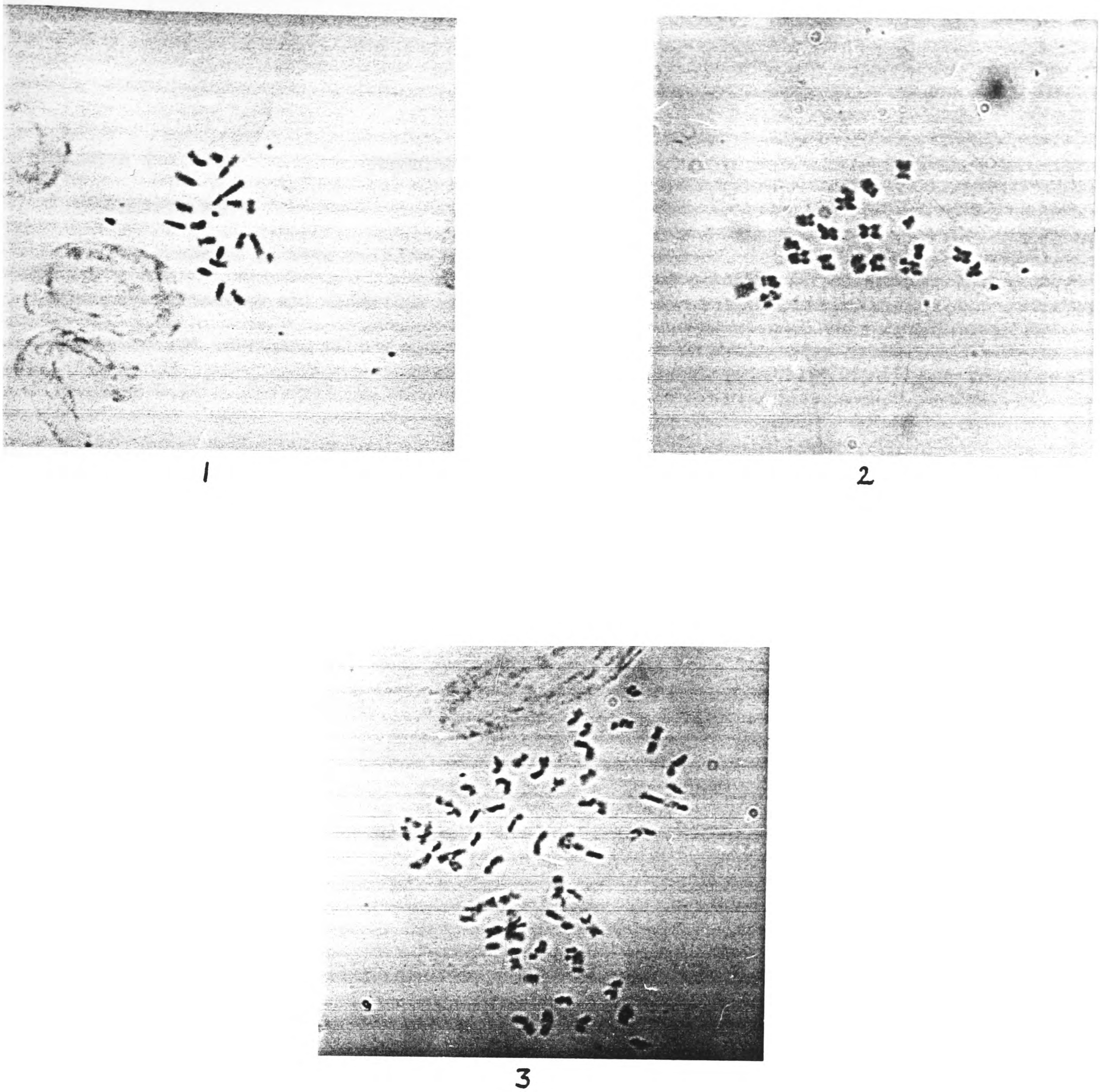


FIG. 13 PHOTOGRAPHS OF CHROMOSOME PREPARATIONS

1. S. desfontainei (73) x 970: 2n = 20. 2. S. balansae (18) x 1470: 2n = 20.
3. S. hoggariensis (45) x 1510: 2n = 60. Root tip squashes stained with lactopropionic orceine (see 5.32).

CHAPTER 6 PHENOTYPIC PLASTICITY

6.1 INTRODUCTION

Two kinds of plastic response have been recognised by Schmalhausen (1949). Where the intensity and direction of the response is directly related to the direction and intensity of the environmental stimulus, he used the term 'dependent morphogenesis'. Bostrack and Millington (1962) demonstrated this type of response in Ranunculus flabellaris Raf. where a decrease in temperature or photoperiod caused a corresponding increase in leaf dissection. Schmalhausen contrasts this with autoregulatory dependent morphogenesis in which the response is not proportional to the intensity and direction of the stimulus. The initiation of the response depends upon a threshold of stimulation being reached, whereupon the full response takes place. This might be more conveniently termed a threshold or 'all or nothing' response. The development of dissected and undissected leaves in Ranunculus aquatilis L. was shown by Cook (1968) to be of this type. He found that development of entire leaves was initiated by long photoperiod provided that the apex of the plant was submerged.

According to Cook (1968) the taxonomic confusion arising from the threshold type of response is much worse than from the dependent response as in the latter, the plasticity can be more clearly correlated with environmental factors. R. flabellaris, with a dependent response, has five synonyms, while the threshold response in R. aquatilis has given rise to over 25 synonyms! However, extreme cases of dependent response as demonstrated in Senecio joppensis (1) described in 6.4 could be equally confusing to the taxonomist.

6.2 MATERIAL AND METHODS

The phenotypic plasticity of ten different **accessions** was investigated. In each case seed from a single capitulum was taken and split into two samples. As the seed was taken from wild gatherings, identical parentage within each sample could not be guaranteed. One sample of each **accession** was planted in dune sand in an unshaded greenhouse with restricted water; this involved keeping a close watch on the plants and watering them only when they were about to wilt. The second samples were planted in a shaded greenhouse in John Innes no.1 potting compost with unrestricted water. On a cloudless day the incident light in the two greenhouses was measured with a Weston meter. Compared with readings obtained in the open, the unshaded greenhouse received 87% sunlight and the shaded greenhouse received 25%. In each case six plants were raised. After four weeks, three plants were thinned from each sample, and specimens of leaves and whole plants taken. After eleven weeks the remaining plants were picked and further specimens prepared. The plants in each sample were recorded as being either vegetative, in bud, or in flower, and the height of each plant was noted. Halfway through the experiment, both samples of oneaccessionwere discarded as the plants showed too much variation for comparisons between samples to be at all reliable.

As the two artificial environments differed in soil type, light intensity and water availability, it is not possible to attribute morphological differences to particular factors. A similar problem is encountered in trying to assess the effects of environmental factors from herbarium specimens. Heywood (1967) stresses that individual factors 'do not operate singly in nature but form part of an intricate interrelated environmental complex;it is usually difficult to sort out which factor is responsible for any particular effect'. It is recognised that neither of the experimental regimes accurately represents wild conditions. However, the results give an idea of the range of plasticity that can occur in the group.

6.3 RESULTS

Details of maturity, height, node number and internode length are given in Fig. 14. The classification of maturity into vegetative, budding or flowering is somewhat arbitrary as only one day separates buds from flowers. The most distinctive leaf shape seems to be developed once flowering has been initiated, the plant then being physiologically mature. Where expression of leaf shape is

		TREATMENT A				TREATMENT B			
Soil type		dune sand				potting compost			
Light		90%				40%			
Water		restricted				unrestricted			
	Accession no.	Maturity	Average height cm.	No. of nodes	Average internode cm.	Maturity	Average height cm.	No. of nodes	Average internode cm.
joppensis	1	F	35	20	1.8	F	68	21	3.2
gallicus	24	B	13	13	1.0	V	47	26	1.8
hesperidium	52	F	21	15	1.4	B	56	22	2.5
mauritanicus	22	F	21	15	1.4	F	52	23	2.3
leucanthemifolius	63	F	10	11	0.9	V	53	15	3.5
mauritanicus	14	V	3	11	0.3	V	21	17	1.2
leucanthemifolius	74	B	5	11	0.5	V	18	18	1.0
gallicus v. araneosus	79	V	2	8	0.3	V	20	17	1.2
pinguiculus	10	F	15	16	0.9	B	36	25	1.4
average height cm.			13.9				41.3		
average internode cm.					0.95				2.02

FIG. 14. HEIGHT AND NODE NUMBERS FOR PLANTS OF NINE DIFFERENT ACCESSIONS GROWN IN TWO CONTRASTING ENVIRONMENTS.

V: plant vegetative, B: plant in bud, F: plant in flower.

See 6.2 for cultivation details.

concerned, the important distinction is between plants that are purely vegetative and those that are in bud or in flower. The final leaf spectra for each sample at eleven weeks old are shown in Figs. 15-23. Leaves from 87% sunlight are shown life size, while those from 25% sunlight, being in general much larger, have been reduced to $\frac{5}{8}$. This was necessary in order to show both samples of each accession on the same page. Details of the preparation of leaf spectra are given in 5.2.

6.4 DISCUSSION AND CONCLUSIONS

Fig. 14 shows that plants from light conditions were in general physiologically older than those from the shade. In the latter environment, flowering was initiated in only four accessions. Numbers 14 and 79 remained vegetative in both treatments. Some variation between accessions is shown by the differences in node number between the treatments. Numbers 24 and 79 both show about twice as many nodes in shady conditions as they do in the light. These have both been referred to S. gallicus. However, morphological and breeding criteria suggest that no.79 (S. gallicus var. araneosus) belongs to the leucanthemifolius group.

Most of the other numbers show increases of between 30% and 50% in node number. However no. 1, which appears most plastic in leaf shape (Fig.15) has developed only one more node in shady conditions. While it is tempting to put taxonomic interpretations on these differences, it is probably not very sound. Bradshaw (1965) states that marked differences in plasticity are shown not only by different species within one genus but also by different varieties within one species.

Figs. 15-23 show considerable variation in the degree of plastic response. In general, depth of lobing and number of lobes is greater in shade conditions, though no. 24 (S. gallicus) has deeper lobes in light conditions but most lobes in the shade (Fig. 16). No.63 (S. leucanthemifolius) produced very curly leaves in shady conditions which were more or less entire except towards the top of the plant (Fig.18). This contrasts with the results of a series of experiments on

Ipomoea caerulea by Njoku (1956), who concluded that where other factors remain constant, depth of lobing is directly proportional to light intensity. He raised seedlings singly in baskets of 'ordinary garden soil'. On germination, half of the baskets were moved to a verandah where they received 40% daylight. The other half remained in full daylight. Both samples were watered regularly. Leaf silhouettes from Njoku's experiment are shown in Fig.24. In the experiment described here, the additional factors of poor soil and lack of water may have produced depauperate forms with poorly developed lobing.

S. joppensis (1) shows the most plastic phenotype (Fig. 15). The average taxonomist might well put plants exposed to these two treatments into separate species. Greater stability is shown by no. 24 (S. gallicus). Though there are fewer and deeper lobes in light conditions, the general facies of plant and leaf is similar in both treatments. Different populations of the same species show different degrees of plasticity. No. 22 (Fig.18) produced leaves with a few very shallow lobes in light conditions which are very different from the deeply lobed leaves from the shade. No. 14 (Fig. 20) on the other hand, is far more stable. Both of these biotypes have been referred to S. mauritanicus. This raises the eternal problem of sampling. Where only one population of a particular species has been investigated one can infer only that the biotype in question showed a particular degree of plasticity and not generalise for the taxon as a whole.

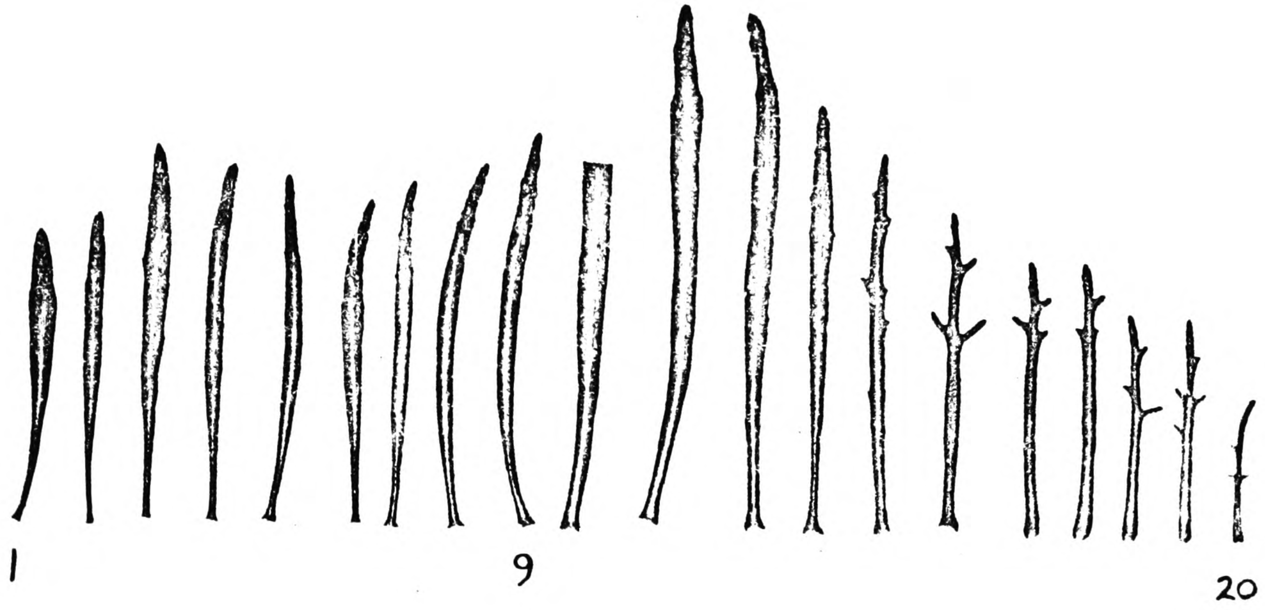
It is interesting to make rough groupings based on leaf shapes produced in the two regimes. In light conditions marked similarity is shown by nos. 63, 74, 14 and 79 (Figs. 19-22). This grouping is taxonomically quite suggestive as no. 79 (S. gallicus var. araneosus) fits better in the leucanthemifolius group. However the similarity shown by nos. 1, 22 and 10 is probably misleading as no. 1 (S. joppensis) on both morphological and breeding criteria belongs in the gallicus group.

The occurrence of very different degrees of plasticity in two fairly close species, S. joppensis (1) and S. gallicus (24), bears out Bradshaw's remark, quoted previously, that plasticity evolves separately in related taxa. S. joppensis with a broad range of expression could be described as a euryplastic species compared with the stenoplastic S. gallicus (Davis & Heywood, 1963:337). The adaptive significance of plasticity is not always clear. In this case, it could be argued that S. joppensis, usually a sand dune plant, experiences greater environmental extremes than does S. gallicus, a plant of sandy pine woods. However, the fluctuation of temperature and moisture availability on sand dunes is often very rapid, and it is hard to believe that phenotypic plasticity can play any part in coping with short term changes. There can be little selective advantage to be gained by producing a xeromorphic leaf with reduced assimilatory capacity unless there is likely to be a shortage of water for several weeks. In addition, the final shape of a given leaf appears to be determined very early in its ontogeny (Ashby, 1950; Njoku, 1956). Thus the only environmental fluctuations which could exert a profound selective pressure on leaf shape operate over periods varying from the time it takes a leaf to become physiologically active to some period less than the time in which the plant completes its reproductive cycle. Longer periods than this are catered for by genetic mechanisms of variation and mutation. The other situation in which phenotypic plasticity might give considerable advantage occurs when an expanding population colonises a variety of peripheral habitats which are ecologically different from each other and from the original habitat. There is no evidence that this is occurring in S. joppensis, as all the material examined comes from coastal sands. In general, xerophytic plants from coast and desert are not noted for their plasticity. Bradshaw (1965) argues that phenotypic plasticity is not always adaptively significant; this may be the case with S. joppensis.

FIGS. 15 - 23 LEAF SPECTRA FROM PLANTS OF NINE DIFFERENT ACCESSIONS GROWN IN TWO CONTRASTING ENVIRONMENTS

In each figure, spectrum 1 is from plants grown in dune sand and 87% daylight with restricted water; spectrum 2 is from plants grown in John Innes no. 1 potting compost and 25% daylight with unrestricted water. Further details of cultivation are given in 6.2. Leaves from light conditions are shown life-size; those from the shade are reduced to $\frac{5}{8}$. The plants were 80 days old when dissected. Numbers under leaves refer to nodes.

1.



2.

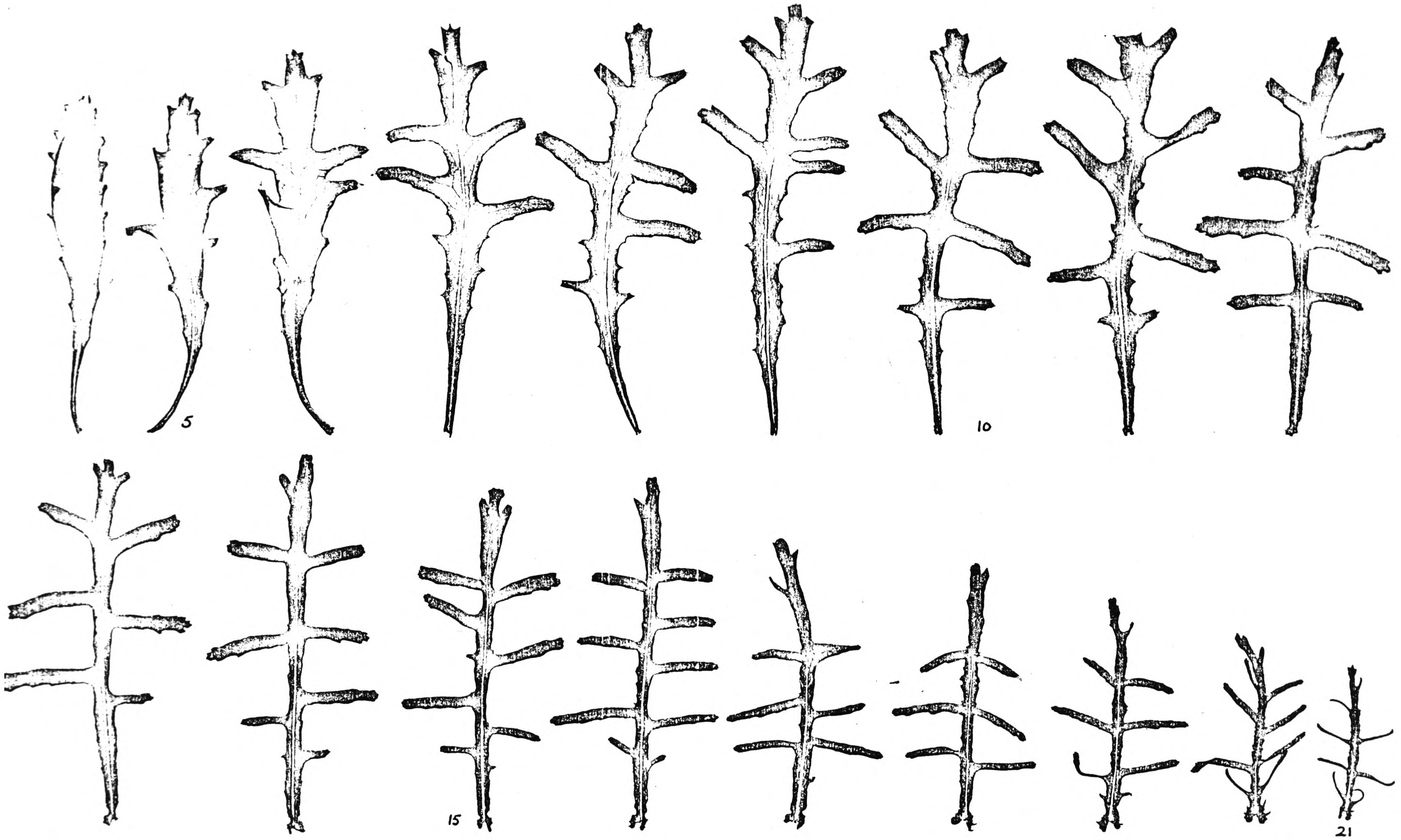


FIG. 15. LEAF SPECTRA OF S. JOPPENSIS (1)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$

FIG. 16. LEAF SPECTRA OF <u>S. GALLICUS</u> (24)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$

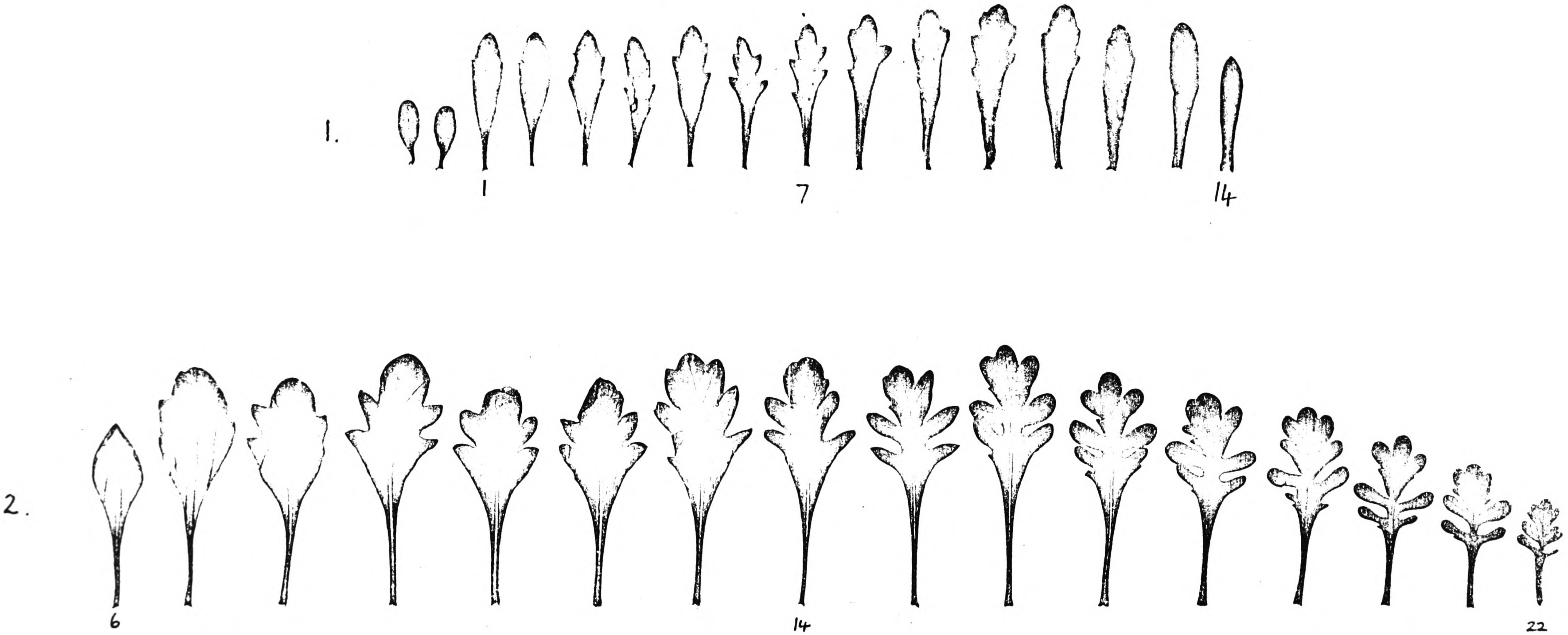


FIG. 17. LEAF SPECTRA OF <u>S. HESPERIDIUM</u> (52)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$

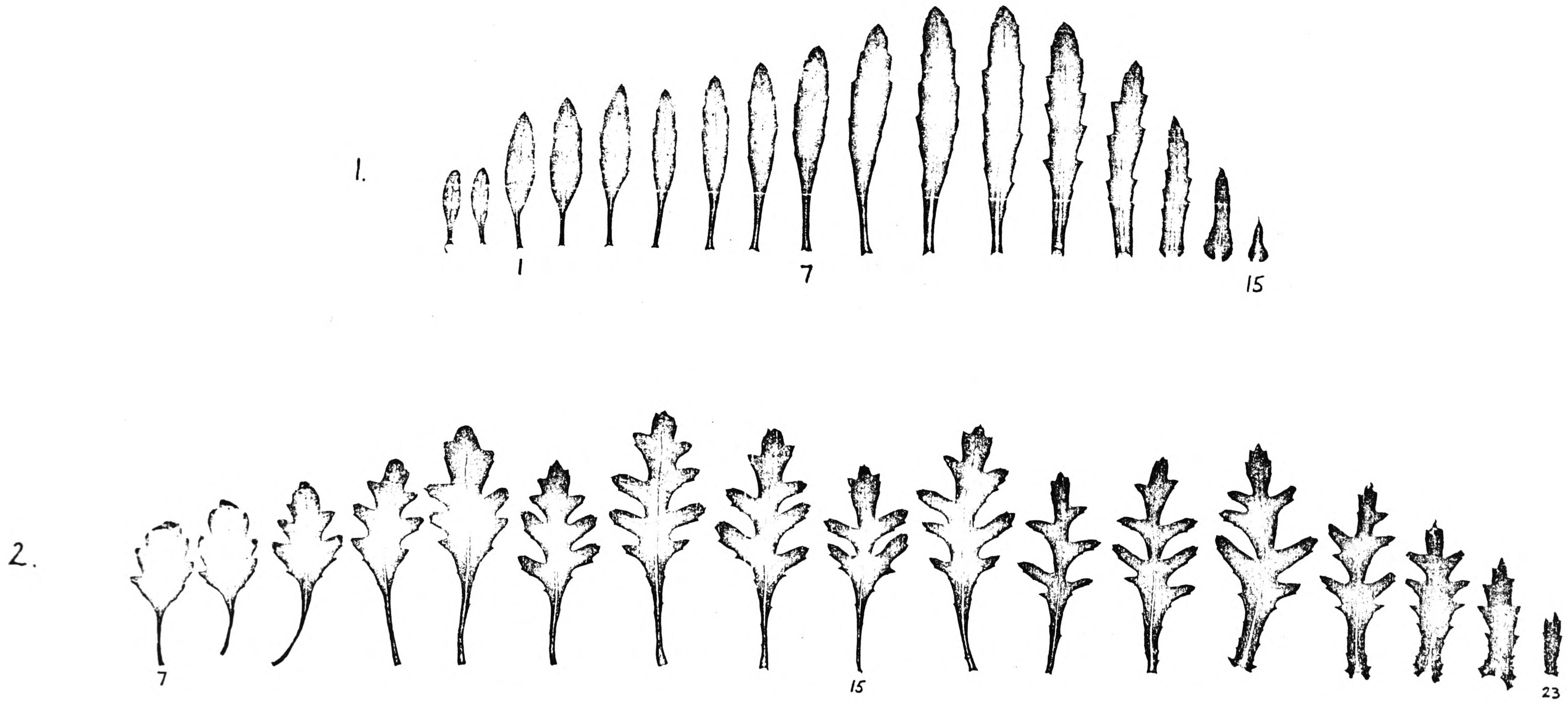


FIG. 18. LEAF SPECTRA OF <u>S. MAURITANICUS</u> (22)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$

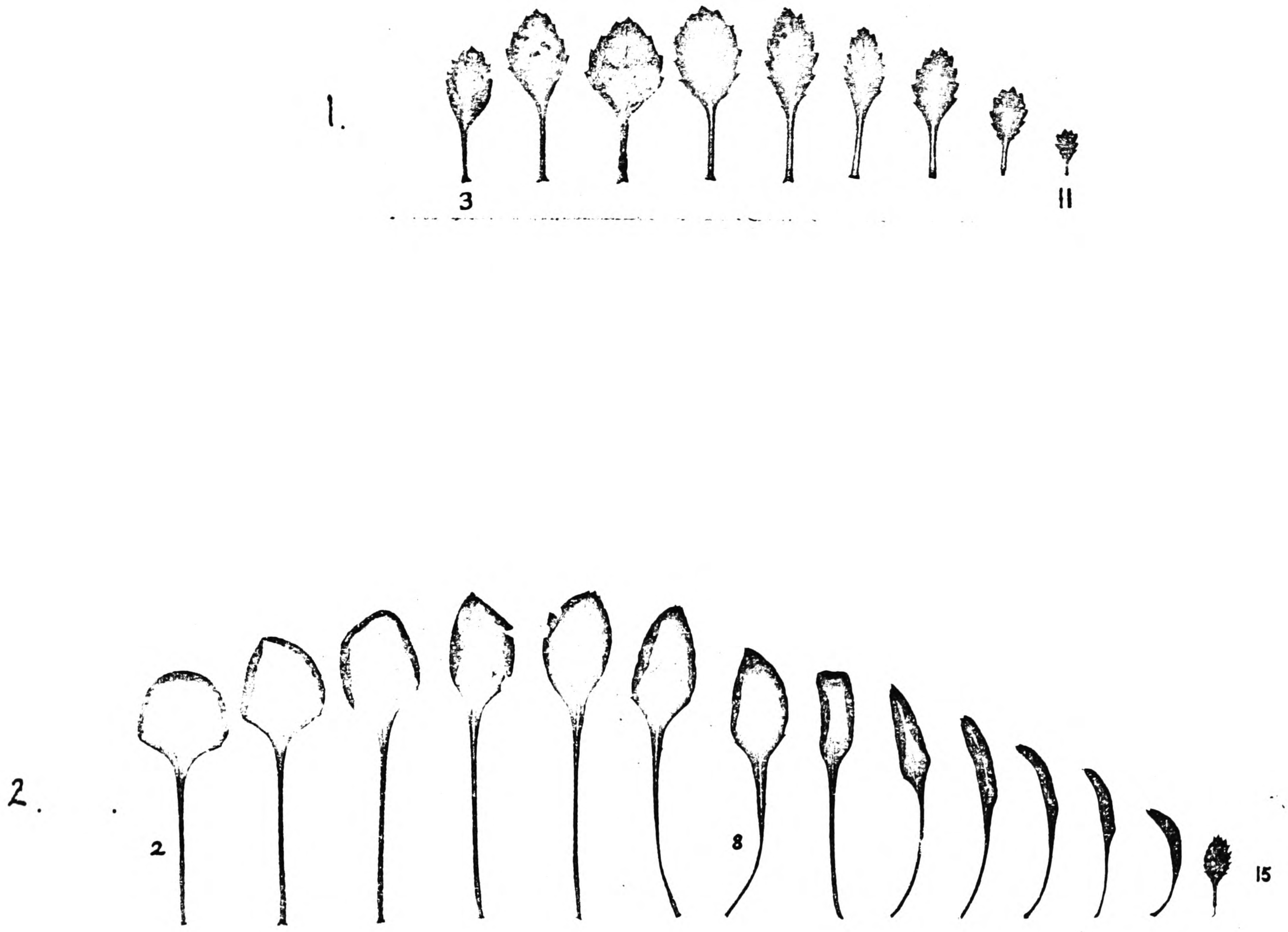


FIG. 19. LEAF SPECTRA OF <u>S. LEUCANTHEMIFOLIUS</u> (63)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$

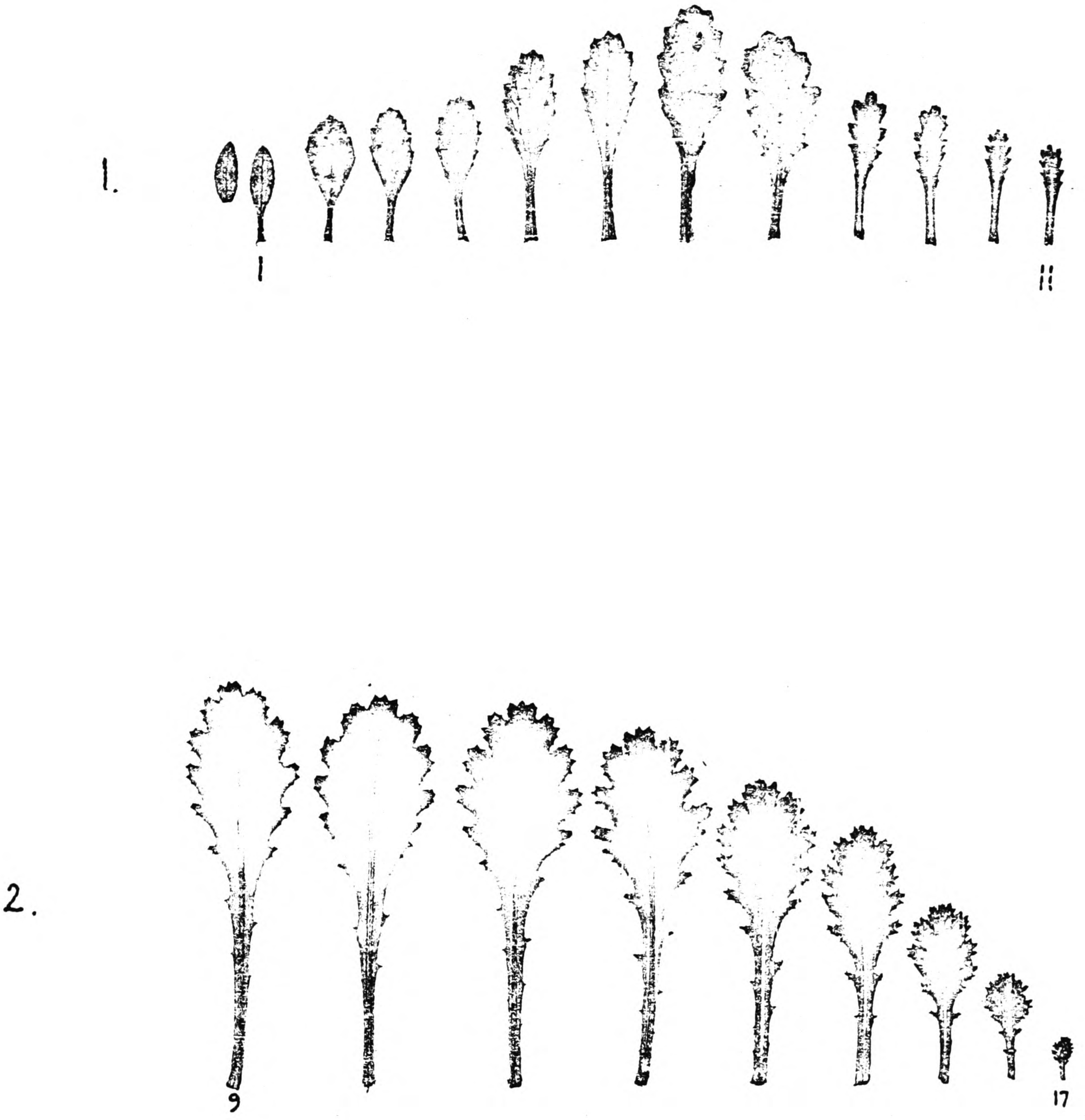
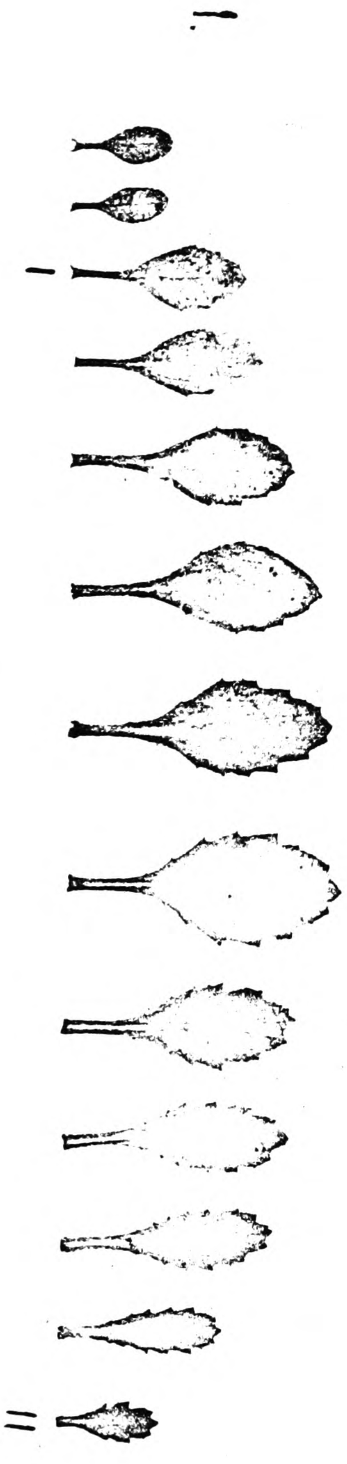


FIG. 20. LEAF SPECTRA OF <u>S. MAURITANICUS</u> (14)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$



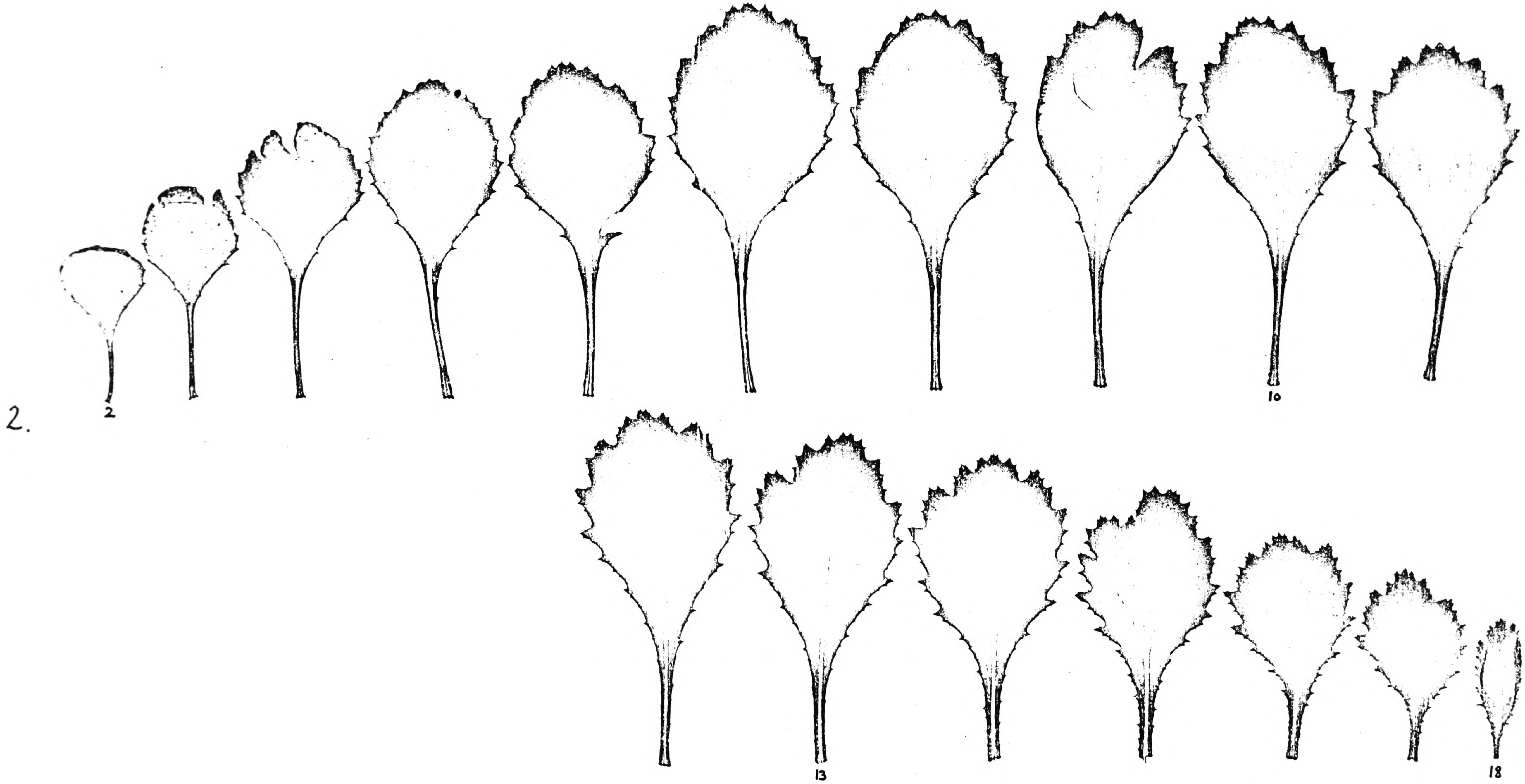


FIG. 21. LEAF SPECTRA OF <u>S. LEUCANTHEMIFOLIUS</u> (74)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$

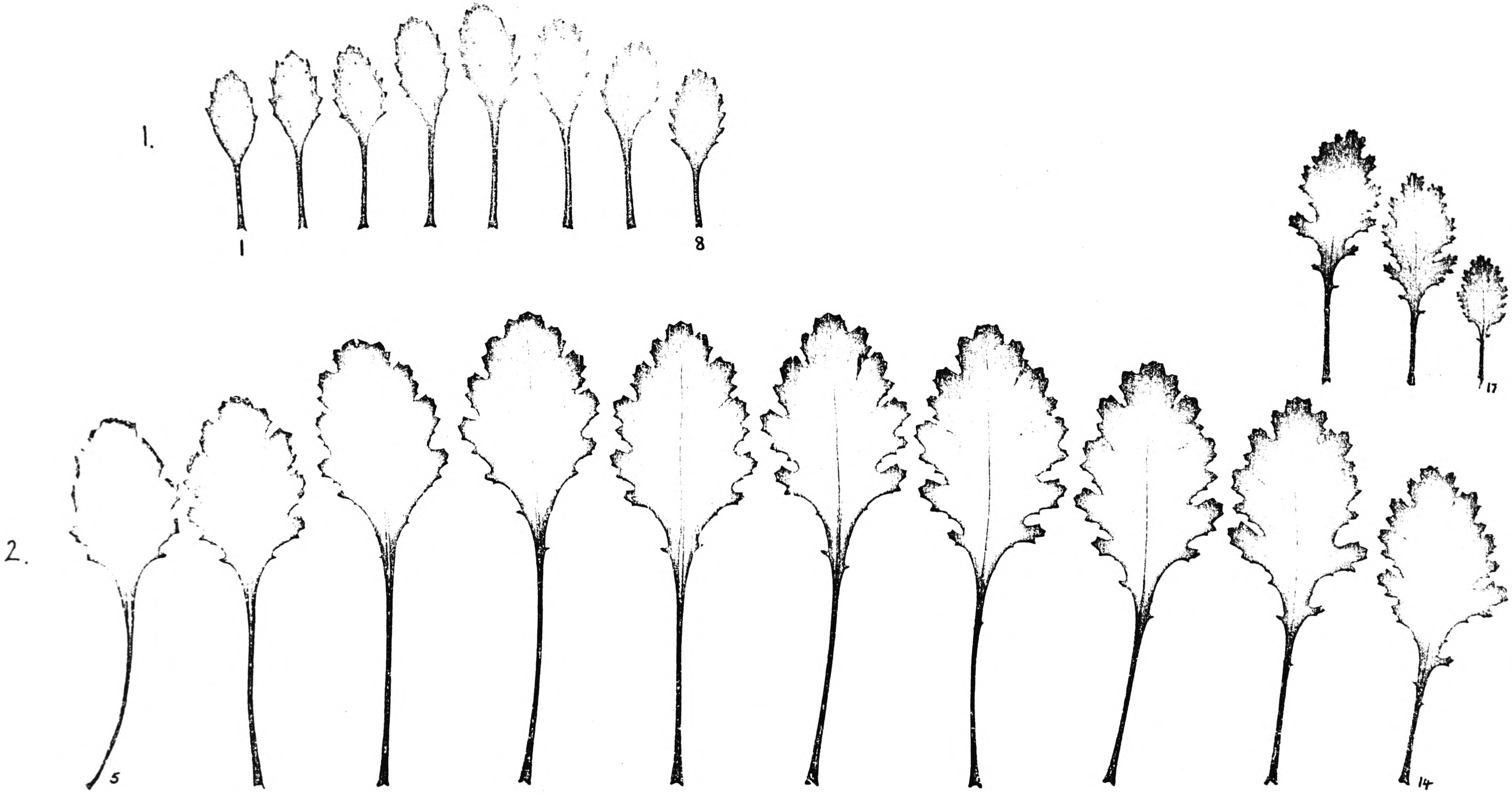


FIG. 22. LEAF SPECTRA OF S. GALLICUS VAR. ARANEOSUS (79)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$

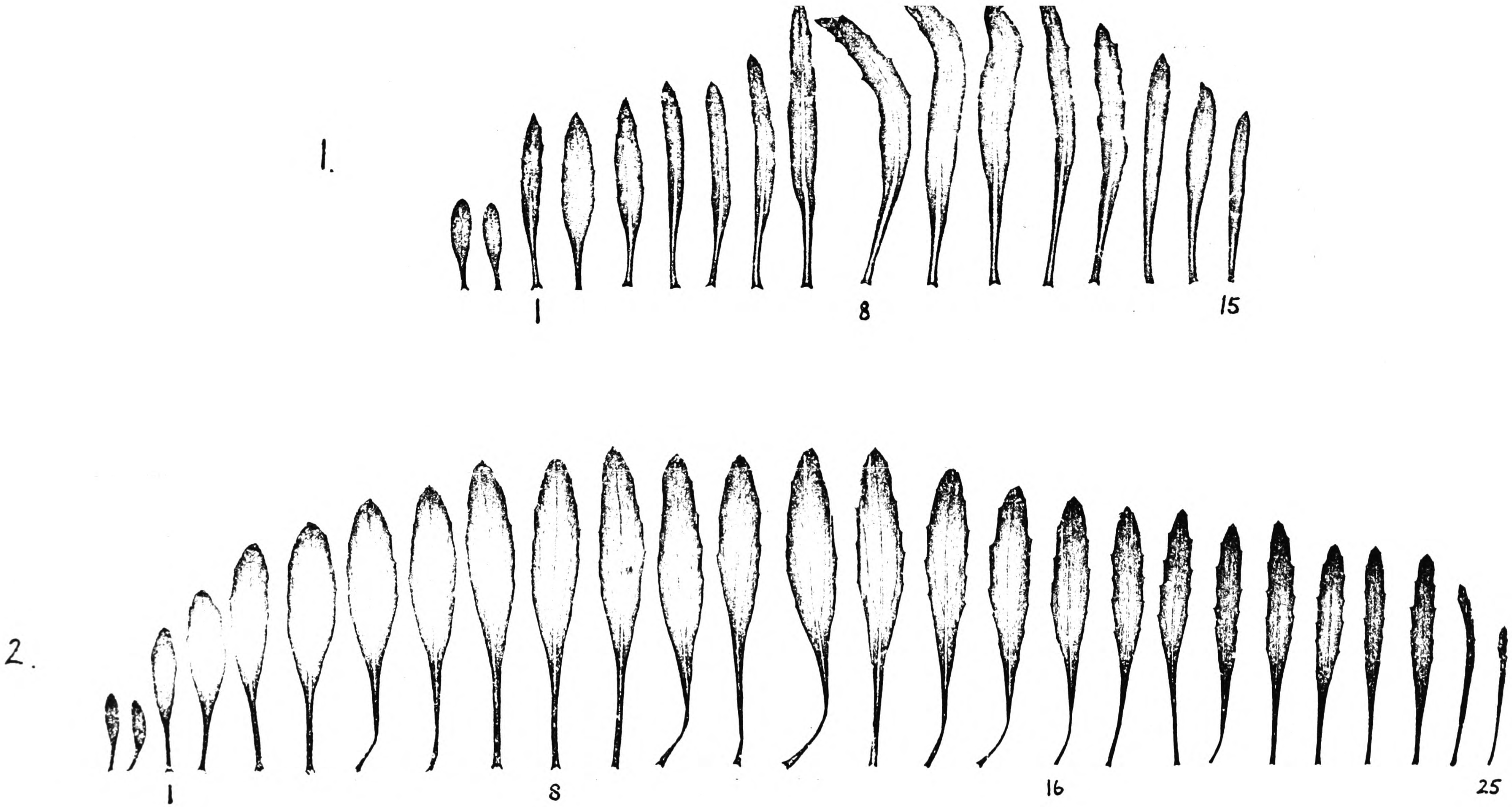


FIG. 23. LEAF SPECTRA OF S. PINGUICULUS (10)

1. 87% daylight x 1, 2. 25% daylight x $\frac{5}{8}$

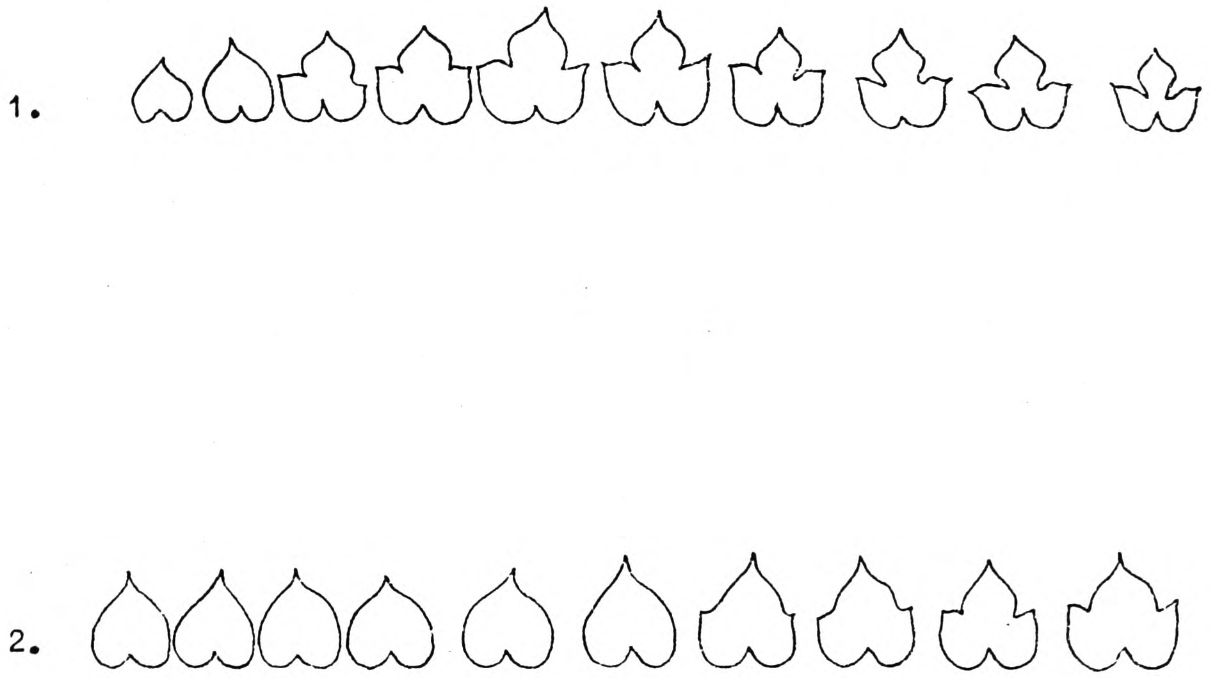


FIG. 24. LEAF SPECTRA OF *IPOMOEA CAERULEA* AFTER NJOKU (1956)
1. 100% daylight, 2. 40% daylight. One seventh life size.
Soil and water conditions uniform.

CHAPTER 7. BREEDING EXPERIMENTS

7.1 INTRODUCTION

The technique of artificial hybridisation followed by analysis of the F1 and subsequent generations is one of the major tools of experimental taxonomy. Several revisions of taxonomically difficult genera have been based on or influenced by data obtained in this way. Babcock (1947), in a detailed study of *Crepis*, used crossability data more in evolutionary interpretations of sectional relationships than for classification at the species level. He constructed an elaborate classification of the F1 plants produced, using ten different categories of fertility and vigour. Fertility was estimated by counting the proportion of plump achenes produced. Marsden-Jones and Turrill (1954), working with British species of *Centaurea*, found a high degree of interspecific fertility except for some sterility barriers which cut across what they refer to as 'taxonomic boundaries'. Presumably they mean morphological discontinuities between the species investigated. They assessed the fertility of a particular cross on the number of mature plants raised from each cross-pollinated capitulum. More recently, Strid (1970) investigating the *Nigella arvensis* complex in the Aegean area made a detailed analysis of hybrids produced in a series of reciprocal crosses. Morphological development, pollen fertility and in some cases meiosis and seed set were examined in the F1 hybrids. Some F2 families were also analysed.

Very little experimental work on the species involved in this study has been published. Crisp and Jones (1970) have investigated possible introgression from *S. squalidus* into *S. vulgaris* in Britain. The sterile triploid hybrid between these two species, [*S. x baxteri* Druce (Ellis, 1944),] has given rise to the fertile allohexaploid *S. cambrensis* Rosser (Rosser, 1955). Experimental crossing of *S. viscosus* and *S. vulgaris* has produced infertile hybrid seed (Gibbs, 1971).

Intensive work has been done on the complex around *S. lautus* Forst ex Willd. in Australasia (Ali, 1964a, 1964b, 1966 and 1969; Ornduff, 1960 and 1964). This group has many similarities to the pinnatifid annuals from around the

Mediterranean, both in morphology and taxonomic problems. The complex was shown to consist of about six groups, separated from each other by their ecological preferences. In some cases, the groups are still capable of exchanging genetic material, while in others reproductive barriers are present. The latter groups correspond to the geno-ecodeme of Gilmour and Heslop-Harrison (1954).

In the investigation recorded here, shortage of time made it impossible to grow the hybrids further than the F1 generation. In this chapter, the breeding experiments are divided into two parts. Section 7.3 deals with breeding systems. The synthesis, cultivation and analysis of hybrids is described in 7.4.

7.2 SPECIAL TECHNIQUES

None of the accessions cultivated appeared to be wholly self-incompatible so it was necessary to develop a reliable method of emasculation. Ornduff (1962) emasculated self-compatible races of S. lautus by removing the upper portions of young capitula with a razor blade, and then washing the cut heads twice a day to remove any pollen remaining in the flowers. In the progenies he found only a few individuals resulting from self-pollination. Gibbs (1971) working with short rayed and rayless species of Senecio has found that by cutting off the apical 1 mm of the capitulum at the correct stage of development, it is possible to remove "most of the anther tissue and virtually all of the pollen". In S. viscosus, 14% of the capitula treated this way produced a few achenes, though the average was only three to four per capitulum.

In the experiments described here, it was necessary to investigate the breeding systems and later cross-pollinate over thirty different accessions, so it was not possible to replicate each operation. For this reason a method of emasculation had to be developed which could be relied upon to produce no selfed seed. Dissection of disc flowers from annual species in various stages of development showed that about twenty-four hours before each flower opens there is a small gap between the top of the stigma and the bottom of the anther tube. This means that complete emasculation is possible in one operation (see Fig. 25). However, this operation will damage the stigmas of the older flowers and leave some pollen in the younger flowers. These flowers can all be removed from the capitulum with forceps. The blades of most fine forceps are too wide for this operation, but a pair with the points filed down to about 0.5 mm wide is quite efficient.

Emasculation stimulates the growth of the style, and twenty-four hours after the operation, the stigmas are found protruding from the cut ends of the flowers. They can then be closely examined with a high powered lens to see if there is any pollen on them. Several workers have emasculated capitula by removing all the hermaphrodite disc flowers leaving only the female ray flowers. In <u>Senecio</u>, I found this method unsatisfactory as very few achenes developed. Possibly the developing achenes became too dry without the disc flowers beside them. Humphries (in litt.) has used an ingenious technique in which the disc flowers are covered with typewriter correction fluid which sets sufficiently firmly to prevent the disc flowers from opening until the ray flowers have been fertilised. To ensure that the supply of pollen from male parents used in breeding system and hybridisation experiments was uncontaminated, only capitula which had been isolated before any of the flowers had opened were used as pollen sources. Pollination was effected by cutting bagged capitula, loaded with pollen, off the male parent and rubbing them against the emasculated capitula on the female parent.

Breeding experiments carried out on numbers of plants in the same glasshouse require a satisfactory method of isolating treated flowers. Many different methods have been employed. Whole plants can be isolated inside muslin cages. This is only suitable if all the flowers on the plant have been given the same treatment; small insects such as greenfly and whitefly, which are almost impossible to eradicate totally, can move pollen from flower to flower. Many different materials have been used to make bags in which to isolate individual flowers or capitula. Manila

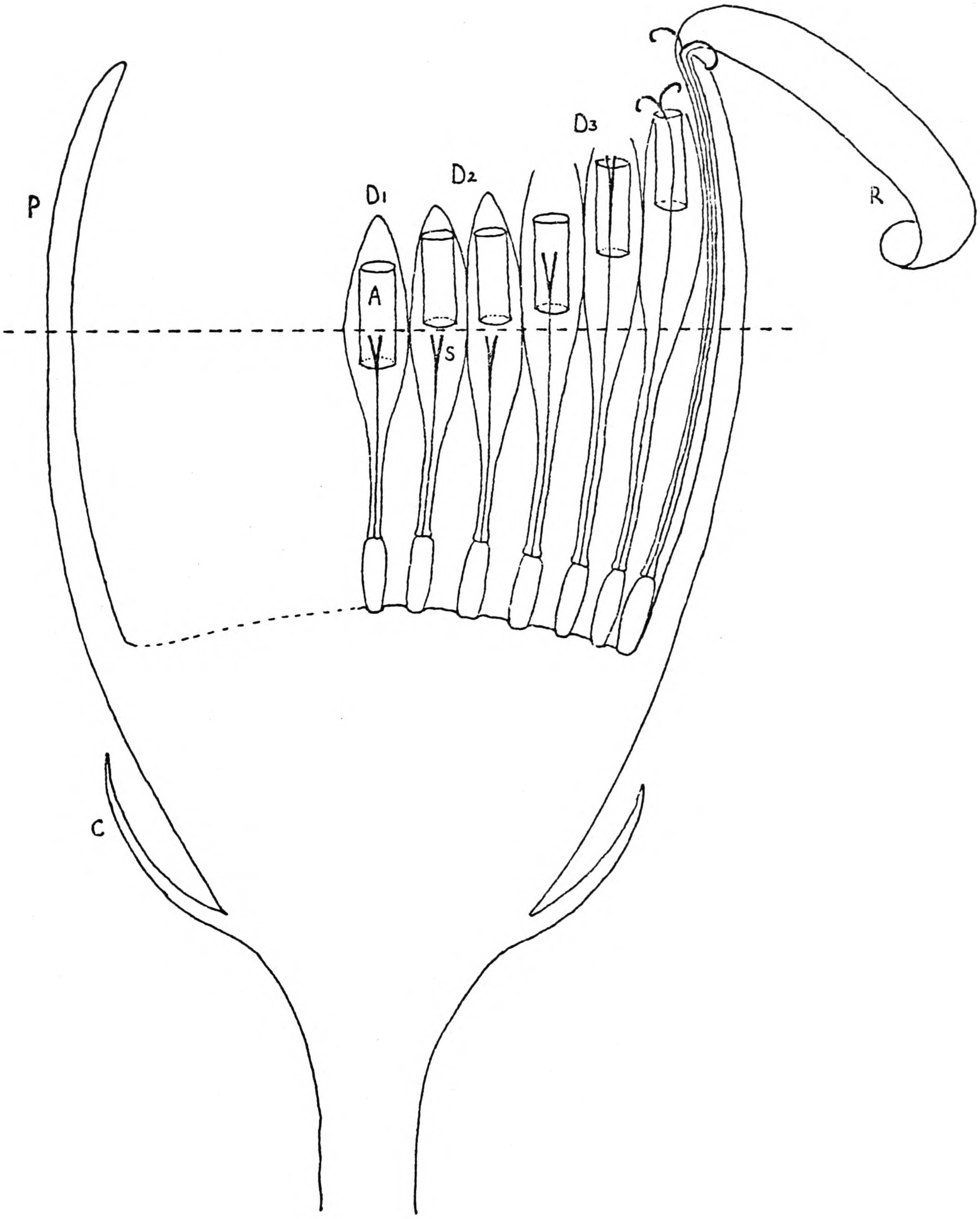


FIG. 25. DIAGRAMMATIC LONGITUDINAL SECTION THROUGH CAPITULUM x 15
A: Anther tube, C: Calyculus bract, D1: Youngest disc flower, D2: Disc flowers shortly before opening, D3: Open disc flowers, P: Phyllary, R: Ray flowers, S: Stigma. Pappus hairs and filaments omitted. Cutting at level indicated emasculates flowers D2.

envelopes, frequently employed in experiments with grasses, are too heavy for Senecio capitula. Initially I made bags from narrow muslin-tubing fastened at the top with sticky labels and drawn in at the base with threads from the muslin. I hoped that muslin would allow adequate ventilation and prevent moisture building up in the bags. However if the bags became damp, the muslin held the moisture and many capitula succumbed to fungal attack. Also there was a tendency for stigmas to protrude through the holes in the muslin. Bags were also made from cellophane ("Visking") dialysis tubing, which has the advantage that the progress of the ripening capitulum can be seen without removing the bag. However these bags are only slowly permeable to water and moisture from respiration soon accumulated inside. Eventually a technique was developed for making bags out of lens tissue, by glueing sheets together with narrow lines of paste. When the paste is dry, the tissue can be cut along the lines with a guillotine. These bags are easily made in large numbers and have several advantages over other materials used:-

a) They are totally pervious to water, preventing build up of humidity. If accidentally moistened, they dry out rapidly.

b) They are extremely light and do not weigh down the capitula.

c) Information about the cross can be written on the bag itself thus avoiding separate labelling.

d) They are easily sealed at the bottom with a small dab of glue, and cannot easily be blown off. This also prevents small insects entering from below.

e) Being semi-transparent, the state of the bagged capitulum is easily seen without removing the bag.

7.3 INVESTIGATION OF BREEDING SYSTEMS

7.3.1 MATERIALS AND METHODS

Four operations were carried out on capitula of all accessions cultivated:-

a) Isolation before flowers open

b) Emasculation and isolation

c) Emasculation, self-pollination and isolation

d) Emasculation, cross-pollination and isolation

In this context, self-pollination means pollination with pollen from the same plant and cross-pollination means pollination with pollen from another plant in the same accession. These experiments were designed to test for obligate and facultative outbreeding, facultative inbreeding and apomixis. It is realised that apomictic development of seed stimulated by pollination would not be detected. The three perennials, nos. 9, 31 and 18 could not be emasculated (see 7.4) and had to be crossed by rubbing pollen onto entire capitula. Each operation was performed at least twice for each accession. Further replication would have been desirable but as it was, these experiments involved bagging over 200 capitula.

7.3.2 RESULTS

The results of the breeding system experiments are tabulated in Fig. 26 together with average figures for ligule length during the first fortnight's flowering. There was little difficulty in deciding whether the achenes were developed or not, as they fell into two very obvious groups. Plump, dark achenes were considered developed and thin pale ones undeveloped. Subsequent crosses between accessions (see 7.4) produced a range of achene development and achenes were classified into four types.

7.3.3 DISCUSSION AND CONCLUSIONS

As no plants set seed after emasculation, it was assumed that all accessions were amphimictic. If apomixis stimulated by pollination was taking place, it would probably have been indicated in the results of crosses between accessions (7.4) by total resemblance of presumed hybrids to the female parent. This did not occur, although in one notable case the hybrids showed more resemblance to the female parent. As the hybrids from the reciprocal cross were also morphologically much

FIG. 26 TABLE OF SEED SET AFTER BREEDING SYSTEM EXPERIMENTS, AND LIGULE LENGTH

M = Many: More than half the achenes per capitulum developed.

S = Some: Less than half, but more than five achenes developed per capitulum.

F = Few: Five or fewer achenes developed per capitulum.

0 No achenes developed. In the last two columns, no quantitative results are given, as emasculation usually leaves only 10-15 flowers per capitulum, some of which may be damaged. Ligule lengths are averages over the first two weeks flowering (see 3.7.1).

No.	Name	Ligule mm	Isolated	Emasculated	Selfed	Crossed
43	vulgaris	-	M	0	+	+
34	aegyptius	-	M	0	+	+
66	massaicus	-	M	0	+	+
7	flavus	1.5	M	0	+	+
45	hoggariensis	5.0	S	0	+	+
63	leucanthemifolius	6.1	F	0	+	+
30	leucanthemifolius	6.8	0	0	+	+
6	vernalis	7.2	0	0	+	+
1	joppensis	7.4	0	0	0	+
21	mauritanicus	8.0	F	0	+	+
3	desfontainei	8.4	F	0	0	+
24	gallicus	9.2	F	0	+	+
4	joppensis	10.4	0	0	+	+
2	joppensis	10.9	0	0	+	+
22	mauritanicus	10.9	F	0	0	+
10	pinguiculus	11.0	F	0	+	+
9	gallicus v. araneosus	11.1	0	-	0	+
31	squalidus	11.5	0	-	F	+
44	vernalis	11.6	0	0	+	+
41	petraeus	11.7	0	0	0	+
52	hesperidium	12.4	F	0	+	+
18	balansae	14.4	0	-	F	+

closer to their female parent, this can be explained by cytoplasmic inheritance (7.6). No record of apomixis in Senecio has been found (Nygren 1954).

The rayless and short-rayed species, nos. 43, 34, 66 and 7, set plenty of seed when isolated and also when crossed. They are clearly inbreeders which are probably capable of outbreeding. S. hoggariensis (45), though having slightly longer rays, also comes into this category. Apart from no. 7 which is diploid, all the inbreeders are either tetraploid or hexaploid. This correlation of polyploidy and inbreeding has already been mentioned in 5.3. It is not surprising that these species should also show a reduction in size or number of attractive parts (Baker, 1961).

The rest of the annuals show some differences in seed set when isolated and when self-pollinated. Half of them did not set seed on isolation. Most of these, however, set seed when emasculated and self-pollinated. They cannot therefore be regarded as self-incompatible. I suspect that further replication of simple isolation experiments would show that all of them can set a few seeds. A slight increase in number of seeds set on isolation can be obtained by rubbing together capitula from the same plant. This could mean that the poor seed set is due to a failure of the usual Composite self-fertilisation mechanism (Small, 1915). However, a much greater increase in seed set results from self-pollination following emasculation. It is possible that surgical interference with the corolla and stamens lessens the already incomplete self-incompatibility barrier. Further experiments are necessary to determine the exact mechanism involved. The two annuals which set no seed on isolation or on self-pollination (nos. 1 and 41) may represent self-incompatible races of species which are generally self-compatible. S. petraeus, represented only by accession 41, could alternatively be a self-incompatible species.

The situation in the perennials seems similar. None of them sets any seed on isolation. Two of them, nos. 31 and 18, set a very few seeds when selfed simply by rubbing. The third perennial, S. gallicus var. araneosus (9), might also be truly self-incompatible, though it is probably capable of self fertilisation.

All accessions set seed when emasculated and cross-pollinated.

From the results of these experiments it seems likely that all accessions are self-compatible. Those having no ligules, or ligules of 5 mm or less are habitual inbreeders. The remainder, both annuals and perennials, while being habitual outbreeders are capable of self-fertilisation.

A very similar situation exists in the S. lautus complex in New Zealand. Ornduff (1960) records a number of experiments on breeding systems and interspecific fertility and concludes that, despite the primary outbreeding nature of the species investigated, all the taxa are in fact self-compatible. He recognises four species in the complex, two of them having subspecies which are normally inbreeders. Not surprisingly, these two taxa, S. glaucophyllus ssp. discoideus (Cheesem.) Ornduff and S. lautus ssp. carnulosus (T. Kirk) Ornduff, have respectively no ligules and ligules only 3-4 mm long. The Australian representatives of this complex are all long-rayed (Ali, 1966). He found an average set of only 0.12 seeds per capitulum on selfing. Whether the capitula were merely isolated or rubbed together is not mentioned. The level of self-compatibility was considered low enough to make emasculation unnecessary.

7.4 SYNTHESIS AND CULTIVATION OF HYBRIDS

7.4.1 MATERIALS AND METHODS

Thirty-two accessions were used as parents in the crossing programme. Emasculation and preparation of capitula of male parents are described in 7.2. Emasculation was performed about 24 hrs before the capitula were required, and capitula for pollen sources were bagged three or four days before the cross in question was made.

The emasculation technique described in 7.2 was found to be quite satisfactory on all the annuals. Dissection of flowers from the perennials showed that at no stage was the anther tube clear of the top of the stigma. Removal of all the pollen always resulted in damage to the stigmas. In a few cases, successful fertilisation was achieved by pollinating cut styles. As this was not reliable, I decided to use the perennials as male parents only.

The inbreeding polyploids, particularly S. vulgaris produced very limited quantities of pollen and are very easy to emasculate. The gap between anther tube and stigma is quite wide, and the flowers in any given capitulum are closer in age than in the outbreeders. This means that a larger proportion of the flowers can be satisfactorily emasculated without damage. Because of this, the inbreeding polyploids were used largely as female parents, though S. massaicus (66) produced more pollen than the other inbreeders and was used as a male parent as well. In a few accessions (nos. 2, 3 and 68), some male sterile plants were used as female parents, the anthers being atrophied. This worked well except that male sterility was found to be dominant, and the offspring were also male sterile. Lack of pollen in these hybrids does not necessarily mean that the parents are intersterile. Ali (1966) encountered the same phenomenon in the S. lautus complex of Australia.

The achenes usually took about three weeks to ripen. The reflexed state of the phyllaries, an indication of ripeness, was easily seen without removing the bags. When ripe, the capitula were removed from the plants, and the achenes were stored in the laboratory for a few months before sowing to overcome any dormancy problems. The degree of development of the achenes was scored in four categories:-

1. Soft, pale and thin, as unfertilised achenes
2. Hard, coloured and thin; or appearing fat but hollow
3. Hard, coloured and medium
4. Hard, coloured and fat.

In some cases, only very few achenes were produced. Up to 30 achenes from each cross were sown. Greenhouse space being at a premium, the achenes were initially sown in trays of 3 cm square "jiffypots" in the laboratory where they could be closely watched. As there were large numbers of achenes to deal with, they were planted in six batches at fortnightly intervals. After the first three batches had been planted, it was apparent that none of the poorest seed (grade 1) was germinating. As a considerable number of crosses had produced seed of this grade, to save time and space, I decided to plant seed of only grades 2, 3 and 4 in subsequent batches. Of those that germinated and survived, nine were transferred to 4 in. clay pots in the temperate greenhouse. Very often, the dry atmosphere in the laboratory kept the pericarp too dry and the cotyledons were trapped inside. Frequent application of drops of water from a bulb pipette softened the pericarp and allowed the cotyledons to burst through. Five plants from each cross were grown to maturity, the discarded plants being pressed whole or dissected for leaf spectra. When the plants flowered measurements of the floral parts were taken and pollen fertility was estimated by staining with propionic carmine. Grains that were evenly shaped and darkly stained were considered fertile. A sample of 300 grains was counted for every mature hybrid plant.

7.4.2 RESULTS

The success rate for all 139 crosses made was as follows:-

63 crosses gave hybrids which flowered and produced pollen
12 crosses gave hybrids which flowered and produced no pollen
8 crosses gave hybrid seedlings which perished
25 crosses gave good seed (grades 2, 3 or 4) which failed to germinate
31 crosses gave poor seed (grade 1)
139

Percentage fertility of pollen in those hybrids which produce pollen is shown in Fig. 27 which also gives details of crosses which failed to produce viable seed, and of hybrid plants which failed to produce pollen. Most of the latter are the results of using a female parent which was male sterile (see also 7.6).

			3	68	73	1	2	4	24	29	7
	desfontainei	3									
	"	68	N↑ ←N								
	"	73									
	joppensis	1									
	"	2		←85		92↑ ←89					
	"	4	95↑ NP↑		N↑	85↑ ←65					
	gallicus	24	35↑		26↑	52↑ ←P					
	"	29							80↑ ←93		
	inter. desf/maur	76									
	"	77		←95							
	hesperidium	52	N↑	←75	N↑	←L	N↑		←42		99
	mauritanicus	22			NP↑				N↑		←
	leucanthemifolius	30	N↑				NP↑			41↑	
	"	74		72↑			NP↑			68↑	←
	"	63								47↑	
	mauritanicus	13	65↑		NP↑		NP↑		N↑		87
	"	21									
	vernalis	6	N↑							N↑	
	"	44					NP↑			N↑	
	pinguiculus	10	N↑	L↑			NP↑			57↑	
	petraeus	41								87↑	
	flavus	7	←P					←P			
perennial	gallicus v. araneosus	9					L↑			58↑	87
	"	79									
	squalidus	31					NP↑			39↑	
	balansae	16									
	"	18	30↑								
4x	vulgaris	43	←18			←17			←10	N↑	
"	"	59									
"	massaicus	66	←14	←P		←3					
"	aegyptius	34	L↑			O↑ ←O					
6x	hoggariensis	45	←P	←P		←P			←P		
			3	68	73	1	2	4	24	29	76

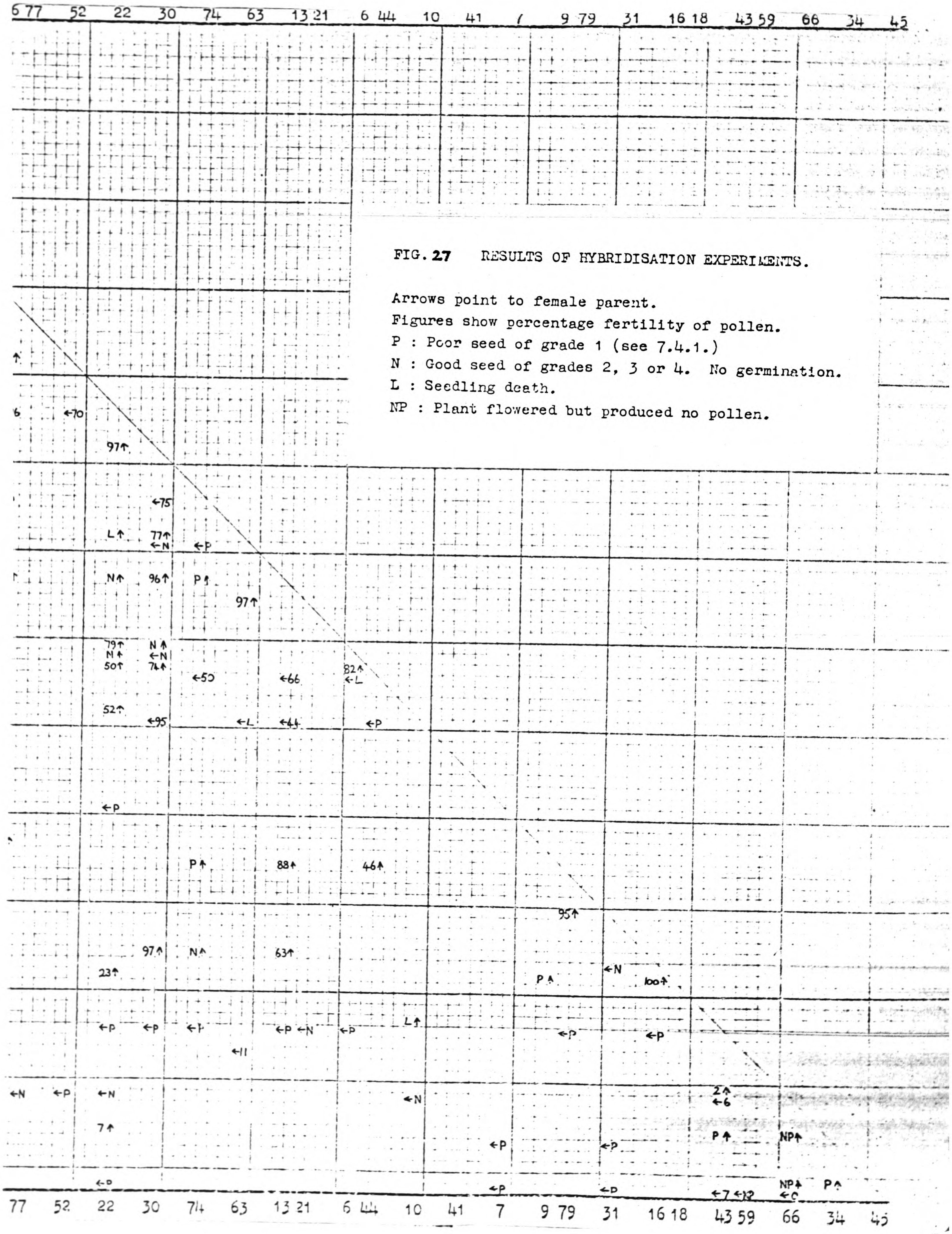


FIG. **27** RESULTS OF HYBRIDISATION EXPERIMENTS.

Arrows point to female parent.

Figures show percentage fertility of pollen.

P : Poor seed of grade 1 (see 7.4.1.)

N : Good seed of grades 2, 3 or 4. No germination.

L : Seedling death.

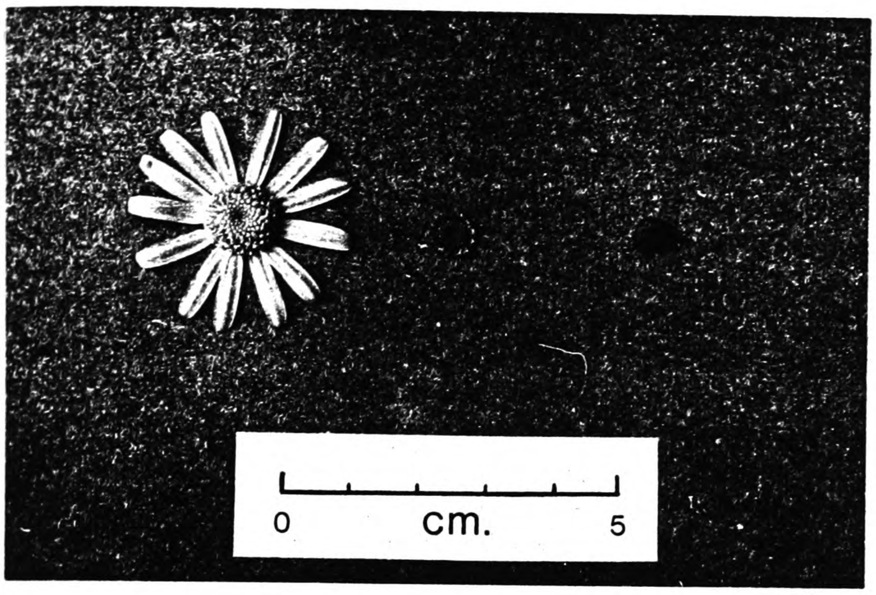
NP : Plant flowered but produced no pollen.

Morphologically, most hybrids were clearly intermediate between their parents in habit, leaf shape (App.II), and floral characters. Fig. 28 shows photographs of three hybrid capitula placed between their parents. In each case shown, the rayless S. vulgaris (43) was used as the female parent. Though there is little difference in ligule length between the male parents used in Fig. 28:1 and 2, the hybrid with S. gallicus (24) had much longer ligules. Absence of rays is probably caused by a gene or gene complex which partially suppresses the action of a supergene controlling ray length, flower sex and breeding system. Cross 43 x 1 could be another example of cytoplasmic inheritance. The reciprocal cross, which was not performed, might produce hybrids with much longer rays (see 7.6). Cross 43 x 45 in which the parents are respectively rayless and purple-rayed produce a hybrid with rays very nearly as long as the male parent and of a dull yellow colour (Fig. 28:3). Presumably S. vulgaris (43), though rayless, does carry a factor for yellow rays. Cases attributable to cytoplasmic inheritance in which offspring show a closer resemblance to the female parent are discussed in 7.6. The teratology of hybrids is described in 7.5.

7.4.3 DISCUSSION AND CONCLUSIONS

There is a distinct lack of correlation between seed score and pollen fertility (see Fig.27). In this group at least, taxonomic conclusions made on the basis of degree of hybrid seed development would be highly misleading. Seed development has frequently been used to assess relatedness of different plants used in crossing experiments (Babcock, 1947). Nearly 20% of my crosses produced seed of grades 2, 3 or 4 which failed to germinate. There may be a longer dormancy than was realised, and subsequent planting of these achenes might produce hybrid plants. Negative results must be treated with caution.

As different populations of the same morphological species often gave very different results when used in the same cross, I decided not to present the results



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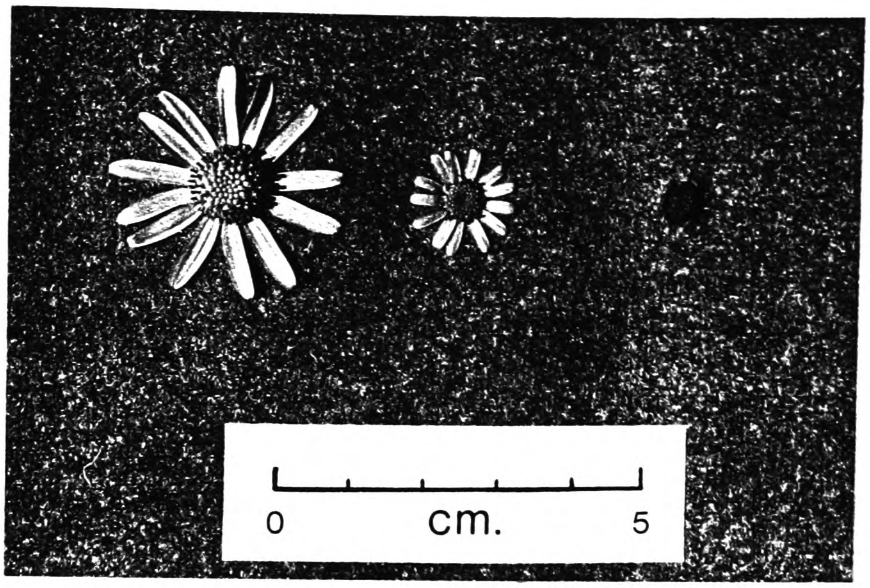

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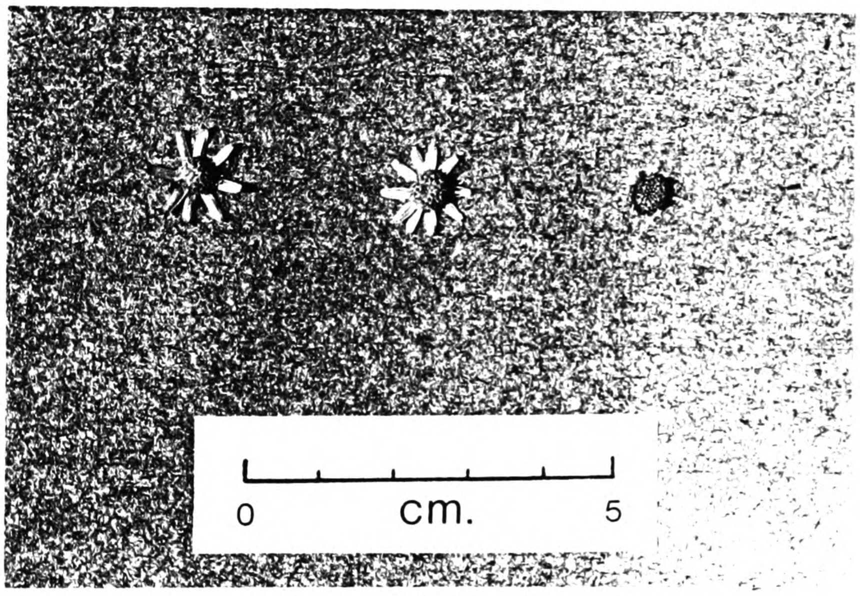


3

FIG. 28 PHOTOGRAPHS OF CAPITULA: PARENTS AND HYBRIDS

1. S. vulgaris (43) x S. joppensis (1). 2. S. vulgaris (43) x S. gallicus (24) 3. S. vulgaris (43) x S. hoggariensis (45). Hybrids are shown between their parents with the female parent on the right.

in the form of a crossing polygon as is frequently done in reports of breeding experiments (Clausen et al, 1941; Strid, 1970). To do so would have entailed either representing each accession used individually on the polygon, which because of the large numbers involved would not have communicated the results clearly; or combining the results obtained from different accessions of one morphological species to give a meaningless average. Conversely, the results do not suggest the presence of breeding groups, as distinct from morphological groups, which could have been used as points on a polygon. In addition, many results which would require averaging, involve descriptions of seed quality or pollen failure which cannot be expressed in figures. The situation is further complicated by cases in which reciprocal crosses gave contrasting results. Sometimes two different pollen fertilities were found; more often the seed from one cross failed to germinate, or the seedling died, e.g. 63 x 30, 44 x 6 and 24 x 1. Differences of this nature were also found between replicated crosses made in the same direction, e.g. 22 x 6. Instead, the results are presented in the form of a crossing chart (Fig. 27), which shows the result of each cross made. Unless otherwise indicated the parents are annual and diploid.

In general, the pollen fertility of hybrids was very high when compared with data similarly obtained in other groups of plants e.g. Nigella (Strid, 1970). However, other work on annual *Senecio* species shows very similar results (Ali, 1966 and 1969; Ornduff, 1960 and 1962). There was no obvious correlation between morphology and crossability of parents. Plants of very different morphology, long regarded as different species, produced hybrids with highly fertile pollen. Crosses 10 x 30, 29 x 41, 13 x 79, 79 x 31 and 30 x 16 all had pollen fertilities of over 85% (Fig. 27). In each case, the parents are morphologically distinct. The last three crosses mentioned are between annuals and perennials. This calls into question the use of life-form in delimiting sections within *Senecio*. Numbers 79 and 16 would have been put into Section *Jacobaea* (Cass.) Dumort. by de Candolle (1837).

Conversely parents which are very close morphologically sometimes gave hybrids of low fertility. Cross 73 x 24 between accessions often referred to *S. gallicus* had a pollen fertility of only 26% (Fig. 27). More often though, crosses between morphologically similar parents yielded hybrids of high pollen fertility.

As expected, interploid crosses were less fertile than any others; they were nevertheless surprisingly high. The tetraploid *S. vulgaris* (43 and 59) when crossed with four different diploids, in each case produced hybrids with pollen which was more than 10% fertile. Ornduff (1960) found no fertile pollen in interploid crosses in the *S. lautus* complex in New Zealand.

A discussion on the performance of different morphological groups used in the crossing experiments follows.

Number 3 (*S. desfontainei* from Israel) appears more similar to no. 4 (*S. joppensis*) than to any other accession. This cross when replicated failed to produce pollen, probably because a male sterile plant of no. 3 was used as the female parent. The seed produced when no. 3 was crossed with other accessions of the same species from Morocco (68 and 73) failed to germinate. These two show most affinity with no. 2 (*S. joppensis*), no. 76 (a morphological intermediate between *S. mauritanicus* and *S. desfontainei*) and with no. 52 (*S. hesperidium*) which on morphological grounds can be classified as a coastal variant of Moroccan *S. desfontainei*.

The three accessions of *S. joppensis* (nos. 1, 2 and 4), apart from affinities with nos. 3 and 68 just mentioned, produce negative results again due to the use of a male sterile parent.

Numbers 24 and 29 (*S. gallicus*) though showing a high fertility with *S. petraeus* (41) a local Spanish endemic, seem fairly isolated from other accessions.

Numbers 76 and 77 have affinities with members of both main groups. This is reflected in their morphology.

Number 52 (*S. hesperidium*) shows greatest affinity with the intermediates just mentioned, but is also quite fertile with members of both main groups.

Numbers 22, 30, 74, 63, 13 and 21, all members of the leucanthemifolius group, do not show very coherent results when crossed with the same parents, but show a higher fertility within their group than when crossed with members of the gallicus group.

Numbers 6 and 44, though rather different in morphology and habit, have both been referred to S. vernalis. Their affinity seems to be with the leucanthemifolius group. On morphological grounds it is very hard to distinguish S. vernalis from leucanthemifolius.

Number 10 (S. pinguiculus), often regarded as a separate species, gave highly fertile hybrids when crossed with no. 30 (S. leucanthemifolius).

The behaviour of the perennials and the annual tetraploids and hexaploid are discussed in the general remarks about the crossing experiments above.

While an indication of the genetic affinities of certain accessions can be gained from these results, it must be stressed that statistically they are not valid. At most levels in the investigation the sampling has not been extensive enough to give results upon which to construct a reliable classification. Only a very few populations, and in some cases only one population, were sampled for each species represented. Shortage of space and time made it impossible to perform most of the crosses more than once, and only a proportion of the total crosses possible was made. Ideally, larger families of F1 plants should have been grown and tested for pollen fertility. With the aim of getting an idea of the affinities within the group as a whole, it was decided to cover as much of the group as possible experimentally while bearing in mind the drawbacks just mentioned arising from the need to restrict the depth of study of each taxon involved.

7.5 HYBRID TERATOLOGY

A considerable number of the hybrids were deformed. In several cases, the achenes produced by the female parent after crossing were twisted and wrinkled while appearing well filled. Cross 66 x 1 gave very twisted achenes which germinated successfully. The twisting was seen to be caused by contortion of the cotyledons which appeared to be too long to fit neatly into the achenes (Fig. 29 : 1 and 2). Once the seedlings emerged, the cotyledons expanded normally and the plants survived to maturity. In one case (63 x 22) several achenes produced two seedlings each, most of which were deformed. Fig. 29 : 3 and 4 shows a pair of seedlings which emerged from one achene . In one of them (Fig. 29 : 4), the cotyledons were fused together and very reduced, forming a saucer-shaped depression on tcp of the young stem. The other one (Fig. 29 : 3) had much larger cotyledons,which were fused together along one side; the next leaf and terminal bud appeared at their base. This fusion of cotyledons was also found in 22 x 18 and 29 x 74. Almost total fusion of cotyledons up both sides was seen in 22 x 10 (Fig. 29 : 5); some of these seedlings had to be operated on to allow the growing point to emerge. Cross 2 x 9 produced an albino seedling which only survived for a few days. Most crosses producing fused but relatively undeformed cotyledons survived to maturity.

No vegetative deformities were seen in mature plants apart from albino patches on the leaves of 30 x 16.

A variety of deformed capitula and flowers were observed. Crosses 73 x 13 and 73 x 22 both produced shrunken, wrinkled capitula which failed to open. Dissection showed that a mass of deformed floral tissue had been developed, but no pollen was found. In one cross (22 x 34) a minute capitulum was found growing out from between the phyllaries of a normal head (Fig. 30 : 1). Most capitula, which opened normally, developed well formed flowers, but in a few cases, bizarre forms of ray and disc flowers were found. Cross 66 x 45 produced disc flowers having various numbers of lobes, none of them being five-lobed. Most of them were three-lobed with trifid stigmas (Fig. 30 : 2). This cross also produced very tattered ray flowers (Fig. 30 : 3 and 4). A bilabiate ray flower was developed in cross 1 x 34 (Fig. 30 : 5) similar to that found in Seris (Mutisieae). This has been

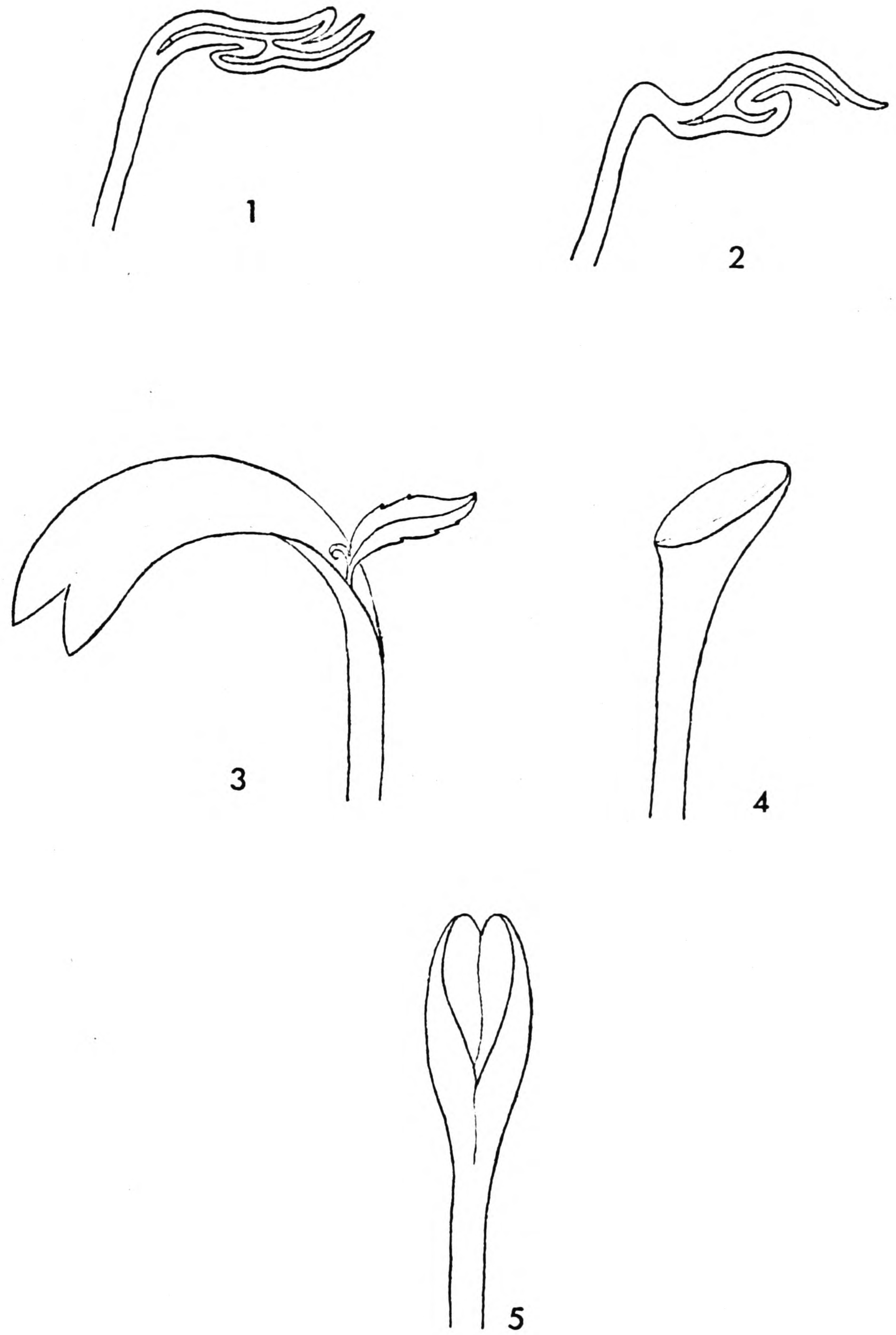


FIG. 29. HYBRID TERATOLOGY: COTYLEDONS

1 and 2. *S. massaicus* (66) x *S. joppensis* (1)

3 and 4. *S. leucanthemifolius* (63) x *S. mauritanicus* (22)

5 *S. mauritanicus* (22) x *S. pinguiculus* (10). All x 5.

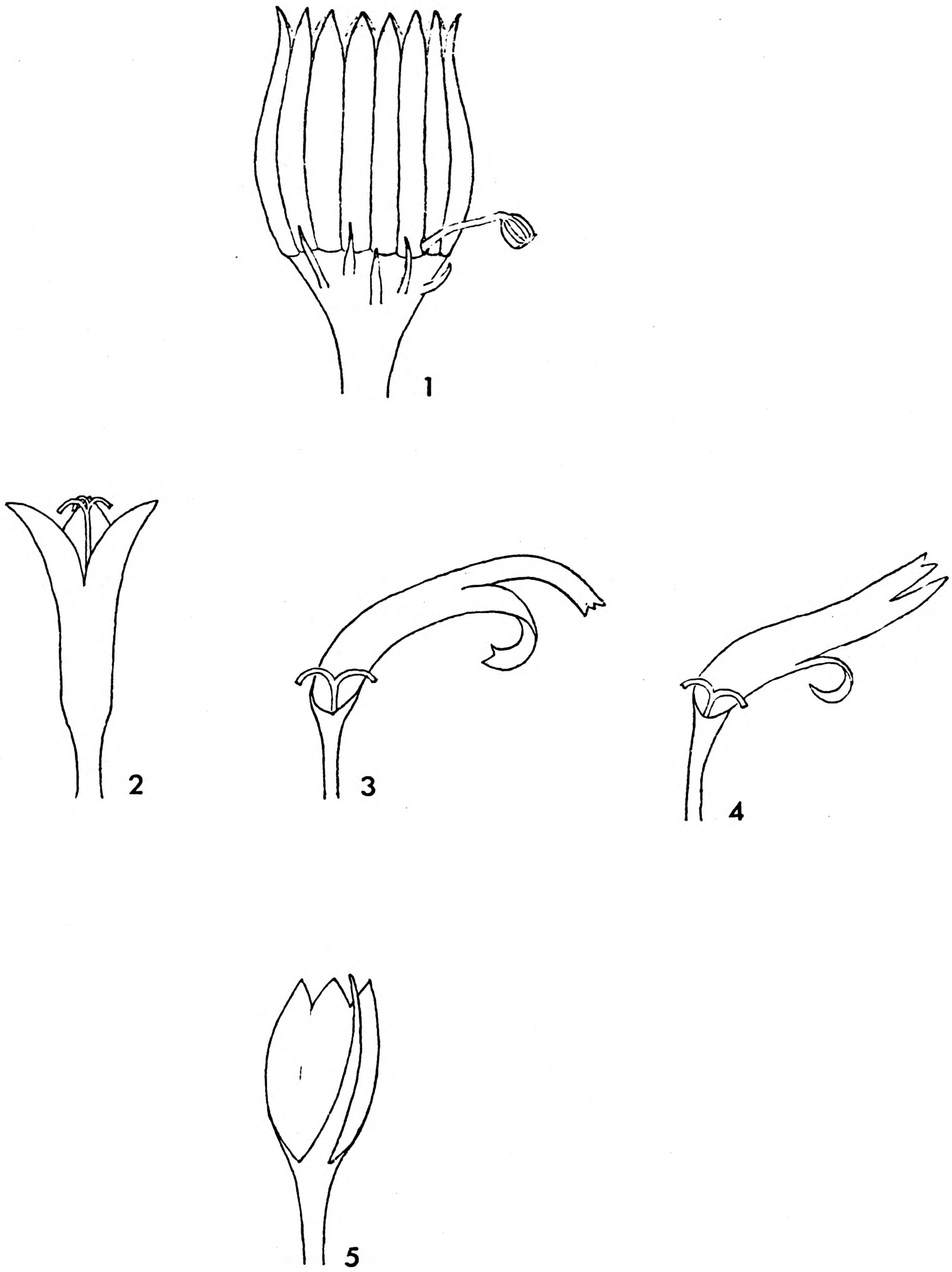


FIG. 30. HYBRID TERATOLOGY: CAPITULUM AND RAY FLOWERS

1. Capitulum x 6 of S. mauritanicus (22) x S. aegyptius (34),

2. Disc flower x 20 of S. massaicus (66) x S. hoggariensis (45),

3 and 4. Ray flowers x 20 of S. massaicus (66) x S. hoggariensis (45).

5. Ray flower x 20 of S. joppensis (1) x S. aegyptus (34)

sporadically recorded in Senecio (Small, 1919: 80). Several crosses between rayed and rayless forms produced short rays with vestigial anthers in the ray flowers.

There was no apparent correlation between deformity of seedling and low pollen fertility. Deformities of flowers were often the result of crosses between different ploidy levels and were usually accompanied by very low pollen fertility.

7.6 CYTOPLASMIC INHERITANCE IN CROSS 45X66

The hybrids resulting from one of the crosses which was made reciprocally, while clearly intermediate between their parents, were in each case morphologically closer to the female parent. Some of the characters of the parents and hybrids are tabulated in Fig. 31.

Using no. 45 as the female parent, the hybrids produced pale yellow ligules which were slightly shorter than in no. 45, with purple veins. Using no. 66,which has no ligules,as the female parent, the hybrids produced shorter ligules without any purple veins. That both F1 populations examined were hybrids is shown by their failure to produce any stainable pollen grains (see Fig. 27). Cases such as this in which hybrids show a morphology closer to the female parent have been shown to be the result of inheritance of characters controlled by particles carried in the cytoplasm of the female cells.

As the zygote receives a much larger quantity of cytoplasm from the female parent than from the male parent, the offspring may show a closer resemblance to the female parent. In some cases it has been suggested that the particles may be viral in origin and not truly part of the plants hereditary material (Swanson, 1963). Several of the hybrids failed to produce any pollen as distinct from producing pollen with 0% fertility. In most cases one of the parents used was male-sterile, a character which has been shown to be carried in the cytoplasm.

	hoggariensis (45)	45 x 66	66 x 45	massaicus 66
2n	60	-	-	40
ligule no.	8-10	7-8	12-13	0
" length mm	4.5-5.5	3.5-4.0	2.0	-
" breadth mm	1.0-1.5	1.0-1.5	0.5	-
" colour	pale petunia purple, RHS 32/2	pale barium yellow, RHS 503/3, purple lines	pale sulphur yellow, RHS 1/2, no lines	-

Fig. 31. TABLE OF LIGULE CHARACTERS FOR S. HOGGARIENSIS (45), S. MASSAICUS (66) AND THEIR HYBRIDS AFTER RECIPROCAL CROSSES.

Colours are taken from the Royal Horticultural Society Colour Chart.

CHAPTER 8 ADDITIONAL TECHNIQUES

8.1 FLAVONOID CHROMATOGRAPHY

8.1.1 INTRODUCTION

Considerable work has been done on the alkaloids in Senecio as surveyed by Darnley Gibbs (1974). One group in particular, the pyrrolizidine alkaloids, has been called the 'Senecio alkaloids' (Manske & Holmes, 1954). Apart from this and various isolated reports of other chemicals, the genus is relatively unexplored chemically. Glennie et al (1971) surveyed the flavonoid chemistry of the complex around S. radicans (L. f.) Sch. Bip. with a view to finding data which might be taxonomically useful. However, they found a much stronger correlation between chemistry and geography than between chemistry and morphology or cytology.
Some work on the occurrence of esterases in rayed and non-rayed forms of S. vulgaris in central Scotland has been done by Hull (1974b). He found that esterase patterns in rayed forms showed certain similarities to patterns found in S. squalidus from the same area, and cites these data as further evidence that introgression is occurring from S.squalidus into S. vulgaris. This has previously been suggested by Crisp & Jones (1970) and by Hull (1974a). Hull (1974b) mentions in passing that S. viscosus also occurs in the areas which he sampled for S. vulgaris and S. squalidus. As S. viscosus has rays, albeit short ones, it would be pertinent to explore the esterases of that species as well. Hull does not mention that S. vulgaris, like S. viscosus, is tetraploid with 2n = 40 (see 5.3.1), while S. squalidus is diploid. Neither Crisp & Jones nor Hull make any suggestion as to how introgression can occur between species on different ploidy levels, whose hybrids would normally be triploid and sterile. Possible interaction between S. vulgaris and S. squalidus is discussed further under S. vulgaris in 9.2.3.

8.1.2 PRACTICAL DETAILS

As a pilot study, eighteen accessions covering a range of morphology, ploidy and life-form were selected for a survey of leaf flavonoids. In each case, 1 gm of fresh leaf was ground up with 1% hydrochloric acid in methanol with a pestle and mortar to extract the phenolic compounds (Alston & Turner, 1963). The leaf particles were removed by centrifuge and the supernatant extract stored at 4°C. Some of the extracts turned brownish-blue on standing. As this reaction might have involved the deterioration of flavonoids, further extractions were made after poisoning the extractant with 0.1% potassium cyanide. Equal quantities of the extracts were then 'spotted' onto 45 x 57 cm. Whatman no. 3 chromatography paper, and the flavonoids separated by partition chromatography using n-butanol: acetic acid: water in the proportions of 4:1:5 (Harborne, 1973). After shaking, the water phase of the mixture was placed in the bottom of a chromatography tank and the alcohol phase used to elute the extracts by descent for about 16 hours. The presence of flavonoids on the paper was then detected in three ways:-

1. Examination in visible light: spots greenish-brown.
2. Examination in ultra-violet light: spots fluorescent
3. Examination in visible light after spraying with a mixture of equal volumes of 1% solutions of ferric chloride and potassium ferricyanide in water: spots blue, pink, or paler than surrounding paper.

Good separation of spots was observed. For each accession, about ten spots were definable by the three methods described. However, few qualitative differences were found, and where present they showed no correlation with morphology, geography or cytology. In some cases, quantitative differences were noticed between accessions in the degree of development of certain spots, but again there was no correlation. Quantitative differences were also noticed between poisoned and non-poisoned extracts of the same accession. As the taxa involved in this investigation form a closely knit group, it is not very surprising that their flavonoid chemistry should be fairly uniform. The pilot study was not extended.

8.2 SCANNING ELECTRON MICROSCOPY

8.2.1 INTRODUCTION

One of the first papers to recognise the application of scanning electron microscopy (SEM) to morphology and taxonomy was published by Thornhill et al (1965). They remarked that SEM is particularly useful for examining structures too small or detailed to give good replicas for transmission electron microscopy (TEM). They don't mention the additional advantages of easy specimen preparation and tremendous depth of focus. Since then, numerous papers describing SEM of a wide range of biological material have been published.

Heslop-Harrison & Heslop-Harrison (1969) looked at the leaves of several angiosperms and gymnosperms. They consider that xerophytes make better specimens than mesophytes, as they possess a more solid structural skeleton which will not be destroyed by desiccation during preparation and viewing. They suggest that a technique be developed for impregnation of mesophyte tissue with a polymerising agent which would hold the tissue in place when dessicated. A more recent paper by Heslop-Harrison (1970) describes how fresh moist material may be viewed uncoated for a few seconds before it collapses. Several workers have examined the bloom on leaves of many glaucous species as seen by SEM (Heslop-Harrison & Heslop-Harrison, 1969; Holloway, 1971; Baker & Holloway, 1971; Page, 1972). This is due to superficial crystaline deposits of wax, the exact form of which may be highly specific. Examination of the cuticular surface below the wax may require removal of the crystals, either by previous polishing of the leaf, or by melting the wax in the electron beam of the microscope.

Pollen has also received much attention since the development of SEM. The fossil pollen of Scandinavian species of <u>Artemisia</u> was examined by Praglowski (1971). He noted that the genus was 'stenopalynous' having very uniform pollen morphology and concluded that these data were of little use for specific identification in the genus. Earlier working involving TEM in other species of the Compositae suggests that in general, pollen studies are of little value at the lower taxonomic levels. Skvarla & Larson (1965) examined pollen from a wide range of species in the family and concluded that both the Heliantheae and the Anthemideae were uniform in pollen morphology. Payne & Skvarla (1970) used TEM to examine representatives of all evolutionary groups in Ambrosia and found no significant differences between species or between Ambrosia and Franseria which they consider should be congeneric. I have not found any comparative work on Senecioneae pollen.

8.2.2 MATERIALS, METHODS AND RESULTS

A brief survey was made of pollen and leaf surfaces of a few cultivated accessions. Fresh material was fixed with double-sided 'Sellotape' onto aluminium stubs, coated with gold-palladium and examined in a Cambridge mk II 'Stereoscan'. Photographs were taken. The results are shown in Figs. 32-34.

8.2.3. LEAF SURFACES

Number 22 (Fig. 32:1 and 2), a non-glaucous plant has a cuticle devoid of superficial wax crystals. The highly wrinkled surface is presumably due to desiccation and is not natural. A considerable deposit of wax is seen on the upper and lower surfaces of no. 10 (Figs. 32 : 3, 4, 5 and 6) which are very glaucous. The crystals on the upper surface are capitate, while those on the lower surface are flat and adpressed to the cuticle. This accession came from a sandy river terrace near sea-level and is presumably subject to desiccation by wind and sun. Number 22 is a weed of fallow fields and is less likely to experience such desiccation. Inspite of ecological and morphological differences, these two accessions are fairly interfertile, their hybrid having a pollen fertility of 52% (Fig. 27). Number 7 (Figs. 32 : 7 and 8) is a distinct species both

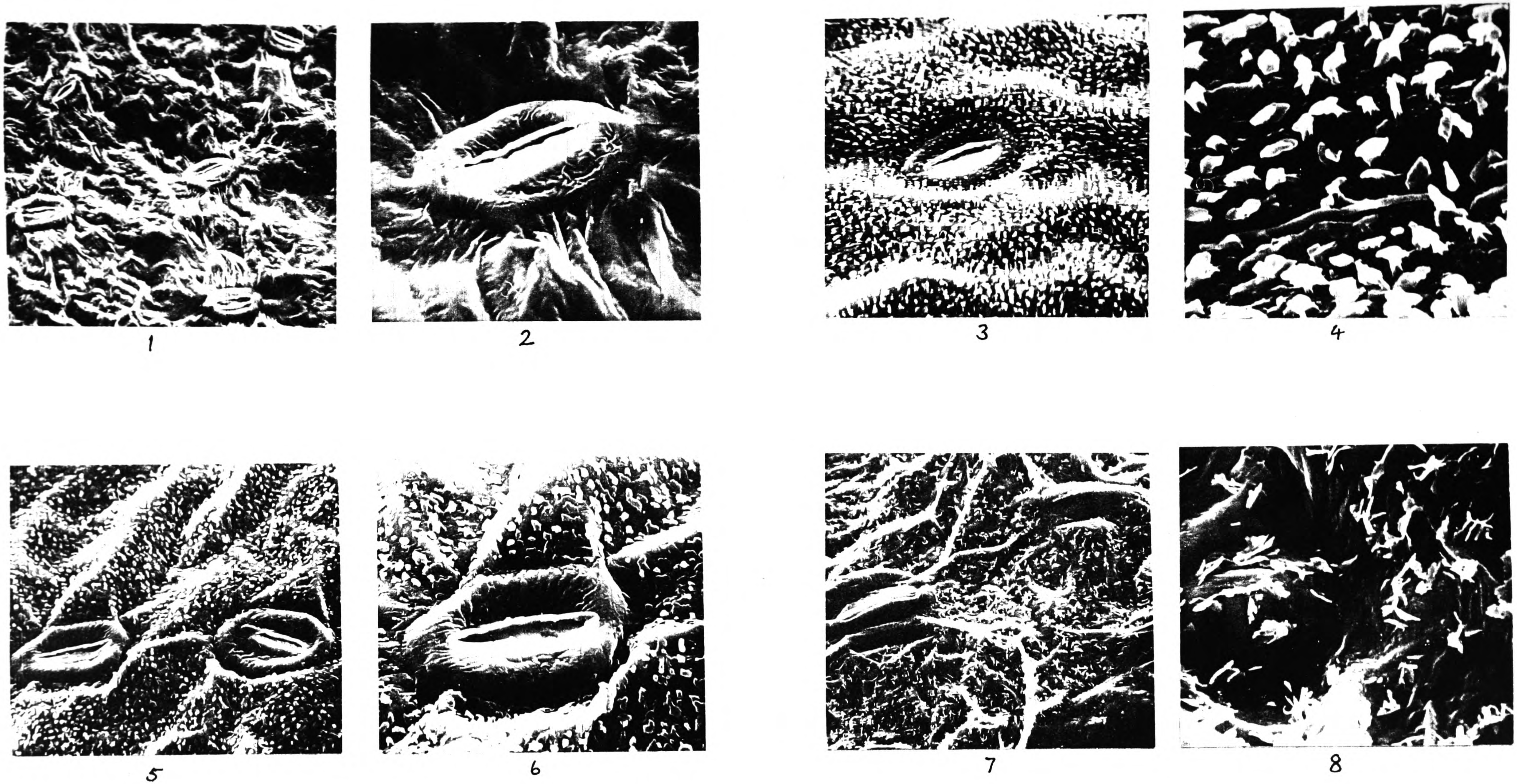


FIG. 32 SCANNING ELECTRON MICROGRAPHS OF LEAF SURFACES

S. mauritanicus (22), upper surface:- 1 x 250, 2 x 1000. *S. pinguiculus* (10), upper surface:- 3 x 550, 4 x 2,750, lower surface:- 5 x 500, 6 x 1000. *S. flavus* (7) lower surface:- 7 x 450, 8 x 2,250.

morphologically and genetically. Here the glaucousness assumes the form of flat plates set at right angles to the leaf surface. In general, the glaucous forms come from desert or maritime sands, though non-glaucous species are also found in these habitats. There could be more useful data to be found from a detailed study of leaf surfaces at the population level.

8.2.4 POLLEN MORPHOLOGY

The pollen of all diploids examined is very similar in morphology (Figs. 33: 1, 2, 3, 4, and 6; 34 : 1, 2 and 3). Terminology used in description of pollen grains is taken from Erdtman (1972). The grains are tricolpate, isopolar, broadly three-lobed in polar view and elliptic in equatorial view. The non-apertural surfaces, the mesocolpia and polar apocolpia, are echinate, the spines being 2μ in length and 2.5-3.0μ broad at the base. In the lower region of the spines (Fig. 34 : 3), there are numerous small pores. In Cosmos, these have been shown to communicate with cavities in the sexine (Heslop-Harrison, 1969). A few of these pores also occur on the surface of the grain between the spines. Grain size is discussed in 3 .7.3. The two diploids examined, nos. 34 and 43, are rather different in shape. Number 43 (Fig. 33: 5) is similar in form to the diploids, while no. 34 (Fig. 34: 4 and 5) has more angular grains which are trigonal when seen in T.S. and have a more pronounced angle at the equator. Several quadripolar grains were found in this sample. The structure and disposition of the spines is as in the diploids.

The hexaploid has larger grains (see 3.7.3) with more spines per unit area. The majority of the spines are of the type found in the diploids and tetraploids, with pores in their lower regions and concave sides as seen in T.S. Scattered among these are a few spines with large smooth hemispherical bases and acuminate tips (Fig. 34:9). The only perennial examined, no. 79 (Fig. 33: 6), is similar to the other diploids in size, shape and spineness. Photographs and descriptions

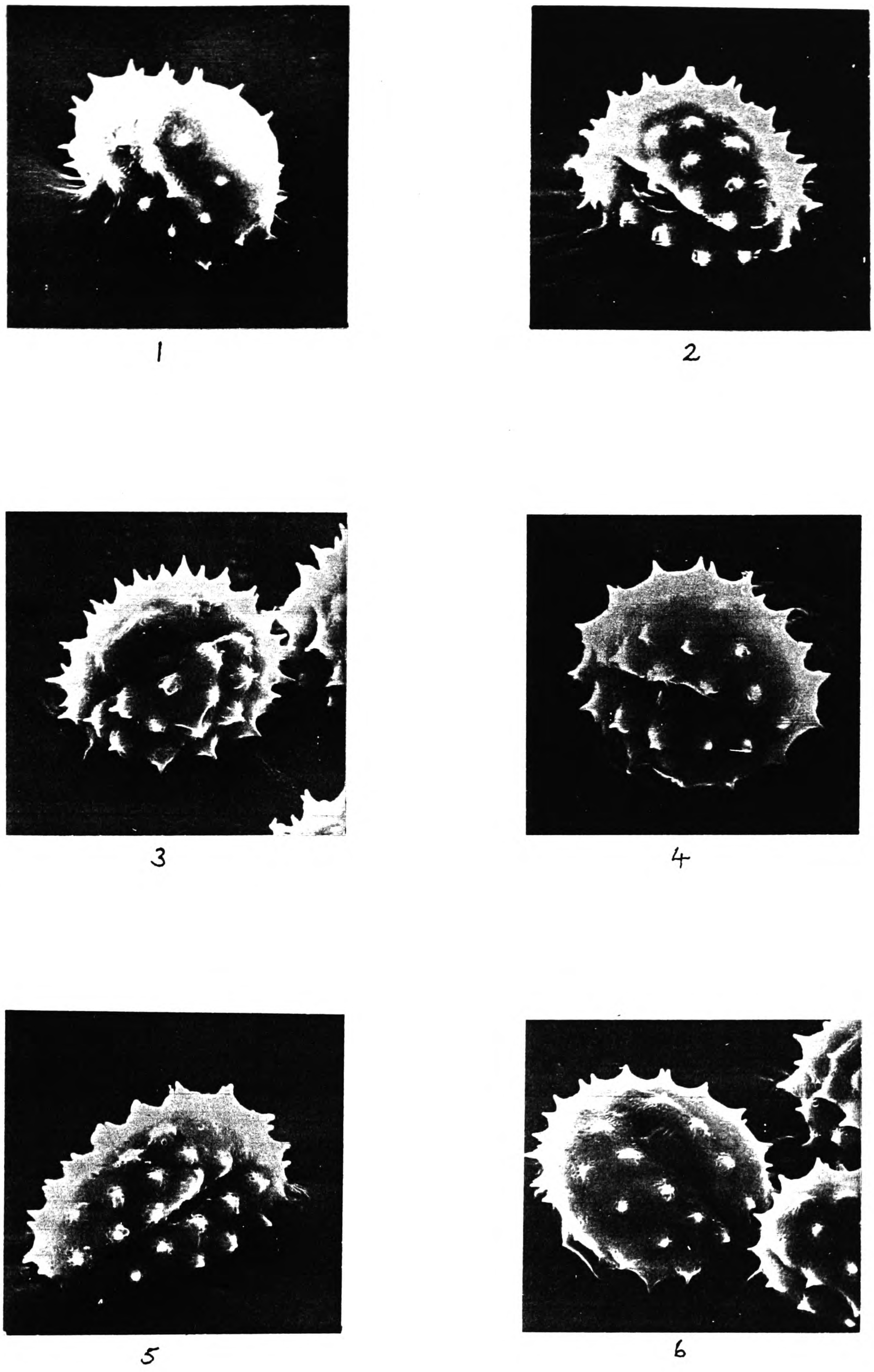


FIG. 33 SCANNING ELECTRON MICROGRAPHS OF POLLEN GRAINS

1. *S. desfontainei* (3), 2. *S. gallicus* (24), 3. *S. leucanthemifolius* (30), 4. *S. leucanthemifolius* (74), 5. *S. vulgaris* (43), 6. *S. gallicus* v. *araneosus* (79). All x 1100.

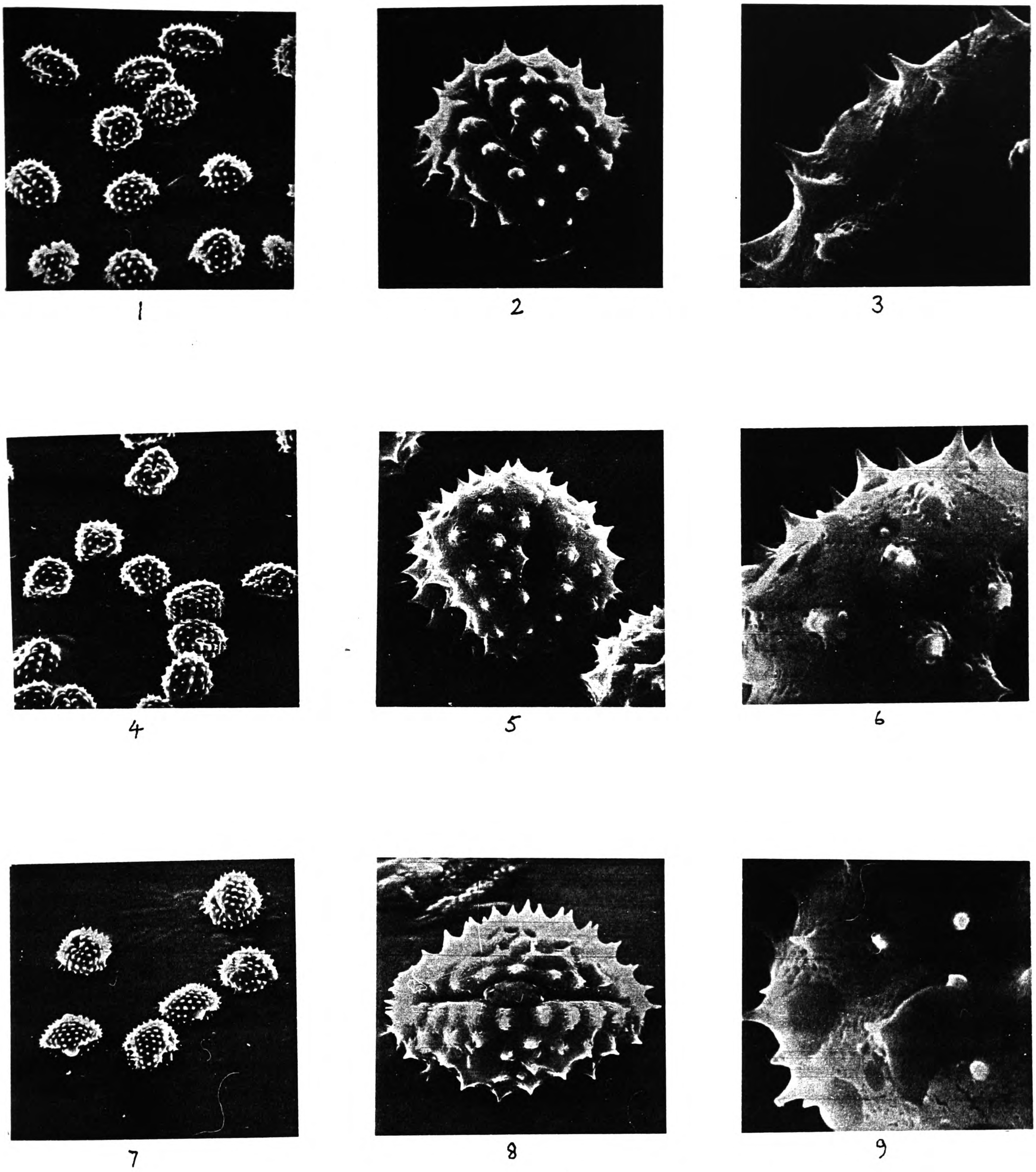


FIG. 34 SCANNING ELECTRON MICROGRAPHS OF POLLEN GRAINS

S. mauritanicus (22):- 1 x 275, 2 x 1100, 3 x 2750. S. aegyptius (34):- 4 x 275, 5 x 1100, 6 x 2750. S. hoggariensis (45):- 7 x 275, 8 x 1100, 9 x 2750.

PART III

CONCLUSIONS AND SPECULATIONS

CHAPTER 9 TAXONOMIC CONCLUSIONS

9.1 TAXONOMIC PRINCIPLES

9.1.1 THE CONFLICT OF CHARACTERS

The conflict between the 'biological' and 'morphological' species concepts is a well worn topic. Throughout the history of biological classification, the species concept in favour at any particular time seems largely to have reflected newly developed and therefore currently fashionable techniques. Although Linnaeus himself (1774) developed a theory of small scale evolution of species through hybridisation, apparently none of his followers took his advice on experimental work. A fundamentally morphological concept, rooted in religious belief about the immutability of species, held sway until the latter half of the 19th century. With the increasing use of experimental methods during the first half of the 20th century, the influence of breeding data on taxonomy became evident. Clausen, Keck and Hiesey (1936) remarked that inherent isolating mechanisms, demonstrable by experiment, had put the species concept on an objective rather than a subjective basis. Few present-day taxonomists would agree that a useful classification can ever be totally objective. Admittedly objective classifications, either morphological or biological, are comparatively easy to construct but their value, in many cases would be rather limited. More recently, the development of computer techniques, together with new tools for examining morphology such as the scanning electron microscope have accompanied a return to a more morphologically based concept.

As discussed in Ch. 7, the data from breeding experiments and from morphological observations are extremely difficult and in some cases impossible to reconcile. Ideally a taxonomic treatment should aim to synthesise all available data, resulting in a species concept which is not unduly biased in either a genetical or a morphological direction. In some groups, species limits are distinct and there is a satisfactory correlation between data from all sources. In most groups, however, there is a greater or lesser degree of conflict between data. What is required is informed subjectivity rather than pure objectivity. Cases of conflict between biological and morphological criteria can involve more or less uniform morphology embracing several breeding groups, a situation common in the Fungi, or several morphological groups which all have some degree of interfertility, which is more common in the higher plants.

Burger (1975) discusses the situation in Quercus, and suggests that in this genus the biological 'species' is probably equivalent to the subgenus or section. He adds that ideally the binomial and the biological species should be equivalent. This would make for such gross morphological inconsistencies in the delimitation of taxa that it is an ideal best not attempted. There is clearly a great deal to be gained from understanding what the differences are between the biological and morphological species in any particular group, but unless the division of a genus on biological data happens to coincide with morphologically recognisable units, it is better not to try to equate the two at species level. The problem is partly a semantic one in that the word 'species' is used in both concepts. Several authors have employed other terms for the biological species, e.g. the 'syngameon', used by Grant (1971, and earlier) and the 'genodeme', a category in the -deme terminology proposed by Gilmour & Gregor (1939) which has been so misused by many authors as to have greatly detracted from its value. The use and misuse of the -deme terminology are discussed by Gilmour & Heslop-Harrison (1954) and Bennett (1964) who gives a list of works in which the term 'deme' is used on its own for a local breeding population, rather than the suggested derivative 'topogamodeme'. The fact that the word 'deme' appears in the title of the original paper by Gilmour & Gregor may have caused the word to be used without a prefix from the start.

The problem of reconciling morphological and experimental data would be simpler if the results of breeding experiments were always either positive or negative, as is apparently the case among the mammals and birds. Fertility in angiosperms can be anywhere between 0% and 100%. A purely objective approach to such results would mean selecting a certain level of hybrid fertility on which to base delimitation of taxa. Unfortunately such consistency of treatment, though often advocated in other contexts, would result in taxonomic chaos. Useful taxa can only be delimited by balancing the various data available. In some cases one may have to be governed by morphological considerations, e.g. to avoid having an enormous and morphologically variable species in cases where plants of very different morphology are interfertile. In other cases, breeding data may help one to 'weight' morphological characters and thus help to split up a large group in which morphological differences are less pronounced. As we only have experimental data for a very small percentage of the angiosperms, it is hard to foresee a time when a biological species concept could be widely applied.

9.1.2 THE SPECIES CONCEPT IN THIS GROUP

A comparison of the results of the breeding experiments (Fig. 27) with the leaf spectra of the parents used (Figs. 46-64) shows that in this group there is a wide range of phenotypes, many of which have very high interfertility. In most cases, the species limits have been set on morphological grounds, based on the premise that a specific name should be used to describe something which is recognisable in the field. Data from the breeding experiments have been used mainly to tip the balance in cases where the morphological data do not point clearly in any particular direction, and also to get some idea of the relationships between species and between groups of species. Geographical and ecological/data have been considered in attempts to interpret what the situation is in the field. Two populations, highly interfertile in the greenhouse, may be geographically or ecologically isolated. In several cases sterility barriers appear to be stronger between sympatric taxa than between taxa which are allopatric. This phenomenon, first described by Wallace (1889) and later by other workers has been named the "Wallace effect" by Grant (1966).

Consistency of treatment has not always been possible, and in cases where more morphological or breeding information is required a fairly conservative view has been taken. For instance:- *S. vernalis* has been maintained as a separate species although morphologically close to populations of *S. leucanthemifolius*, some of their hybrids having pollen fertility of 79%. *S. squalidus* var. *aurasiacus* (*S. balansae*) has not been elevated to subspecific rank although it is morphologically fairly distinct and probably ecologically isolated from var. *squalidus*. These points are further amplified in the discussion under the species in question.

Because this research was experimentally orientated, it was necessary to design and perform the hybridisation experiments before a complete survey of all available herbarium material had been made. The result is that some significant taxa were not 'discovered' until it was too late to obtain living material of them, e.g. *S. leucanthemifolius* var. *vernus*. In the time available it was not possible to delay the breeding experiments until loans from foreign herbaria had been received and fully examined. In such cases, taxa have had to be delimited on a purely morpho-geographical basis.

9.2 TAXONOMIC TREATMENT

9.2.1 INTRODUCTION

As discussed in 2.3, the name changes resulting from this work are not used in the thesis until the final delimitation of species in this chapter. As many of the changes can be described as 'lumping' it was useful to have names by which to refer to groups which were eventually amalgamated. The major nomenclatural changes are shown in Fig. 35. A conspectus of species recognised is given in Fig. 36 together with life-form and chromosome number. This is followed by an indented dichotomous key, which includes several species which are peripheral, geographically or morphologically, to the group studied. Some of these are perennials which have

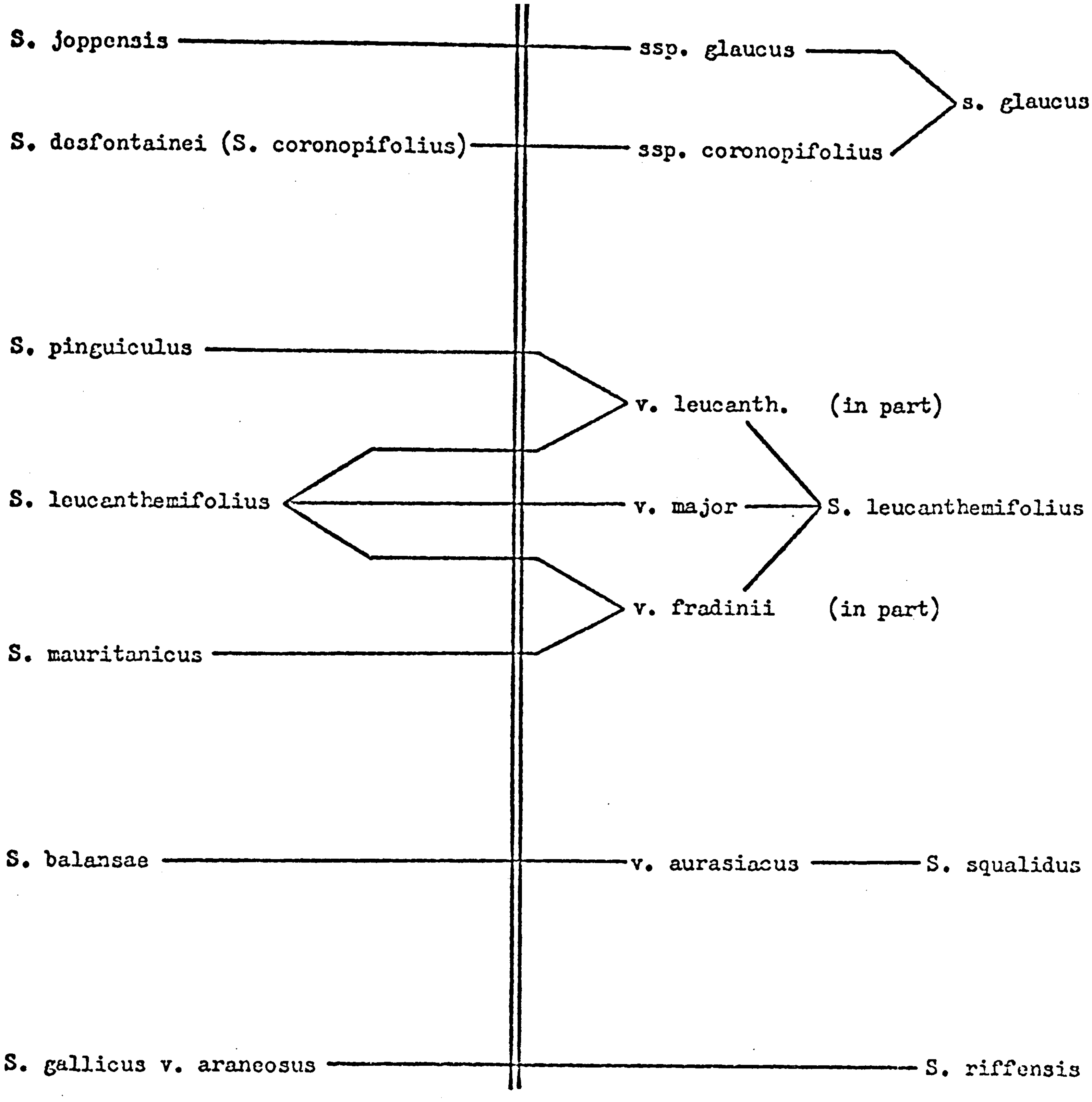


Fig. 35. MAJOR NOMENCLATURAL CHANGES IN THIS THESIS.

Names on the left are used in parts I and II, those on the right in part III. Other names are constant.

pinnatifid or pinnatisect leaves, e.g. S. erraticus, others are annuals which being distinct and easily recognisable have had very little attention paid to them during this investigation, e.g. S. sylvaticus and S. lividus.

Descriptive terms and measurements used in the key are the same as in Ch. 3. Unqualified measurements apply to length. Capitulum diameter, used only in discoid or very short-rayed species, is measured across the tips of the phyllaries at anthesis.

The key is followed by species description and diagnoses. Full descriptions are given for widespread and difficult species, and for species around whose names there has been some confusion, e.g. S. squalidus and S. nebrodensis. Other species are diagnosed from those having a full description, except for a few which are merely given brief descriptions, e.g. S. minutus and S. delphinifolius. When arranging the descriptions and diagnoses in a logical order, it was not always possible to place diagnosed species immediately after the full description from which the diagnosis was made. However the species in question are always referred to by a number, indicating their systematic position in this chapter, which should not be confused with the accession numbers used in earlier chapters.

The separation of the perennials, otherwise similar to the annuals, into Sect. Jacobaea (Cass.) Dumort. cannot easily be upheld in view of the high interfertility between the two groups, especially as some of the perennials, e.g. S. squalidus may sometimes be annual. Accordingly these perennials and all but two of the annuals are placed in Sect. Senecio, the type species of the genus being S. vulgaris. The remaining two annuals, S. delphinifolius and S. minutus, constitute the separate Sect. Delphinifolius Reichenb., differing from Sect. Senecio in indumentum, achene and pappus characters.

Several synonyms often cited under the more common species were found to refer to cases in which the original name had been misused by a later author; these have not been included. A question mark in front of a synonym means that the reference has been consulted but that from the description it is not possible to be certain that the name should be placed in synonymy. All other synonyms have been checked.

The descriptions are based almost entirely on herbarium specimens, although some use has been made of living material for floral characters which are considered less plastic than vegetative ones. Chromosome numbers are taken mostly from my own counts (5.3.2) and also from Cave (1956-1964), Moore (1965-1971) and Fedorov (1969). Flowering times, habitat notes and altitudinal range are taken from herbarium specimens. Following the citation of herbarium specimens, reference is made to living accessions used in the experimental work. Distributions were compiled largely from herbarium material. As there is a long history of misidentification in this group, literature records have not been relied upon except for easily identifiable species, e.g. S. hoggariensis and S. flavus.

	Name	Life-form	2n
	Sect. SENECIO (incl. JACOBAEA)		
1.	nebrodensis	P	
2.	riffensis	P	20
3.	chalureaui	P	
4.	erraticus	B	
5.	squalidus	P	20
6.	chrysanthemifolius	P	
7.	aethnensis	P	
8.	leucanthemifolius	A	20
9.	rodriguezii	A	20
10.	vernalis	A	20
11.	vulgaris	A	40
12.	gallicus	A	20
13.	glaucus	A	20
14.	hesperidium	A	20
15.	krascheninnikovii	A	
16.	vulcanicus	A	
17.	massaicus	A	40
18.	hoggariensis	A	60
19.	petraeus	A	20
20.	sylvaticus	A	40
21.	viscosus	A	40
22.	lividus	A	40
23.	aegyptius	A	40
24.	flavus	A	20
25.	trilobus	A	
	Sect. DELPHINIFOLIUS		
26.	delphinifolius	A	40
27.	minutus	A	

Fig. 36. CONSPECTUS OF SPECIES DESCRIBED AND DIAGNOSED

P = Perennial, B = Biennial, A = Annual

9.2.2 DICHOTOMOUS KEY TO SPECIES DESCRIBED AND DIAGNOSED

1. Ray flowers absent
  2. Leaves pinnatifid or pinnatipartite
    3. Lanate **perennial**; capitulum diam. more than 7 mm .... 3. *chalureaui*
    3. Glabrous to pubescent annual; capitulum diam. less than 6 mm
      4. Phyllary length more than 6 mm; calyculus bracts 10-20, black-tipped .... 11. *vulgaris*
      4. Phyllary length less than 6 mm; calyculus bracts 4-10, brown-tipped
        5. Pappus c. 2 mm; capitula diam 3-4 mm; corymbs dense .... 23. *aegyptius*
        5. Pappus c. 5 mm; capitulum diam. 5-6 mm; corymbs lax .... 17. *massaicus*
  2. Leaves entire or shallowly lobed
    6. Basal leaves linear, distantly toothed or lobed .... 17. *massaicus*
    6. Basal leaves ovate-spathulate or orbicular, crenate or shallowly lobed
      7. Plant glaucous; middle cauline leaves triangular, auriculate, crenate; phyllaries 6-9 mm .... 24. *flavus*
      7. Plant not glaucous; middle cauline leaves lanceolate to ovate-spathulate, entire or sinuately lobed; phyllaries less than 5 mm .... 8. *leucanthemifolius*
1. Ray flowers present
  8. Ligules less than 3 mm
    9. Plant glandular, at least in inflorescence
      10. Achenes glabrous; plant viscid in all parts .... 21. *viscosus*
      10. Achenes at least strigulose; plant glandular in inflorescence

11. Phyllaries 8-10 mm; middle cauline leaves toothed, crenate or pinnatifid, upper cauline leaves broadly auriculate; capitula in lax corymbs .... 22. lividus

11. Phyllaries 5-7 mm; middle cauline leaves pinnatipartite, upper cauline leaves narrowly auriculate; capitula in dense corymbs .... 20. sylvaticus

9. Plant not glandular

12. Phyllaries more than 6 mm

13. Plant glaucous; middle cauline leaves triangular, auriculate, crenate; calyculus bracts 0-5 .... 24. flavus

13. Plant not glaucous; middle cauline leaves ovate to oblong in outline; calyculus bracts 10-20 .... 11. vulgaris

12. Phyllaries less than 5 mm

14. Middle cauline leaves more than 4 cm, pinnatifid or pinnatipartite; phyllaries more than 15 .... 23. aegyptius

14. Middle cauline leaves less than 4 cm, entire, sinuately lobed or shallowly pinnatifid; phyllaries fewer than 10 .... 8. leucanthemifolius

8. Ligules more than 3 mm

15. Leaves unlobed, sinuate or trifid, not pinnatifid

16. Ligules purple or lilac

17. Disc flowers purple, ligules lilac .... 9. rodriguezii

17. Disc flowers yellow, ligules purple ....8. leucanthemifolius

16. Ligules yellow

18. Perennial, stems suffrutescent at base

19. Plant glaucous, fleshy; leaves lanceolate to elliptic, entire, occasionally distantly toothed .... 7. aethnensis

19. Plant green, not or slightly fleshy; leaves elliptic to oblong, dentate .... 5. squalidus

18. Annual, stems not woody at base

  20. Ligules more than 10 mm

    21. Calyculus of 8-20 bracts .... 8. <u>leucanthemifolius</u>

    21. Calyculus absent .... 19. <u>petraeus</u>

  20. Ligules less than 8 mm

    22. Calyculus lacerate; peduncles arachnoid .... 25. <u>trilobus</u>

    22. Calyculus entire; peduncles glabrous

      23. Leaves denticulate, not trifid; almost always with a few scattered hairs on leaf surface .... 10. <u>vernalis</u>

      23. Leaves dentate or crenate, sometimes trifid; leaf surface almost always glabrous .... 8. <u>leucanthemifolius</u>

15. Leaves pinnatifid to pinnatisect

  24. Achenes glabrous, ridged or papillose

    25. Phyllaries glabrous

      26. Lanate perennial; calyculus of 6 or more bracts .... 3. <u>chalureaui</u>

      26. Glabrous or pubescent annual or biennial; calyculus of 5 or fewer bracts

        27. Subacaulous annual less than 10 cm; leaves linear to broadly lanceolate, unlobed or shallowly lobed .... 16. <u>vulcanicus</u>

        27. Biennial, stems 25-100 cm; middle cauline leaves lyrate-pinnatisect .... 4. <u>erraticus</u>

    25. Phyllaries glandular or sericeous or with a few short scattered hairs

      28. Plant viscid; achenes subcylindric, ridged, 3-4 mm ..... 21. <u>viscosus</u>

      28. Plant glabrous or pubescent; achenes elliptic to ovate, papillose 1-2 mm

        29. Calyculus absent; phyllaries c.13, sericeous; stem less than 25 cm... 27. <u>minutus</u>

29. Calyculus of 6-10 bracts; phyllaries c. 21, sparsely strigose; stems 20-60 cm .... 26. *delphinifolius*

24. Achenes strigulose

30. Plant glandular at least in inflorescence

31. Perennial; phyllaries c. 10 mm, calyculus of 1-5 bracts; ligules 6-9 mm .... 1. *nebrodensis*

31. Annual; phyllaries 5-7 mm; calyculus of 5-13 bracts; ligules 2-3.5 mm .... 20. *sylvaticus*

30. Plant not glandular

32. Ligules purple .... 18. *hoggariensis*

32. Ligules yellow

33. Middle cauline leaves narrowly lobed, lobes linear, not triangular or denticulate, at least 3.5 x longer than broad, sinuses at least 3.5 x lobe width. If lobes closer and broader then fleshy and rounded, and ligules more than 8 mm

34. Erect perennial, usually over 35 cm, stems densely leafy, branching in inflorescence .... 6. *chrysanthemifolius*

34. Decumbent or erect annual, usually under 35 cm, stems not densely leafy, branching above and below

35. Calyculus of 0-3 bracts; leaves rarely more than 5 cm, lobes patent .... 12. *gallicus*

35. Calyculus of 3 or more bracts; leaf lobes antrorse, if patent then leaves fleshy and some more than 5 cm

36. Ligule breadth more than 4 mm; leaf lobes rounded; phyllaries 6-8 mm; plant not glaucous ....14. *hesperidium*

36. Ligule breadth less than 4 mm; leaf lobes dentate or acute-tipped; phyllaries 4-6 mm; plant often glaucous .... 13. *glaucus*

33. Middle cauline leaves more broadly and closely lobed, lobes oblong to elliptic, sometimes denticulate, if narrow and distant then triangular

  37. Perennial, stems woody below; some basal and middle cauline leaves more than 6 cm, if less than leaves closely lobed, lobes tapering towards the midrib; ligules usually more than 2.5 mm broad

    38. Plant glabrous or sparsely arachnoid, branching above and below; leaf tips acute or if obtuse then leaves lyrate-pinnatifid; pappus 4.5-6 mm .... 5. <u>squalidus</u>

    38. Plant sparsely to densely arachnoid, branching mostly in upper half; leaf tips obtuse, leaves never lyrate-pinnatifid; pappus 6-7 mm (endemic to N.Morocco) .... 2. <u>riffensis</u>

  37. Annual, stems not woody, leaves less than 6 mm, if longer then lobes rounded or triangular, isodiametric and denticulate. Ligules usually less than 2.5 mm broad

    39. Lobes of middle cauline leaves patent; rounded; triangular or oblong, sometimes denticulate

      40. Calyculus of 5 or more bracts; leaves usually denticulate; achnes 2.5-3 mm .... 10. <u>vernalis</u>

      40. Calyculus of 0-3 bracts; leaves not denticulate; achenes 1.5-2.5 mm .... 12. <u>gallicus</u>

    39. Lobes of middle cauline leaves antrorse, triangular or oblong, never denticulate .... 8. <u>leucanthemifolius</u>

9.2.3 SPECIES DESCRIPTIONS AND DIAGNOSES

Sect. SENECIO

Syn: Subgen. JACOBAEA Cass., Dict. 24: 110 (1822)
Subgen. OBAEJACA Cass., Dict. 35: 270 (1825)
§. SENECIOTYPUS Dumort., Fl. Belg. Prodr. 65 (1827)
§. JACOBAEA (Cass.) Dumort., Fl. Belg. Prodr. 65 (1827)
Sect. OBAEJACAE DC., Prodr. 6: 341 (1838)
Sect. OBAEJACOIDEAE DC., Prodr. 6: 343 (1838)

Acaulous, decumbent or erect annuals, biennials or short-lived perennials. Glabrous to arachnoid or lanate, occasionally glandular. Stems terete, ridged, sometimes suffrutescent below, often branched. Leaves linear, elliptic to oblong in outline, usually pinnatifid to pinnatisect or lyrate pinnatisect, sometimes unlobed; leaf margins entire, toothed, crenate or denticulate; leaf bases often auriculate-amplexicaul. Capitula urceolate, oblong or cup-shaped in lax or dense corymbs, occasionally solitary, sometimes plant more or less scapose; peduncles usually bracteate. Calyculus of 1-25 linear, subulate or triangular, rarely lacerate bracts, occasionally absent, often black-tipped. Involucre a single whorl of 8-30 phyllaries, often black-tipped. Ray flowers female, 5-30, with long or short, yellow, rarely lilac or purple ligules, often absent. Disc flowers many, hermaphrodite, tubular, 5-toothed, yellow, rarely purple. Achenes subcylindric, glabrous, strigulose or lanate. Pappus of shortly toothed hairs, usually a few fluked or clavate hairs present in outer pappus whorl.

The reason for treating Sect. Jacobaea Cass. under Sect. Senecio are discussed in 9.2.1.

Dumortier (1827) did not specify whether his taxa were sections or subgenera. The sign used by him to designate these taxa has been copied directly from his work.

1. S. nebrodensis L., Sp. Pl. ed. 2: 1217 (1763)

Syn: S. duriaei J. Gay in Ann. Sci. Nat. Ser. 2 (6): 346 (1836)

Erect viscous perennial, 20-80 cm, stems tufted from woody rootstock. Leaves brownish-green, pinnatifid to pinnatipartite. Capitula large, cup-shaped, in lax or dense corymbs; calyculus of 1-5 glandular bracts; phyllaries c. 10 mm, glandular-strigose. Ligules yellow, 6.0-9.0 mm. Achenes c. 3.5 mm, subcylindric, sparsely strigulose. Pappus c. 6 mm.

Fl. 6-7. Rocky montane habitats. c. 2000 m.

Described in error from Sicily. Hb. Linn. 996.23!

Spain: Granada, Sierra Nevada, Heywood & Davis 697 (E)! Above Capileira, Alpujarra Allen 7.vi.1969 (E)!

Distribution: Restricted to mountains in Central and S. Spain. (Map. Fig.37).

Described by Linnaeus as an annual from Sicily, apparently in error as the Linnean specimen and all others seen are perennials from Spain. This error has resulted in countless misidentifications of specimens clearly referable to S. rupestris and S. laciniatus (both = S. squalidus L.), from central and S. Europe, Sicily and N. Africa.

Not used experimentally.

2. S. riffensis Alexander, sp. nov.

Syn: S. gallicus v. araneosus Emb. & Maire in Mem. Soc. Sci. Nat. Maroc 18: 54 (1927)!

Erect sparsely or densely arachnoid perennial, occasionally glabrescent. Stems terete, ridged, 20-60 cm, woody below, arising from previous year's stem bases in older plants, branching mostly in inflorescence. Lower cauline leaves elliptic, dentate, entire or shallowly pinnatifid, lobes oblong; middle cauline leaves 3.5-10.0 x 1.5-3.5 cm, elliptic to oblong, dentate, pinnatifid to pinnatipartite, occasionally bipinnatipartite, lobes oblong, rounded, antrorse. Upper cauline leaves with narrow simple lobes, or merely dentate. Capitula in lax or dense corymbs, peduncles < 5 cm, with a few scattered subulate bracts. Calyculus of 5-10 narrow triangular bracts, 1.0-3.0 mm, often with pronounced black tips. Phyllaries 21-27, 6.0-8.0 mm, with small black tips, occasionally purplish. Ligules yellow, c. 13, (7.0) 9.0-17.0 x 1.5-3.0 mm. Achenes 3.0-3.5 mm, sparsely strigulose. Pappus hairs 6.0-7.0 mm, clavate hairs present. 2n = 20.

Fl. 4-6. Eroded banks, rocky hillsides and dry gulleys on marls, shales and schists, occasionally on calcareous rock. 800-2000 m.

Holotype: Morocco, Tizi Ouzli, between El Hoceima and Taza. Roadside bank. 1200 m. 17.v.1972 Alexander & Kupicha 260 (E)! Iso. (BM, MO)!

70 km Talamerhait to Taza, Alexander & Kupicha 253 (E, BM)! Above Oued Nahor, Davis 51374 (E)! Pass N. of Aknoul, Davis 51279 (E)! Jbel Tazaote, Riff, Sauvage 15604 (RAB)!

Accessions 9 and 79 (Figs. 59 as gallicus v. araneosus).

Distribution: Endemic to the Eastern end of the Riff Mts., N. Morocco (Map. Fig. 43).

Although originally described as a variety of S. gallicus, this plant is much closer to S. leucanthemifolius on both morphological and breeding criteria. Its most fertile hybrids, produced by crossing with S. squalidus, had 95% stainable pollen, However, its morphological distinctness makes it reasonable to recognise it as a species. Unfortunately the isotype examined of S. gallicus v. araneosus is a poor specimen in which it is hard to distinguish the leaf characters clearly.

However, the woodiness of the stem bases and the general habit of the plant, together with its site of gathering agree with other specimens examined, as does the original description of Emberger & Maire (1972). The specific epithet is taken from the Riff Mts. to which this species is endemic.

3. S. chalureaui Humb. in Bull. Soc. Hist. Nat. Afr. Nord 15: 207 (1924)

Differs from no. 2, S. riffensis, in being densely lanate, with finely divided pinnatipartite to pinnatisect leaves. Stems woody, often tufted from below, < 20 cm. Discoid or with ligules < 5 mm. Perennial. Peaks of calcareous mountains, 3000-3500 m.

Isotype, Morocco: Ari Ayachi, Grand Atlas Oriental, Eboulis calcaires de la croups culminante et des pentes voisines, 3300-3500 m. Humbert 1055 (MPU)!

Distribution: Endemic to the Eastern end of the Gt. Atlas Mts., Morocco. Not used experimentally.

4. S. erraticus Bertol., Rar. Ital. Pl. Dec. 3: 62 (1810)

Distinguished from no. 5, S. squalidus, by having leaves lyrate-pinnatisect into narrow pointed lobes. Phyllaries broad with two prominent longitudinal ridges, c. 4.0 x 1.5 mm. Achenes glabrous. Biennial.

Described from Italy. Recorded from central and S. Europe and N. Africa.

Not used experimentally.

5. S. squalidus L., Sp. Pl. 2: 869 (1753)

Erect glabrous to arachnoid perennial, occasionally annual. Stems terete, ridged, (20)30-80 cm, leafy, branching mostly above, suffrutescent, often arising from a horizontal woody rootstock. Lower cauline leaves elliptic, petiolate, widely dentate or shallowly pinnatifid; middle and upper cauline leaves elliptic in outline, usually deeply pinnatipartite, rarely unlobed and dentate; lobes distantly and acutely toothed; leaf tips acute or if rounded then leaves lyrate-pinnatifid. Middle cauline leaves 4.0-15.0 x 1.5-6.5 cm. Capitula in lax corymbs. Calyculus of 4-20 bracts, 2.0-3.5 mm, phyllaries c. 21, 5.0-10.0 mm, calyculus and phyllaries often black-tipped. Ligules yellow, 13-21, 9.0-15.0 mm. Achenes 2.0-3.5 mm, sparsely strigulose. Pappus 4.5-6.0 mm, fluked hairs present. 2n = 20.

1. Middle cauline leaves pinnatipartite, leaf tips acute, plant glabrous or sparsely arachnoid .... var. squalidus
1. Middle cauline leaves lyrate-pinnatipartite, leaf tips rounded, plant usually arachnoid .... var. aurasiacus

var. squalidus

Syn: S. montanus Willd., Sp. Pl. 3: 1989 (1803)

S. paradoxus Hoppe, in Sched., cited in Willd., Sp. Pl. 3: 1989 (1803)

S. rupestris Waldst. & Kit., Pl. Rar. Hung. 2: 136 (1803)

S. laciniatus Bertol. in Desv. Journ. Bot. 2: 76 (1813)

?S. glaucescens Sprengel, Syst. Veg. 3: 561 (1826)

S. nebrodensis v. glabratus DC., Prodr. 6: 350 (1838)

S. nebrodensis auct. mult. non L., e.g.:-DC., Prodr. 6: 350 (1838); Nyman, Consp. 1: 356 (1879); Batt. & Trab., Fl. de l'Alg. 1: 474 (1889); Fiori & Paol., Fl. Anal. d'It. 3: 212 (1903); Jah. & Maire, Cat. Pl. Maroc 3: 786 (1934)

Fl. 5-10. Ruderal of open sandy and rocky places; hillsides, waste-ground and railway-sidings. s.l.-2200 m.

Described from Southern Europe. Hb. Linn. 996.33!

Italy: Mt. Grigna, *Lacaita* 24.ix.1890 (BM)! Jugoslavia: Cattaro, Dalmatia, *Krebs* 5.ix.1896 (E)! Austria: Gailthal, *Krebs* 11.ix.1900 (E)! Greece: Lakonia, *Heldreich* 1547 (E)! Switzerland: Silva Plana, Engadin, *Browning* vii.1910 (E)! Rumania: Transilvania, *Gurtler et al* 831 (BM)! Sicily: Rocca Busambra, Ficuzza, *Davis* 40005 (E)! Algeria: Djebel Mahmel, *Maire* 30.vi.1920 (MPU)! Palestro, *Davis* 51968 (E)! Accession 31 (Fig. 60).

Distribution: Southern and Eastern Europe, North Africa. Introduced to Britain and apparently spreading from there to N.W. Europe (Map. Fig. 37).

Rather variable morphologically, but almost always with pinnatifid to pinnatisect leaves, the lobes being narrow and forward-pointing, sometimes triangular (*S. laciniatus* Bert.). P. Crisp (in litt.) has suggested that *S. squalidus* arose on Mt. Etna in Sicily as a result of hybridisation between *S. chrysanthemifolius* and *S. aethnensis*, which have both been described as varieties of *S. squalidus*. Several other varietal names are published but no attempt has been made to sort them out here as *S. squalidus* is not central to this thesis.

Material of var. *squalidus* was used in a few experimental crosses. When crossed with *S. gallicus*, the resulting hybrids had 39% stainable pollen. From this and from morphological considerations it seems likely that among the annuals, *S. squalidus* is most closely allied to *S. leucanthemifolius*. Hybrids with 95% stainable pollen resulted from crossing var. *squalidus* with *S. riffensis*.

Many specimens referable to *S. squalidus* from N. Africa and S. Europe have been placed under *S. nebrodensis*. This is almost certainly the result of an error in the Linnean description of *S. nebrodensis* which is described as an annual from Sicily. From the Linnean type of *S. nebrodensis* it is clear that this name applies to a viscid perennial which is endemic to Spain. Any record of *S. nebrodensis* other than from Spain almost certainly refers to *S. squalidus*. Descriptions of

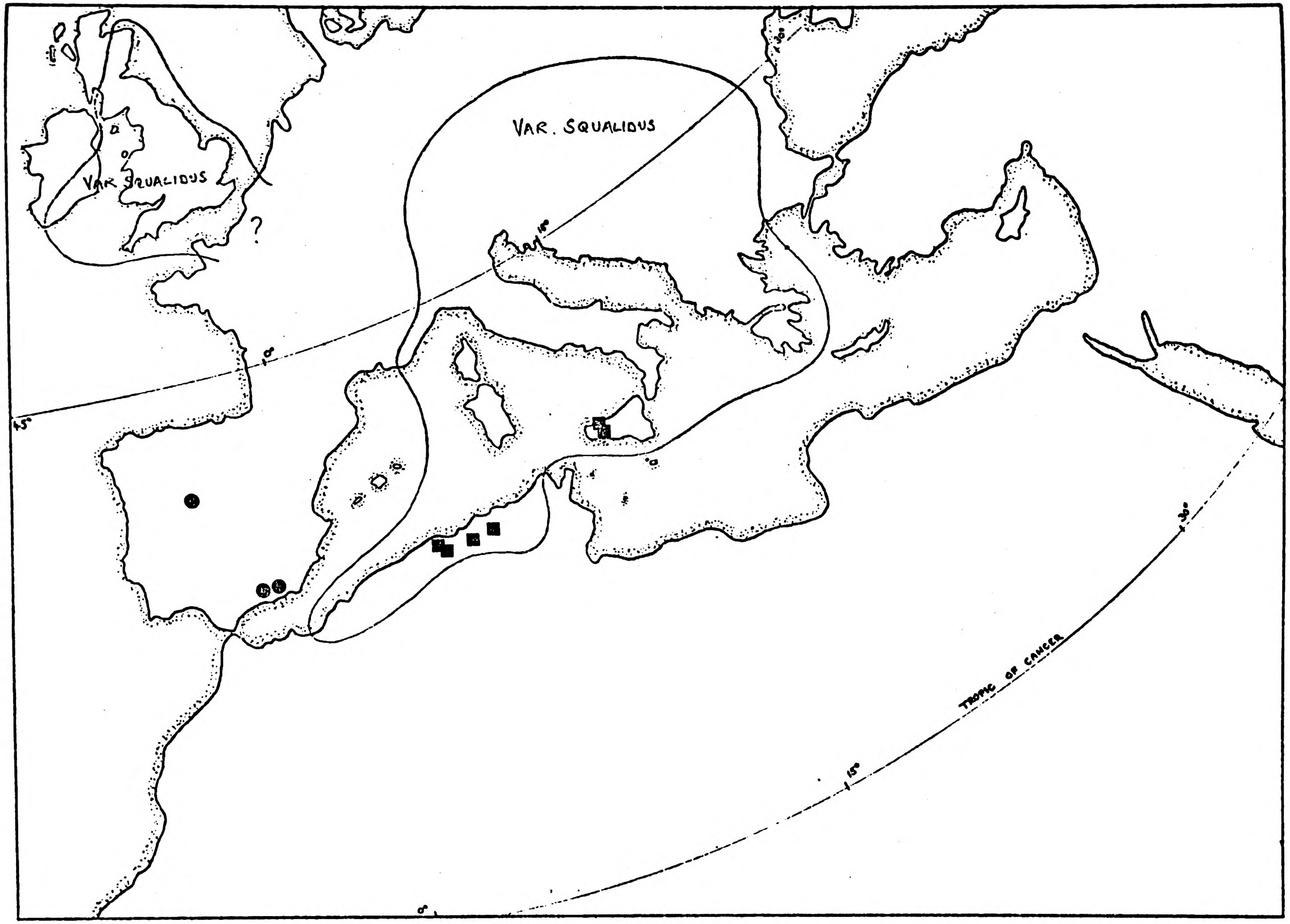


FIG. 37

Distribution of *S. nebrodensis* ● and *S. squalidus* vars. *squalidus* and *aurasiacus* ■.

plants clearly referable to *S. squalidus* are given in many European and N. African floras under the heading of *S. nebrodensis*.

S. glaucescens Sprengel is sometimes cited as a synonym of *S. squalidus*. However, Sprengel's description states that the achenes are glabrous. On leaf characters the name seems acceptable as a synonym.

British material of *S. squalidus* is atypical of the species as a whole. This is attributable to the fact that British plants are all descended from a few individuals cultivated in the Oxford Botanic Garden during the 17th and 18th centuries.

var. *aurasiacus* (Batt. & Trab.) Alexander, *comb. nov.*

Syn: *S. balansae* Boiss. & Reut., Diagn. Ser. 2(3): 32 (1856)
S. nebrodensis v. *aurasiacus* Batt. & Trab., Fl. de L'Alg. 1: 475 (1889)
S. nebrodensis v. *siculus* Fiori, Fl. Anal. d'It. 3: 212 (1903)

Distinguished from var. *squalidus* by having lyrate-pinnatifid leaves with rounded apices. Whole plant often arachnoid. *2n* = 20.

Fl. 4-6. Cliffs and rocky hillsides on limestone. 500-1500 m.

Described from Algeria: In declivitate boreali montis Gebel Tougour, prov. Constantine. *Balansa* s.n. 1853 n.v.

Algeria, Djebel Djurdjura, *Davis* 53197 (E)! *Maire*, 9.vi.1930 (MPU)!
Sicily: Palermo, Ficuzza, *Ross* 546 (E)!

Accession Nos. 16 and 18 (Fig. 61).

Distribution: Restricted to Algeria and Sicily. (Map. Fig. 37).

Although quite distinct morphologically from all the annual species, var. *aurasiacus* when crossed with *S. leucanthemifolius* var. *leucanthemifolius*, produced hybrids with 97% stainable pollen. Morphologically, var. *aurasiacus* merges with var. *squalidus*, both being present in Algeria and Sicily. Crosses between the two varieties produced non-germinable seed. In spite of this close genetic affinity, it seems useful to maintain S. squalidus as a separate morphological species.

Fiori and Paoletti (1903) place S. nebrodensis var. glabratus DC. in synonymy under var. siculus (see above). However, the description and distribution given by de Candolle (1838) suggest that the two varieties are not synonymous, var. glabratus being referable to the type variety as described here.

6. S. chrysanthemifolius Poir., Encycl. Meth. Bot. 7: 96 (1806)

Distinguished from no. 5, S. squalidus, by having much more finely divided leaves, reminiscent of S. glaucus subsp. coronopifolius, and very leafy stems. Perennial.

Described from Sicily and only recorded from there.

Not used experimentally.

7. S. aethnensis Jan. ex DC., Prodr. 6: 345 (1838)

Distinguished from no. 5, S. squalidus, by having unlobed, lanceolate to elliptic glaucous leaves which are usually entire, sometimes widely toothed. Perennial.

Described from Mt. Etna in Sicily, and only recorded from there.

Not used experimentally.

8. S. leucanthemifolius Poiret, Voy. Barb., 2: 238 (1789)
non Phil., Anal. Univ. Chil., 495 (1873)

Extremely variable. Decumbent to erect, glabrous to pubescent or arachnoid annual, 2.0-50.0 cm; stems terete, shallowly ridged; sometimes plant acaulous. Basal leaves spathulate to elliptic or rhomboid, entire to dentate or crenate, attenuate. Middle and upper cauline leaves elliptic to oblong, entire to dentate or crenate, unlobed to sinuate, or pinnatifid to pinnatipartite, 3.0-8.0(10.0) x 1.0-3.0(4.0) cm, auriculate or amplexicaul; lobes of middle cauline leaves oblong, antrorse, lobe length less than 3.5 x lobe width, sinuses less than 3.5 x lobe width. Capitula cylindrical to cup-shaped in lax corymbs, pedicels 0.5-9.0 cm, bracteate. Calyculus of 4-20 bracts, 1.0-3.0 x 0.5-2.0 mm, often black-tipped. Phyllaries 6-21, 4.0-8.0 mm, often black-tipped. Ligules yellow, very rarely purple, 1.5-15.0 x 0.5-4.0 mm, spreading or revolute, sometimes absent. Achenes 1.5-2.5 mm subcylindric, sparsely or densely strigulose. Pappus hairs 2.5-7.0 mm, fluked hairs present. $2n = 20$.

It was found extremely difficult to make satisfactory infra-specific groupings in this species. Examination of a large quantity of herbarium material referable to S. leucanthemifolius showed that several characteristic facies were discernable, but that in most cases there was continuous variation inter-connecting them. Nevertheless it seemed useful to attempt to categorise these facies in a formal manner. Some specimens will not run down satisfactorily to any of the varieties recognised, though it should be possible to identify between 70 and 80% of material examined.

Two major facies groups are distinguishable, each of which has been subdivided into varieties. Group A consists of fleshy, acaulous, decumbent or short-stemmed plants from coastal rocks and sands, with leaves undivided or sometimes pinnatifid into simple lobes. Group B consists of plants from inland or occasionally coastal habitats, not or slightly fleshy, with large undivided or pinnatifid to pinnatipartite leaves. In the latter group five varieties are recognised which probably represent genetic entities. Group A consists of two varieties, one of which, var. leucanthemifolius, occurs throughout the range of the species and has probably been developed repeatedly from inland varieties whenever the latter encounter maritime conditions, and thus has no genetic unity. The other variety in group A, var. pygmaeus appears to be a sporadic variant developed from var. leucanthemifolius. It would have been possible to recognise the two groups as subspecies, but the probable polyphyletic origin and widespread distribution of the maritime group made this seem inadvisable and to recognise the inland varieties as subsp. mauritanicus would, according to Article 20 in the International Code of Botanical Nomenclature, have resulted in the erection of subsp. leucanthemifolius as an autonym.

1. Plant fleshy, acaulous, decumbent or short-stemmed with unlobed or shallowly lobed leaves, lobes simple. (Group A)
  2. Ligules more than 4 mm; phyllaries 13-21, more than 5 mm .... i. var. leucanthemifolius
  2. Ligules less than 4 mm; phyllaries fewer than 12, less than 5 mm .... ii. var. pygmaeus
1. Plant not or a little fleshy, erect, leaves pinnatifid to pinnatipartite or three lobed, if unlobed then some leaves longer than 5 cm and serrate, sinuate or crenate, or with denticulate auricles (Group B)
  3. Phyllaries 7.0-9.0 mm, ligules 10.0-15.0 mm .... vii. var. cyrenaicus
  3. Phyllaries 6 mm or less, ligules less than 10 mm

4. Upper cauline leaves ± unlobed, auricles denticulate, or leaves regularly serrate or crenate
  5. Mid cauline leaves spathulate, auricles denticulate .... iv. var. *major*
  5. Mid cauline leaves triangular, regularly serrate or crenate .... v. var. *casablancensis*
4. Upper cauline leaves trifid or pinnatifid to pinnatipartite
  6. Mid-cauline leaves ± orbicular, attenuate; upper cauline leaves trifid, lobes rounded .... vi. var. *vernus*
  6. Middle and upper cauline leaves pinnatifid to pinnatipartite .... iii. var. *fradinii*

GROUP A

i. var. *leucanthemifolius*

Syn: *S. humilis* Desf., Fl. Atl., 2: 271 (1799)
S. crassifolius Willd., Sp. Pl. 3: 1982 (1803)
S. marmorae Moris, Strip. Sard. Elench. 2: 6 (1827)!
S. apulus Tenore, Syll. Pl. Neap. 432 (1831)!
S. humulis var. *pedunculosus* DC., Prodr. 6: 345 (1838)
S. incrassatus Guss., Fl. Sic. 28 (1826)
S. leucanthemifolius v. *pectinatus* Guss., Fl. Sic. 28 (1826)
S. salisii Gay, MS. nomem (1838)!
S. pinguiculus Pomel, Nouv. Mat. Fl. Atl. 62 (1874)
S. crassifolius v. *pinguiculus* (Pomel) Batt. & Trab., Fl. de l'Alg. 473 (1889)
S. leucanthemifolius v. *pedunculosus* Fiori, Fl. Anal. d'It. 3: 211 (1903)
S. leucanthemifolius v. *typicus* Fiori, Fl. Anal. d'It. 3: 211 (1903)

S. leucanthemifolius v. reichenbachii Fiori, Fl. Anal. d'It. 3: 211 (1903)

S. salzmannii Rouy, Fl. France, 8: 340 (1903), as of uncertain status

? S. crassifolius v. giganteus Caballero in Mem. R. Soc. Esp. Hist. Nat. 8: 288 (1915)

pp. S. leucanthemifolius ssp. poiretianus Maire, Cat. Pl. Maroc. 3: 783 (1934)

S. leucanthemifolius ssp. crassifolius (Willd.) Batt. (citation of combination not found).

Acaulous to decumbent or erect fleshy annual 5.0-30.0 cm, glabrous or sparsely arachnoid. Basal leaves spathulate or elliptic, unlobed or distantly dentate to shallowly lobed, 2.0-5.0 x 0.5-1.5 cm. Middle and upper cauline leaves, elliptic to lanceolate, unlobed, distantly dentate or with simple oblong, pointed or rounded lobes; attenuate, sometimes amplexicaul. Capitula cylindric to cup-shaped, borne in lax corymbs or singly on bracteate peduncles up to 7.0 cm. Phyllaries 13-21, 4.0-6.5 mm, glabrous, often black-tipped. Calyculus of 4-20 bracts, 1.0-3.0 mm x 0.5-2.0 mm, often black-tipped. Ligules yellow, very rarely purple, 4.0-8.5 x 1.0-2.5 mm. Achenes subcylindric, sparsely strigulose, 1.5-2.0 mm. Pappus hairs 2.5-5.0 mm, fluked hairs present.

Fl. 11-6. Sand dunes, strand-lines, rocky places by the sea, coastal plains. 0-100 m.

Described from Algeria. "Cete espèce croît dans les prairies sèche près de Bonne".

Morocco: Oualidia, Davis 54252 (E)! Fedhala, Trethewy ii. 1930 (BM)! Algeria: Mostaganem, Battendier s.n. no date (MPU)! Mostaganem, Balansa 177 (BM)! Lampedusa: Sommier 8-14.iii.1906 (FI)! Sicily: Balestrate, Fiore 21.ii.1906 (FI)!

Italy: Calabria, Fiori 970 (K,E)! Corsica: Porto Vecchio, Mabile 143 (FI)! Calvi, Archibald iii-iv.1962 (E)! Sardinia: Tempio, Reverchon 177 (E, K, FI)! France: Iles de Porquerolles, Bourgeau 239 (K)! Greece: Crete, Mavromuri, Goulimy iii.1954 (K)! Karpathos, Pichler v.1883 (BM)! Jugoslavia: Pelagosa I., Marchesetti iii.1882 (K)!

Accessions 10 and 30 (Figs. 52 and 57).

Distribution: West and central Mediterranean, eastwards to Crete and Karpathos. (Map. Fig. 38).

Only two accessions of this variety were involved in the hybridisation experiments; from Algeria and Malta. When crossed they produced hybrids with 95% fertility, though they are very different in leaf-shape (accessions 10 and 30, figs. 52 and 57). The Algerian material was as fertile with S. gallicus as it was with other accessions of S. leucanthemifolius. The Maltese material was very fertile with vars. major (S. leucanthemifolius, accession 74) and fradinii (S. mauritanicus), and also with Algerian S. squalidus. One gathering from Crete, cited above, has purple ligules, but having a yellow disc, and in leaf characters resembling var. leucanthemifolius, cannot be referred to S. rodriguezii.

The large number of synonyms cited under this variety gives some idea of its variability. The earlier synonyms at specific level were probably based on insufficient material which did not convey an adequate idea of the variation. More recent synonyms are mostly infra-specfic but do not in my opinion represent distinct enough forms, when the species is viewed as a whole, to warrant formal taxonomic recognition.

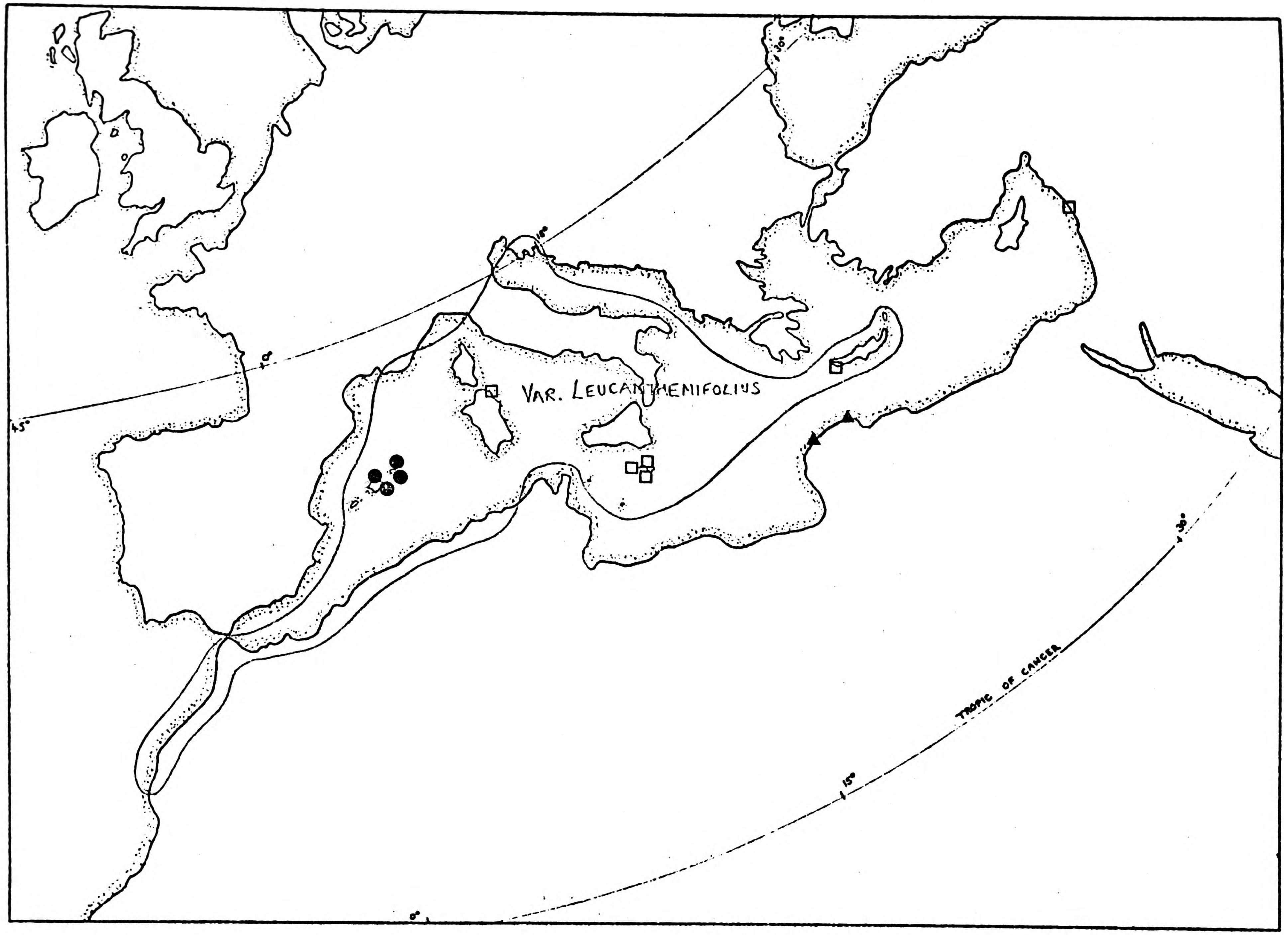


FIG. 38 Distribution of S. rodriguezii ● and S. leucanthemifolius vars. leucanthemifolius, pygmaeus □ and cyrenaicus ▲ .

ii. var. *pygmaeus* (DC.) Fiori, Fl. Anal. d'It. 3: 211 (1903)

Syn: *S. pygmaeus* DC., Prodr. 6: 341 (1838)
S. caroli-malyi Horvatic in Biol. Glasn. Zagreb, 8: 37 (1956)

Differs from var. *leucanthemifolius* in being smaller in all its parts, though sometimes up to 20 cm. Ray flowers absent or if present then ligules less than 4 mm. Phyllaries 8-12, less than 5 mm. Leaves elliptic to lanceolate, entire, dentate or sinuate, 1.0-3.0 cm.

Fl. 2-6. Maritime rocks and sand. s.l.-50 m.

Described from Sicily. "In Sicilia propeCapo-Pojato".

Sardinia: Isola Maddalena, *Vaccari* vi.1893 (FI)! Malta: Gozo, *Fiori & Beguinot* 1148 (BM)! Crete: Palaiokhora, *Davis* 1186 (E)! Lebanon: Beirut, *Herb. Postian* 12.v.1871 (E)!

Distribution: Sporadic in central and East Mediterranean. (Map. Fig. 38).

This was originally described by de Candolle (1838) as a rayless species. However a collection from Crete, cited above, contains both short-rayed and rayless plants, connecting *S. pygmaeus* with *S. caroli-malyi* which has very short rays. The Lebanese and Sardinian gatherings of *S. pygmaeus* have ligules of up to 3.5 mm. All collections are similar in the striking smallness of their capitula. It is probable that var. *pygmaeus* has been derived several times from var. *leucanthemifolius*, as there is some variation in habit and leaf-shape, and its distribution is disjunct. No material was available for experimental work.

GROUP B

iii var. *fradinii* (Pomel) Batt., Fl. de L'Alg. 1: 472 (1889)

Syn: S. mauritanicus Pomel, Nouv. Mat. Fl. Atl. 62 (1874)!

S. fradini Pomel, Nouv. Mat. Fl. Atl. 61 (1874)!

S. leucanthemifolius v. pinnatifidus Fiori, Fl. Anal. d'It. 3: 212 (1903)

S. leucanthemifolius v. lanigerus Batt., Suppl. Fl. Alg. 55: (1910)

S. gallicus ssp. mauritanicus (Pomel) Maire in Mem. Soc. Nat. Maroc 17: 54 (1927)

S. gallicus v. mauritanicus (Pomel) Pau, In Sched. (1927)

S. leucanthemifolius v. paui Maire in Cavanillesia 2: 173 (1929)!

S. leucanthemifolius ssp. crassifolius v. latisectus Pau & Font. Quer, In Sched. (1929)!

S. gallicus ssp. mauritanicus v. eu-mauritanicus Maire in Jah. & Maire, Cat. Pl. Maroc 3: 784 (1934)

S. gallicus ssp. mauritanicus v. lanigerus (Batt.) Maire in Bull. Soc. Hist. Nat. Afr. Nord 25: 304 (1934)

? S. kebdanicus Maire

Erect glabrous, pubescent or arachnoid annual 10.0-50.0 cm, not usually fleshy. Basal leaves elliptic to oblong, unlobed or shallowly lobed, entire to dentate or crenate. Middle and upper cauline leaves, oblong to lanceolate in outline, shallowly lobed or more commonly pinnatifid to pinnatipartite, lobes oblong dentate or secondarily lobed, often amplexicaul, auricles dentate. Middle cauline leaves 2.0-8.0 x 0.7-3.0 cm, lobes less than 3.5 times longer than broad, and closer than 3.5 times the lobe width. Cylindric to cup-shaped capitula borne in lax corymbs. Phyllaries 13-21, 4.0-6.5 mm, glabrous, often black-tipped. Calyculus of 4-20 bracts, 1.0-3.0 x 0.5-2.0 mm, often black-tipped. Ligules yellow, 4.0-8.5 x 1.0-2.5 mm. Achenes subcylindric, sparsely strigulose, 1.5-2.0 mm. Pappus hairs 3.0-5.0 mm, fluked hairs present.

Fl. 12-6. Agrestal and ruderal of forest clearings, roadsides and hillsides mostly on calcareous soils, occasionally on sandy soils. 50-2250 m. 2n = 20.

Isotype: Algeria, Environs d'Alger, Fradin s.n. (MPU)!

Morocco: Bab Bou Idir, Fez, Alexander & Kupicha 281 (E, BM, MO)! Mischliffen, Alexander & Kupicha 345 (E, BM, MO)! Fez, Weiller 316.21 (MPU)! Algeria: Guelma, Davis 52305 (E)! Sicily: Panormum, Todaro 521 (FI)! Palermo, Parlatore 2, 3, 4.47 (K)! Sardinia: Cagliari Cavara s.n., no date (FI)! Libya, Cyrenaica: Tolmetta, Pampanini 9550 (FI)! Baiada, Davis 49961 (E)!

Accessions 13, 21 and 22. (Figs. 52 and 55 as S. mauritanicus).

Distribution: Morocco, N. Algeria, Sardinia, Sicily and Cyrenaica. (Map.Fig.39).

This variety is rather variable in degree of leaf-lobing. Near coasts it intergrades with var. leucanthemifolius. Typical gatherings can be distinguished by having more deeply lobed, not fleshy leaves, with lobes usually dentate or secondarily lobed. The range of indumentum density found made it impracticable to maintain var. lanigerus Batt. (1910) as a separate variety. As European and N. African work has mostly proceeded independently, European plants acceptable in var. fradinii have previously been referred to var. pinnatifidus Fiori (1903). Different accessions of var. fradinii (S. mauritanicus) used in the breeding experiments in general showed high interfertility, though the results were rather mixed (see Fig. 27). Two accessions were also highly fertile with plants from the Great Atlas morphologically intermediate between var. fradinii and S. glaucus subsp. coronopifolius (S. desfontainei).

iv. var. major Ball in J. Linn. Soc. Bot. 16: 514 (1878)

Syn: S. atlanticus Boiss. & Reut., Pugillus 58 (1879) Non Coss. (1856)

S. nebrodensis v. sardous Fiori, Fl. Anal. d'It. 3: 212 (1903)

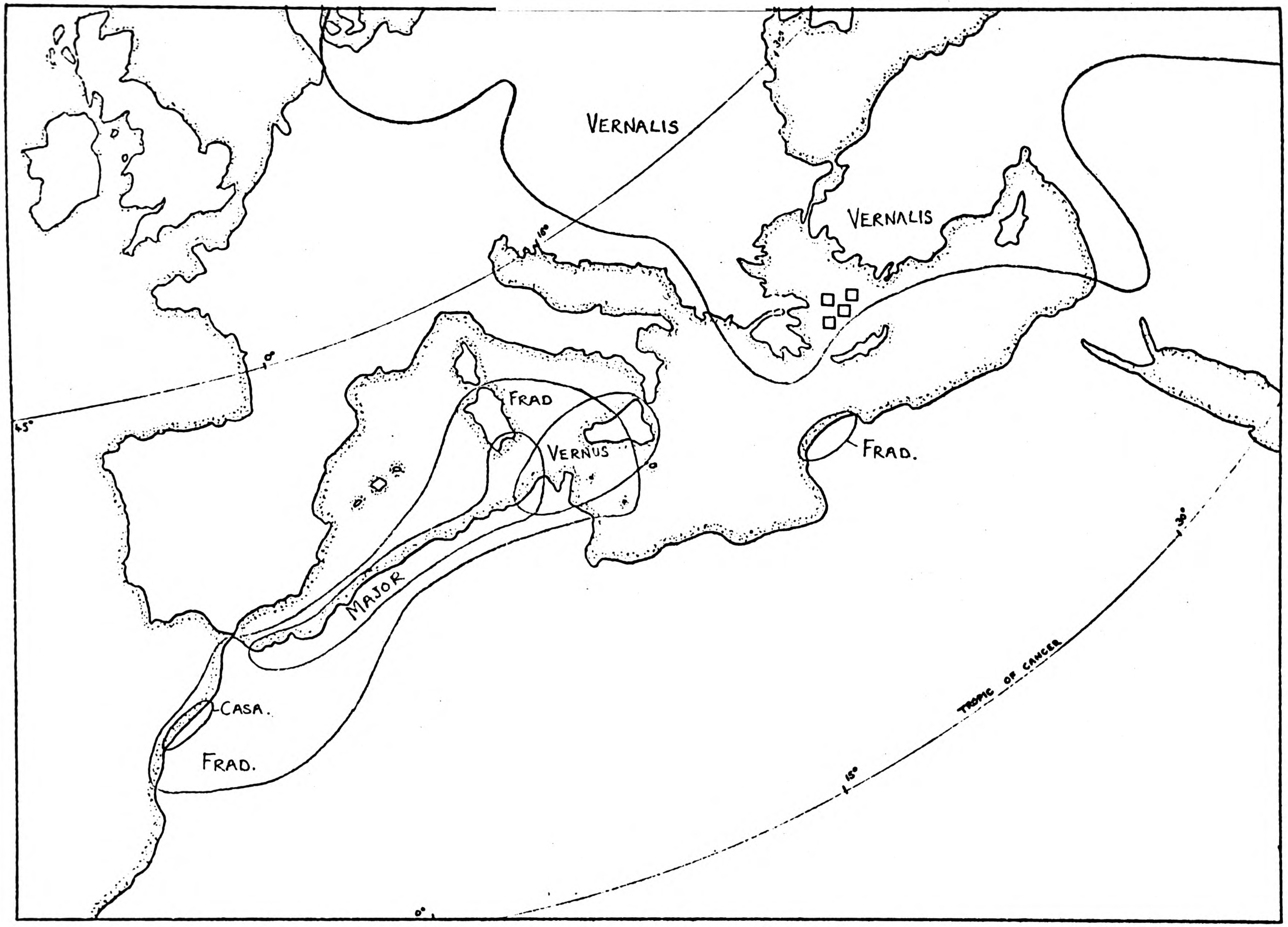


FIG. 39 Distribution of *S. vernalis* and *S. leucanthemifolius* vars. *fradinii*, *major*, *casablancensis* and *vernus*. *S. vernalis/ S. glaucus* intermediates □.

Differs from var. fradinii in having all leaves broadly spathulate to oblong, sinuate to shallowly lobed, dentate, amplexicaul; auricles large and denticulate to lacerate.

Fl. 3-6. Calcareous cliffs and rocky hillsides. 200-1000 m. 2n = 20.

Described from Algeria. "Hab. in Atlante Algeriensi supra Blidah ascendendo ad Ain Telazid in faucibus fluminis Chiffa".

Morocco: Chauen, Font-Quer 406 (BM,MPU)! Beni Hosmar, above Tetuan, Davis 432 (K, E)! Algeria: Nr. Constantine, Bourgeau s.n. (BM)! Sardinia: Capoterra, Fiori 1767 (BM)! Monte Santo, Biondi 7.v.1879 (FI)!

Accession 74 (Fig. 53 as S. leucanthemifolius).

Distribution: N. Morocco, N. Algeria and Sardinia. (Map. Fig. 39).

This variety is probably closest to var. fradinii (S. mauritanicus) with which it intergrades, though its most fertile hybrids were produced with var. leucanthemifolius. It showed higher fertility when crossed with members of the gallicus/glaucus (desfontainei) group than other accessions of S. leucanthemifolius did.

v. var. casablancensis Alexander var. nov.

Erect glabrous or very sparsely pubescent annual, often a little fleshy, (10.0)18.0-60.0 cm. Lower and middle cauline leaves rhomboid, oblong or triangular in outline, not spathulate, regularly serrate or with regular, round shallow overlapping lobes, middle cauline leaves 4.0-8.0 x 1.5-4.0 cm. Upper cauline leaves triangular, often long and narrow, serrate, occasionally lobed at the base, 2.5-6.0 x 0.8-2.0 cm. Capitula in dense corymbs, pedicels bracteate 0.5-5.0 cm. Capitula cylindric to cup-shaped, phyllaries 13-21, 5.0-6.0 mm. Calyculus of 5-10 bracts, 1.0-2.0 x 0.5 mm. Phyllaries and calyculus bracts usually black-tipped. Ligules

FIG. 40

XEROX COPY OF S. LEUCANTHEMIFOLIUS Poiret

VAR. CASABLANCENSIS Alexander, x $\frac{3}{4}$

11.32/73
58

FLORA OF Morocco No. 157
Name. Senecio leucanthemifolius Poir.
Native Name:
Locality Casablanca
Altitude:
Habit, Colour, [illegible]
[illegible]

Type Specimen

Senecio leucanthemifolius Poir.!
[illegible]

yellow, 6.0-10.0 x 1.5-3.0 mm. Achenes strigulose, 1.5-2.0 mm. Pappus hairs 4.0-5.0 mm, fluked hairs present.

Fl. 1-5. Sand dunes, rocky calcareous slopes and cliffs by the sea. s.l.-50 m. (Fig. 40).

Holotype: Morocco, Casablanca *Trethewy* 157 iii.1931 (K)!

Morocco: Cap Blanc, *Davis* 54260 (E)! Casablanca and Chaouia, *Gentil* 1909 (MPU)! Rabat, ?*Zhuby* 27.i.1924, Institut Cherifien 40640, (RAB)! Salé, *Grant* v. 1888 (E)! Fedhala, *Trethewy* 175 (K)!

Distribution: Restricted to about 300 km of the W. Moroccan coast from Beddouza to Salé. (Map. Fig. 39).

Distinguished from var. *fradinii* (*S. mauritanicus*) by having large, oblong rhomboid or triangular leaves, the upper cauline leaves occasionally pinnatifid at the base, never pinnatisect. Shows slight similarity to var. *major* but is more robust and never has truly spathulate leaves. No material was obtainable for experimental work. Var. *casablancensis* is the only variety in Group B with a purely coastal dsitribution.

vi. var. *vernus* (Biv.) Fiori, Fl. Anal. d'It. 3: 211 (1903)
Syn: *S. vernus* Biv., Sicul. Pl. Cent. 1: 73 (1806)

Differs from var. *fradinii* (*S. mauritanicus*) in having suborbicular lower and middle cauline leaves, and trifid upper cauline leaves, the latter sometimes divided into as many as five lobes; the lobes rounded, a little longer than broad. Leaf margins entire to distantly toothed. Approaches var. *major* in sometimes having basal leaves attenuate and thus subspathulate, but typical leaf dimensions are much smaller. Intermediates are found and they could both be treated in one

FIG. 41

XEROX COPY OF S. LEUCANTHEMIFOLIUS Poiret VAR. VERNUS (Biv.) Fiori, x 3/8

Plantae Siculae rariores

Senecio vernus Biv.

In [illegible] maritimis

Selinunt.

13 Quaritossi [illegible]

SICILIA E MALTA

variety. Typical forms are however quite distinct.

Fl. 12-6. Maritime sands and sandy fields near the sea. No information on altitudinal range, but probably below 150 m.(Fig. 41).

Isotype: Sicily, Bivona s.n., no date (BM)!

Sicily: Palermo, Todaro 1855 (FI)! Taormina, Higgins ii.1902 (E)! Algeria: Bône, Meyer 17.v.1875 (MPU)!

Distribution: Central Mediterranean. (Map. Fig. 39).

No material of var. vernus was available for experimental work.

vii. var. cyrenaicus Dur. et Barr., Fl. Lib. Prodr. 135 (1910)

Syn: S. cyrenaicus (Dur. et Barr.) Borzi, Min. Aff. Esteri, Monogr. Rapp. Col. 7: 9 (1912).

Differs from var. fradinii (S. mauritanicus) in being more robust and larger in all its parts. Phyllaries 7.0-9.0 mm, ligules 10.0-15.0 mm, achenes 2.0-2.5 mm. The large capitula are held in lax or more crowded corymbs. The leaves are elliptic to oblong, dentate and sinuate, sometimes pinnatifid above, the lobes close, narrow and antrorse.

Specimens examined in flower during January and February. Coastal.

Type, Libya (Cyrenaica): Derna, Kenissié, Taubert 603 n.v.

Libya (Cyrenaica): Tolmetta, Vaccari 209 (FI)! Tolmetta, Vaccari 1087 (E, FI, BM)!

Distribution: Restricted to Cyrenaica (Map. Fig. 38).

This name has also been applied to other plants from hills behind the Cyrenaican coastline which do not fit the original description at all. In head size and unique calyculus morphology these plants refer well to no. 25. S. trilobus L. Var. cyrenaicus, being easily distinguishable on the size of its capitula, might perhaps warrant subspecific rank; however, only two gatherings have been examined and no material was available for experimental work, so it is probably best kept as a variety until more information on its variation is available.

9. S. rodriguezii Willk. in Anal. Soc. Esp. Hist. Nat. 3: 36 (1874)

Differs from S. leucanthemifolius subsp. leucanthemifolius in having pale lilac ligules and purple disc flowers. Either acaulous with one or several peduncles produced from the basal leaves, or with spreading decumbent branches. Leaves elliptic-spathulate to oblong, widely toothed, not pinnatifid.

Fl. iii-v. Rocky sea-shores. 2n = 20.

Described from the Balearic Isles.

Majorca: C. Formentor, Kennedy 25 (E)! Minorca: C. Mesquieda, Bucknall & White 23.iv.1903 (E)!

Distribution: Restricted to the Balearic Isles. (Map. Fig. 38).

This species is unique among annual species of Senecio from Europe and N. Africa in having purple disc flowers. Purple or lilac rays are also found in S. hoggariensis, and very occasionally in S. leucanthemifolius.

10. S. vernalis Waldst. & Kit., Pl. Rar. Hung., 1: 23, t.24 (1802)

Syn: S. rapistroides DC., Prodr., 6: 346 (1838)

? S. polycephalus Ledeb., Fl. Ross., 2: 630 (1845)

? S. peduncularis Griseb., Spicil. Fl. Rumel., 2: 224 (1846)

Erect, sparsely to densely arachnoid annual, rarely glabrous, (3.0)10.0-40.0 (60.0) cm. Stems terete, unbranched or with a few ascending branches. Lower and middle cauline leaves elliptic to oblong in outline, 3.0-10.0 x 1.0-3.0 cm, usually denticulate, unlobed to sinuate or pinnatifid, the lobes isodiametric, oblong or triangular; bases of lower leaves attenuate, those of middle leaves auriculate and amplexicaul. Upper leaves broader in outline, amplexicaul, pinnatipartite, lobes narrow; becoming more or less unlobed, dentate or denticulate at the top of the stem. Capitula, cylindrical to cup-shaped, in lax or congested corymbs, pedicels 0.5-4.5 cm. Calyculus of 6-20 narrow bracts, 0.5-2.0 mm. Phyllaries 13-21, 5.0-6.0 mm. Phyllaries and calyculus bracts sometimes black-tipped. Ligules 8-13, yellow, 5.0-10.0 mm. Achenes subcylindric, sparsely strigulose, 2.0-3.0 mm. Pappus hairs 4.0-6.0 mm, fluked hairs present. 2n = 20.

Fl. 11-7. Agrestal and ruderal, growing in a variety of disturbed habitats; also grassland, rocky hillsides, limestone turf, maritime rocks and sand-dunes. -30-3500 m.

Described from Hungary. "Crescit ad sepes vinearum et in aggeribus in Comitatu Syrmiensi". The illustration cited above is presumably taken from an uncited specimen in Kitaibel's herbarium (PR).

Sweden: Oland, Kohler 6.vi.1922 (E)! Denmark: Zealand, Jacobsen 97 (E)! Germany: Berlin, Lackowitz 11.vi.1901 (E)! Rumania: Deva, Tauscher 17.iv.1887 (E)! Jugoslavia: Vranje, Krebs v.1895 (E)! Bulgaria: Mt. Vitosa, Stojanov 199 (E)! Greece: Kalimnos, Major 364 (E)! Rhodos, Bourgeau 90 (BM)! Cyprus: Stavios Valley, Foggie 93 (E)! Turkey: Antalya, Heldreich iii.1849 (BM)! Fethiye, Davis 25416 (E)! Syria: Nebk, Davis 5531 (E)! Lebanon: Harissa, Polunin 5273 (E)! Israel: Sharon Plain, Qeisari, Marder 07024 (HUJ)! Jordan: Wadi Musa, Ma'an, Davis 8686 (E)! Iraq: Amadia, Polunin 5120 (E)! Iran: Sanandag, Kurdistan, Archibald 2000 (E)!

Accessions 6 and 44 (Figs. 56 and 57).

Distribution: N., E. and C. Europe, S.W. Asia, Southern Russia and Afghanistan. Apparently spreading into W. Europe. (Map. Fig. 39).

Possible intermediate with S. glaucus (S. desfontainei): Cyclades, Melos, Heldreich iii.1889 (K, BM, E)!

This species shows a considerable clinal range of leaf shape, notably in Turkey where gatherings from the West tend to have rounded denticulate lobes in contrast to Eastern plants with subentire, triangular lobes. A considerable variety of infra-specific taxa have been described. No attempt has been made here to disentangle them or assign specimens to them.

There are no reliable morphological characters for separating S. vernalis from S. leucanthemifolius and there are probably good grounds for treating them as conspecific. The situation is particularly complicated in the Greek Islands, and Israel where there are records of S. leucanthemifolius. Experimental crossing of Israeli S. vernalis with S. leucanthemifolius subsp. fradinii (S. mauritanicus) from Algeria produced hybrids with 80% stainable pollen, and several other crosses between the two species showed over 50% pollen fertility. Non-germinable seed was produced on crossing S. vernalis with members of the gallicus/glaucus (desfontainei) group. However, herbarium specimens have been seen which appear intermediate. More material is required from the Cyclades. It is expected that further hybridisations involving material from the critical areas would confirm that S. vernalis and S. leucanthemifolius should be amalgamated.

Many other names, given as synonyms for S. vernalis, are encountered in the literature and in Index Kewensis. Most of these turn out to be places where the name S. vernalis W. & K. has been misused, rather than true synonyms. In many cases this misuse is suggested only by the localities cited in the description and, without recourse to cited specimens, this circumstantial evidence is not strong enough to place these names in synonymy.

11. S. vulgaris L., Sp. Pl. 2: 867 (1753)

Differs from no. 10, S. vernalis, in having a longer, always cylindric, capitulum, phyllaries 6.0-8.0 mm. Calyculus of 10-20 triangular, overlapping bracts, often with large black tips. Ray flowers usually absent, occasionally 6-12, then ligules 1.5-4.0 mm, yellow. Leaves elliptic to oblong, denticulate, pinnatifid to pinnatipartite, lobes oblong to triangular, patent, with denticulate or lacerate auricles. 2n = 40.

Fl. 1-12. Ruderal and aggrestal of waste places, fields, disturbed habitats and rocky hillsides. s.l. -2000 m.

Described from Europe. Hb. Linn. 996.7!

Portugal: Coimbra, Moller 275 (E)! Spain: Barcelona, Sennen 2.iv.1911 (E)! France: Iles d'Hyeres, Herb. Ball s.n., no date (E)! Balearic Isles: Soller, Bianor 704 (E)! Italy: Mandusia, Groves v.1874 (E)! Sicily: Roca Busambra, Davis 40045 (E)! Turkey: Edirne, Davis 41901 (E)! Cyprus: Yaila, Davis 2838 (E)! Iraq: Baghdad, Wheeler Haines 2.iii.1955 (E)! Lebanon: Harissa, Polunin 5312 (E)! Israel: Jerusalem, Meyers & Dinsmore B1038 (E)! Iran: Jahrum, Koelz 14672 (E)! Egypt: Giza, Davis 8327 (E)! Algeria: Oran, Fauré 12.ii.1936 (E)! Morocco: Tizi n Tichka, Alexander & Kupicha 489 (E)!

Accessions 43 and 59 (Fig. 62).

Distribution: Native to Europe, N. Africa and continental Asia, widely introduced and more or less cosmopolitan.

Hybrids produced when this species was crossed with various diploids produced surprisingly high percentages of stainable pollen (Fig. 27)being over 10% in four cases. Isolation between S. vulgaris and other polyploid species seems to be stronger. Morphologically, S. vulgaris is one of the more distinct species, the capitula are quite characteristic and the leaf shape remotely resembles S. gallicus and S. vernalis. Populations of S. vulgaris from different parts of its range are very similar morphologically when grown under standard conditions. (Fig. 62).

Considerable attention has been paid to the taxonomy and genetics of the rayed variants of S. vulgaris. Trow (1912), on the basis of cultivation experiments described a large number of varieties, some of them with rays. More recent interest stems from the fact that the spread in the British Isles of rayed forms of S. vulgaris appears to be correlated with the spread of S. squalidus. Trow refers obliquely to this, and remarks that it must be coincidental. Crisp & Jones (1970), Hull (1974) and Richards (1975) all attribute the appearance of rays in inland populations of S. vulgaris to introgression from S. squalidus into S. vulgaris. Presumably occasional hybridisation could occur if an unreduced gamete of S. squalidus was involved, when both gametes would be n = 20. The hybrid then being 2n = 40 could presumably back-cross repeatedly with S. vulgaris, giving rise to rayed forms of S. vulgaris. However, the occurrence of rayed forms of S. vulgaris is so common that it is hard to attribute all cases to the formation of unreduced gametes which is usually believed to happen rather rarely. Support for the introgression theory is provided by Hull (1974b) who finds greater similarity in esterase patterns between S. squalidus and rayed S. vulgaris than between rayed and discoid S. vulgaris, when all three are growing in the same area. Additional support is also provided by Richards (1975) who has observed that rayed S. vulgaris is slower growing than discoid S. vulgaris. He attributes this to the effect of genes transferred from the perennial S. squalidus. This correlation of morphological and life-form characters in hybrids between annuals and perennials has been described as M-V linkage by Grant (1967).

More research clearly needs to be done on the interaction between these two species. It may then turn out that the occurrence of unreduced gametes is a comparatively frequent phenomenon. However, if introgression from S. squalidus into S. vulgaris really is taking place, it is surprising that other morphological characters of S. squalidus are not found in populations of S. vulgaris which are thought to have been introgressed.

12. S. gallicus Vill., Hist. Pl. Dauph. 1: 371 (1786)

Syn. pp. S. squalidus sensu Willd., Sp. Pl. 3: 1991 (1803), non L.
S. exsquameus Brot., Fl. Lusit. 1: 388 (1804)
S. desquamatus Willd., Enum. Hort. Berol. Suppl.: 58 (1814)
S. difficilis Dufour in Ann. Sci. Nat. Ser. 1, 5: 428 (1825)!
? S. scheuzeri Gaudin, Fl. Helv. 5: 294 (1829)
S. alboranicus Maire in Bull. Soc. Hist. Nat. Afr. Nord, 24: 218 (1933)!

Glabrous to arachnoid annual, 7-45 cm, stems terete, shallowly ridged, unbranched or branching in upper half, less commonly below. Lower cauline leaves narrowly elliptic to oblong in outline, 2.0-5.0 x 1.0-2.0 cm, widely toothed or pinnatifid, attenuate; middle cauline leaves oblong with small auricles, up to 6.0 x 2.5 cm, pinnatipartite or bipinnatipartite, the lobes patent, oblong or more narrowly linear, entire or dentate; upper cauline and branch leaves more deeply divided into narrow linear lobes, auricles lacerate. Corymbs lax, pedicels up to 3 cm, with a few scattered bracts. Capitula cylindric to cup-shaped, calyculus usually absent, sometimes of up to 3(10) subulate bracts, 1.0-2.0 mm. Phyllaries 13-21, glabrous, sometimes a little glaucous, 4.5-6.0 mm, reflexing in fruit. Ligules 8-13, 5.0-11.0 x 2.0-3.0 mm. Achenes 2.0-2.5 mm, subcylindric, sparsely strigulose. Pappus hairs 4.0-6.0 mm, fluked hairs present. 2n = 20.

Fl. 3-7. Sand dunes, sandy fields and Pinus forests, river banks. Less commonly on schists and calcareous soils. s.l. - 1000 m.

Isotype: Vapinci, in mureis, vineis. (Gap, Dauphine, S.E. France) Villars s.n. (BM)!

Portugal: Aljezur, Lousley 15.v.1969 (BM)! Carrapeteira, Davis 50873 (E)! Spain: La Rabida, Huelva, Gibbs 69. 135 (E)! Madrid, Atchley 434 (K)! France: Sarras, Ardèche, Chabert 2120 (K)! Fontan les Bois, Reverchon 209 (E)! Sicily: Herb. U. Martelli s.n. (FI)! Algeria: Oran, Fauré vii.1910 (E)!

Distribution: S.W. Europe, Sicily, Algeria, Alboran Is. No specimens seen from Balearic Is., Corsica or Sardinia. (Map. Fig. 42).

Intermediates with S. glaucus subsp. coronopifolius (S. desfontainei): Sicily, Pozallo, Fiori 672 (FI, K, BM)! Licata, Ross 545 (E)!

Intermediates with S. leucanthemifolius: Gibraltar, Europa point, Hubbard & Ellman 738 (K)!

The authority for S. gallicus Vill. is often cited as "Chaix apud Vill., Hist. Pl. Dauph., 3: 230 (1788)." However, this description refers back to vol. 1, p.371 of the same work, where a description is given in a footnote. No mention of Chaix is made either in this first description or on the label of the isotype examined.

Other names sometimes cited as synonyms for S. gallicus include "S.squalidus Willd." and S. uliginosus DC. S. squalidus was originally described by Linnaeus (1753) in the first edition of species Plantarum. In Willdenow's edition of this work (1803), he amplifies Linnaeus' description and places S. gallicus in synonymy. S. squalidus sensu Willd. is therefore only partly symonymous with S. gallicus. S. uliginosus was described by de Candolle (1838) as aperennial of unknown provenance. His description is somewhat suggestive of S. gallicus in leaf lobing and absence of calyculus. S. gallicus, however, never shows a perennial tendency. The description of S. scheuzeri Gaudin states that it is a distinct species from

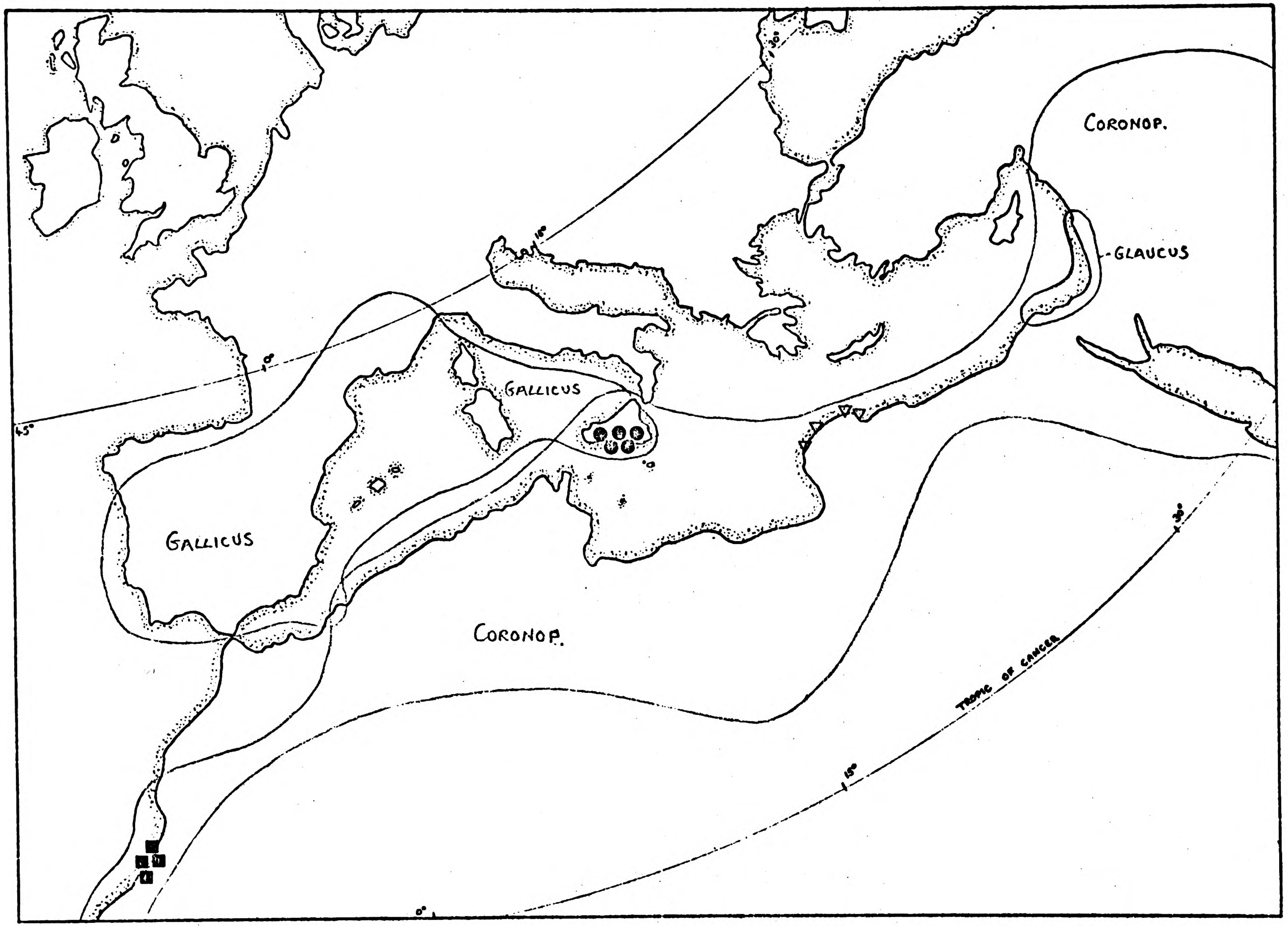


FIG. 42 Distribution of S. gallicus and S. glaucus sspp. glaucus and coronopifolius. S. gallicus/S. glaucus ssp. coronopifolius intermediates ● . S. leucanthemifolius var. fradinii/S. glaucus ssp. coronopifolius intermediates ▽ . S. hesperidium ■ .

S. gallicus but does not say how it differs; the shape of the leaf-lobes sounds very similar to that of *S. gallicus*.

S. gallicus has often been treated as conspecific with *S. glaucus* subsp. *coronopifolius* (*S. desfontainei* Druce or *S. coronopifolius* Desf.) [Jahandiez & Maire, 1933; Flora Europea, in press]. However the area in which intermediates occur is quite small, and breeding experiments have produced hybrids with only 35% stainable pollen. The characteristic facies of the two species are quite different, and little difficulty is experienced in identifying them other than in the area of overlap. One gathering apparently intermediate between *S. gallicus* and *S. leucanthemifolius* has been seen from Gibraltar. It has broader lobes than typical *S. gallicus* and has a calyculus of about 10 bracts. *S. gallicus* is often described as lacking a calyculus, but several specimens from Europe have been seen with up to 3 bracts. Also, specimens from Algeria and the Isle of Alboran, referable to *S. gallicus* on leaf characters, have up to 10 calyculus bracts, as do the intermediates with *S. glaucus* subsp. *coronopifolius* mentioned above. Nevertheless no European material of *S. gallicus* s.s. has been seen with more than three calyculus bracts.

Apart from high interfertility with *S. petraeus* mentioned below, *S. gallicus* seems a fairly distinct species on the basis of breeding experiments. In leaf shape, some populations approach *S. vernalis*. Hybrid seed produced by crossing the two species failed to germinate.

13. *S. glaucus* L., Sp. Pl. 868 (1753)

Decumbent or erect fleshy annual, 8.0-50.0 cm, glabrous to sparsely arachnoid, often glaucous. Stems terete, ridged, sometimes indurated below. Basal leaves linear to narrowly lanceolate, entire or distantly toothed to pinnatipartite, lobes narrow. Middle cauline leaves up to 15 cm, deeply pinnatipartite; lobes linear, some at least 3-5 times longer than broad, sinuses at least 3-5 times the lobe width; lobes antrorse, patent or slightly retrorse, entire, dentate or secondarily lobed; tips of lobes acute, or rounded and bi- or trifurcate. Upper cauline leaves more finely and closely lobed, becoming unlobed and linear above. Capitula in lax corymbs. Phyllaries 13-21, 4.5-8.0 mm. Calyculus of (0)1-12 bracts, 1.0-4.0 mm. Phyllaries and calyculus usually untipped, occasionally with small black tips. Ligules 10-17, yellow, 6.0-12.0 x 1.5-3.0 mm. Achenes 2.0-3.5 mm, sparsely strigulose. Pappus hairs 4.0-7.0 mm, fluked hairs present. $\underline{2n} = 20$.

1. Phyllaries 6.0-8.0 mm, capitula often indurated at base, middle cauline leaves more than 6 cm, if shorter then plant sparsely arachnoid, lobes dentate and bi- or trifurcate at tip .... subsp. *glaucus*

1. Phyllaries 4.5-6.0 mm, capitula never indurated at base, middle cauline leaves less than 6 cm, plant glabrous or very sparsely pubescent, lobes entire or with small remote teeth, tips simple, acute .... subsp. *coronopifolius*

subsp. *glaucus*

Syn: *S. vernalis* v. *carnosus* Post, Fl. Syria, Pal. Sinai ed 1: 442 (1896)
S. joppensis Dinsm., in Post, Fl. Syria, Pal. Sinai ed 2, 2: 69 (1933)

Fl. 12-6. Maritime sand and sandy places not far from the sea. s.l. - 20 m.

Described from Egypt.: Hb. Linn. 996.24!

Israel: Shefalah, *Sheinkar* 07009 (HUJ)! Even Yehuda, *Davis* 4069 (E)!
Egypt: Alexandria, *Bornmüller* 10707 (E)!
Accessions 1, 2 and 4 (Figs. 46 and 47 as *S. joppensis*).

Distribution: Israel and Egypt (Map. Fig. 42).

Generally more robust and fleshier than subsp. *coronopifolius*. The large capitula are often indurated at the base. Typical plants from maritime sands of Israel have broad linear lobes to the leaves and are glaucous and glabrous. Continuous variation connects these coastal forms with smaller leaved, somewhat arachnoid plants from areas behind the coast. It seems likely that hybridisation with *S. vernalis* is taking place inland. Experimental crossing of these two species was performed using a male sterile plant of subsp. *glaucus* resulting in male sterile hybrids. Until these arachnoid inland plants are proved to be hybrid in origin, the manner of leaf lobing refers them to supsp. *glaucus*.

The Linnean name *S. glaucus* was adopted for this species on the evidence of cultivation experiments. An Egyptian accession of *S. joppensis* in cultivation produced upper cauline leaves which closely match specimen 996.24 in the Linnean Herbarium, London, which consists only of the upper part of the plant. Various authors have suggested that the name *S. glaucus* should be applied either to *S. joppensis* or *S. desfontainei*. Ball (1878 p.515) noted under *S. coronopifolius* (= *S. desfontainei*) "Est fere certe *S. glaucus* L. Sp. Pl. 1217; sed nomen ab auctoribus confusum hodie melius negligendum". Also occasional herbarium specimens are found under this name. As *S. joppensis* and *S. desfontainei* are best treated conspecifically on morphological and breeding criteria, it seems appropriate to include them both as supspecies under *S. glaucus* L, in which case *S. desfontainei* becomes subsp. *coronopifolius*. The name *S. coronopifolius* var. *carnosus* (Post) Bornm. has been found on herbarium material of subsp. *glaucus*, but may never have been published.

subsp. *coronopifolius* (Maire) Alexander, *comb. nov.*

Syn: *S. coronopifolius* Desf., Fl. Atl. 2: 273 (1799), non. Burm. (1768)
S. laxiflorus Viv., Fl. Lib.: 55 (1824)
S. subdentatus Ledeb., Fl. Alt. 4: 110 (1833)

S. gallicus var. laxiflorus (Viv.) DC., Prodr. 6: 346 (1838)

? S. ruepellii Sch. Bip. in Schweinf., Beitr. Fl. Aethiop. 157 (1867)

S. coronopifolius var. subdentatus (Ledeb.) Boiss., Fl. Or. 3: 390 (1875)

S. gallicus var. sonchifolius Ball in J. Linn. Soc. Bot. 16: 514 (1878)

S. desfontainei Druce, Br. Pl. List, ed 2: 61 (1928)

S. coronopifolius var. calyculatus Emb. & Maire in Bull. Soc. Bot. Hist. Nat. Afr. Nord 23: 191 (1932)

S. gallicus subsp. coronopifolius Maire in Jahandiez & Maire, Cat. Pl. Maroc 3: 784 (1934)

Fl. 1-7. Agrestal and ruderal of sandy fields, river banks, stony and rocky slopes, and deserts. Also recorded from limestone. s.l. - 2370 m.

Described from N.W. Africa "Habitat in arenis humidis deserti".

Canary Isles: Teneriffe, Burchard 208 (E)! Morocco: Oued Massa, Maire 7. iv.1922 (RAB)! Chichaoua, Maire 5.iv.1921 (MPU)! Tafraoute to Tleta de Tasserirt, Davis 48796 (E)! Algeria: Ain Sefra, Fauré 12.v.1938 (E)! Mzab, Weiller 867 (MPU)! Tunisia: Gafsah, Pitard 413 (E)! Sicily: Licata, Ross 545 (FI)! Licata, ?Lacino 588 (E, BM)! Libya: Tripoli, Davis 49458 (E)! Egypt: Almaza, Lupton 2.iv.1946 (BM)! Israel: Rafiah, Eig 5.v.1924 (HUJ)! Jordan: Wadi Ram, Davis 9095 (E)! Syria: Abu ed Duhur, Rechinger s.n. 1946 (E)! Iraq: Baghdad, K. Mariam, Wheeler-Haines 11.iii.1955 (E)! Iran: Arak, Archibald 1758 (E)! Afghanistan: Ispoli, Kandahar, Hedge & Ekberg 7067 (E)! Pakistan: Surkhab Valley, Baluchistan, Lace 3710 (E)!

Accessions 3, 68 and 73. (Figs. 46, 48 and 49 as S. desfontainei)

Distribution: Canary Isles, N. Africa, Sicily, S.Q. Asia and Western Himalayas (Map. Fig. 42).

This subspecies is usually smaller in all its parts and less fleshy than subsp. *glaucus*. It is never more than sparsely arachnoid, and the leaf lobes end simply in rounded or acute points. The capitula are never indurated at the base. Crosses between this subspecies and subspecies *glaucus* (*S. joppensis*) produced hybrids with 95% and 85% stainable pollen grains, and also some achenes which failed to germinate. Reciprocal crosses between Israeli and Moroccan populations of subsp. *coronopifolius* (*S. desfontainei*) also produced non-germinating achenes. The relationship between *S. glaucus* and *S. gallicus* is discussed under the latter species. Apart from morphological intergrading with *S. gallicus*, *S. glaucus* subsp. *coronopifolius* is fairly distinct both on morphological and breeding criteria. Hybrids with 95% fertility resulted from crossing subsp. *coronopifolius* from Morocco with populations morphologically intermediate between it and *S. leucanthemifolius* var. *fradinii* (*S. mauritanicus*). These intermediates were equally fertile with *S. leucanthemifolius* var. *fradinii*.

Some problems were encountered in choosing the correct name and authority for this subspecies. Maire's combination *S. gallicus* subsp. *coronopifolius* is based on *S. coronopifolius* Desf. which is illegitimate being a later homonym. A note under article 72 in the International Code of Botanical Nomenclature (1972, p.62) states that an illegitimate name can be adopted at a new rank or in a new combination if there are no other objections. The epithet is then treated as new, and the original authority is not mentioned. This subspecies is therefore referred to as subsp. *coronopifolius* (Maire) Alexander rather than subsp. *coronopifolius* (Desf.) Alexander.

14. *S. hesperidium* Jahandiez, Maire & Weiller in Bull. Soc. Hist. Nat. Afr. Nord 22: 297 (1931)

Syn: *S. gallicus* subsp. *hesperidium* (Jahandiez, Maire & Weiller) Maire, Cat. Pl. Maroc 284 (1934)

Differers from S. glaucus subsp. coronopifolius in having larger capitula, phyllaries 6.5-7.5 mm. The ligules c. 13, long and broad, 8.0-14.0 x 4.0-5.0 mm. The plant is fleshy and the leaves pinnatipartite or bipinnatipartite into rounded linear lobes which are entire, never dentate. 2n = 20.

Fl. iii-iv. Colonised sand dunes and sandy slopes by sea. s.l. - 50 m.

Isotypes: Morocco, Sidi Moussa: Jahandiez 81 (RAB)! Máire 22.iv.1931 (MPU)! Morocco, Sidi Moussa: Davis 53536 (E)! Davis 53545 (E)!

Accession 52 (Fig. 49).

Distribution: Sidi Moussa, S.W. Morocco, known only from the type locality. (Map. Fig. 42).

Some of the fleshier populations of S. glaucus from Morocco approach S. hesperidium in having rounded fleshy lobes to the leaves. S. glaucus can almost always be distinguished by having more finely divided leaves, with acute tips to the lobes, and smaller capitula.

Experimental crossing of S. hesperidium with S. glaucus subsp. coronopifolius (S. desfontainei) produced hybrids with 75% stainable pollen, which in this group seems low enough to justify maintaining S. hesperidium as a separate species from S. glaucus. Crossing between S. hesperidium and populations intermediate between S. glaucus subsp. coronopifolius and S. leucanthemifolius var fradinii (S. mauritanicus) produced hybrids with 99% stainable pollen. This is slightly surprising as from leaf morphology one might have expected their parentage to have involved S. glaucus subsp. coronopifolius rather than S. hesperidium.

15. S. kraschenínnikovii Schischk., Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS, 15: 410 (1953)

Syn: S. pedunculatus Edgew., Trans. Linn. Soc. Lond. 20: 74 (1846) non Sch. Bip. (1844)

Differs from S. glaucus subsp. coronopifolius in having smaller oblong capitula and barely exserted ligules less than 4 mm long. The general manner of leaf dissection is much finer than in S. glaucus and the leaves are never fleshy. The achenes are very sparsely and shortly strigulose.

Fl. 7-8. Ruderal, shady places by streams and on cliffs. 2000-3500 m.

Described from Himalayas. "In valle fl. Dhawali, Garwal Orient".

Kashmir: Sind valley, Duthrie 13591 (E)! Pakistan: Hispar glacier snout, Polunin 6366 (E)!

Distribution: Afghanistan, Turkistan, Pakistan and Kashmir; possibly further East into Tibet.

A rayless species otherwise very similar to S. krascheninnikovii was described as S. dubius by Ledebour (1833), from Tibet and Sinkiang. If these are considered conspecific, then S. dubius Ledeb. would be the correct name for the species. Clarke (1876 p. 195), suggests that they could both be included in S. coronopifolius (= S. glaucus subsp. coronopifolius) but nevertheless maintains all three binomials, as do Boissier (1888) and Komarov (1961).

16. S. vulcanicus Boiss., Diagn. Ser. 1 (11): 31 1849)

Differs from S. glaucus subsp. coronopifolius in being a subacaulous montane plant with narrow linear to lanceolate subpinnatifid leaves. Ligules c. 5 mm. Achenes glabrous.

Fl. 7-8. Volcanic rocks and soil. 3000-4000 m.

Syntypes: Iran, Mt. Demavend, Kotschy 667 (n.v.) Iran, Elamout Mts. Aucher 4717 (n.v.).

Iran, Mt. Demavend: Bornmüller 7478 (E)! Jardine 801 (E)!

Distribution: Restricted to the Elburz Mts. in N. Iran.

Although Boissier (1849) describes this species as having achenes which are shortly hirsute, both specimens examined have glabrous achenes, and the species has been keyed out in this manner. From the original description, S. exilis Blanche ex Boiss., Fl. Or. Suppl. 302 (1888) seems similar to S. vulcanicus in being a dwarf montane plant with leaves reminiscent of S. glaucus subsp. coronopifolius. It is described as having glabrous achenes. The type locality is Mt. Makmel in Lebanon. No specimens of S. exilis have been examined. The name S. lacerus Boiss., Diagn. Ser 1(11): 32 (1849) is probably a synonym of S. vulcanicus. The habit description seems very similar, the type locality is the same, and it is also described as having glabrous achenes. Later, Boissier treated S. lacerus as S. coronopifolius var. psilocarpus (1875).

17. S. massaicus (Maire) Maire in Bull. Soc. Hist. Nat. Afr. Nord, 15: 99 (1924)

Syn: S. coronopifolius subsp. massaicus Maire in Bull. Soc. Hist. Nat. Afr. Nord, 14: 153 (1923)

Differs from S. glaucus ssp. coronopifolius in having smaller oblong rayless capitula, diam. 5.0-6.0 mm. The leaves are lanceolate, entire or distantly toothed to pinnatipartite, never bipinnatipartite; lobes narrowly triangular to subulate, antrorse, unbranched or with a few ascending branches above. 2n = 40.

Fl. iii-v. Sandy and gravelly river terraces, often more or less saline. 0-1000 m.

Isotype: Morocco, shores of R. Massa, Maire 8.iv.1922 (MPU)!

Morocco: Mouth of R. Sous, Davis 53902 (E)! Agdz, Maire 14.v.1933 (MPU)! Accession 66 (Fig. 64).

Distribution: Morocco, mouths of R. Sous and R. Massa, Agdz on R. Draa (Map. Fig. 43).

A distinct species both morphologically and genetically. Being a tetraploid, S. massaicus is effectively isolated from local populations of S. glaucus subsp. coronopifolius (S. desfontainei), though artificial hybrids between the two taxa had 14% stainable pollen, when Israeli subsp. coronopifolius was used. When Moroccan subsp. coronopifolius was used, poor seed of grade 1 was produced (see 7.4.1). Hybrids of much lower fertility were produced when S. massaicus was crossed with the tetraploid S. vulgaris, although they are both tetraploid.

The distribution of this species (Map. Fig. 43) is rather surprising, as the localities from which it is recorded are some way apart. Also the inland station is on a different river from the coastal ones. The populations at the coastal localities vary very much from year to year. No S. massaicus could be found at the mouth of the R. Massa in March 1972, when it was abundant on the R. Sous. Unless other records are found for this species, it must be assumed that the inland plants are an isolated case of dispersal. The achenes are quite small enough to be carried on birds' feet.

18. S. hoggariensis Batt. & Trab. in Bull. Soc. Bot. Fr. 58: 671 (1911)

Differs from S. glaucus subsp. coronopifolius in having 8-10 pale purple ligules, 4.0-5.5 x 1.0-1.5 mm. The capitula are narrowly cylindric, phyllaries 6.0-8.0 mm. The leaves are more broadly and closely lobed than in subsp. coronopifolius. 2n = 60.

Fl. iii and "spring". Montane sandy river beds and fallow fields. 1400-2500 m.

Isotype: Algeria, Laperrine, Hoggar Mts., Battendier s.n. no date (MPU)!

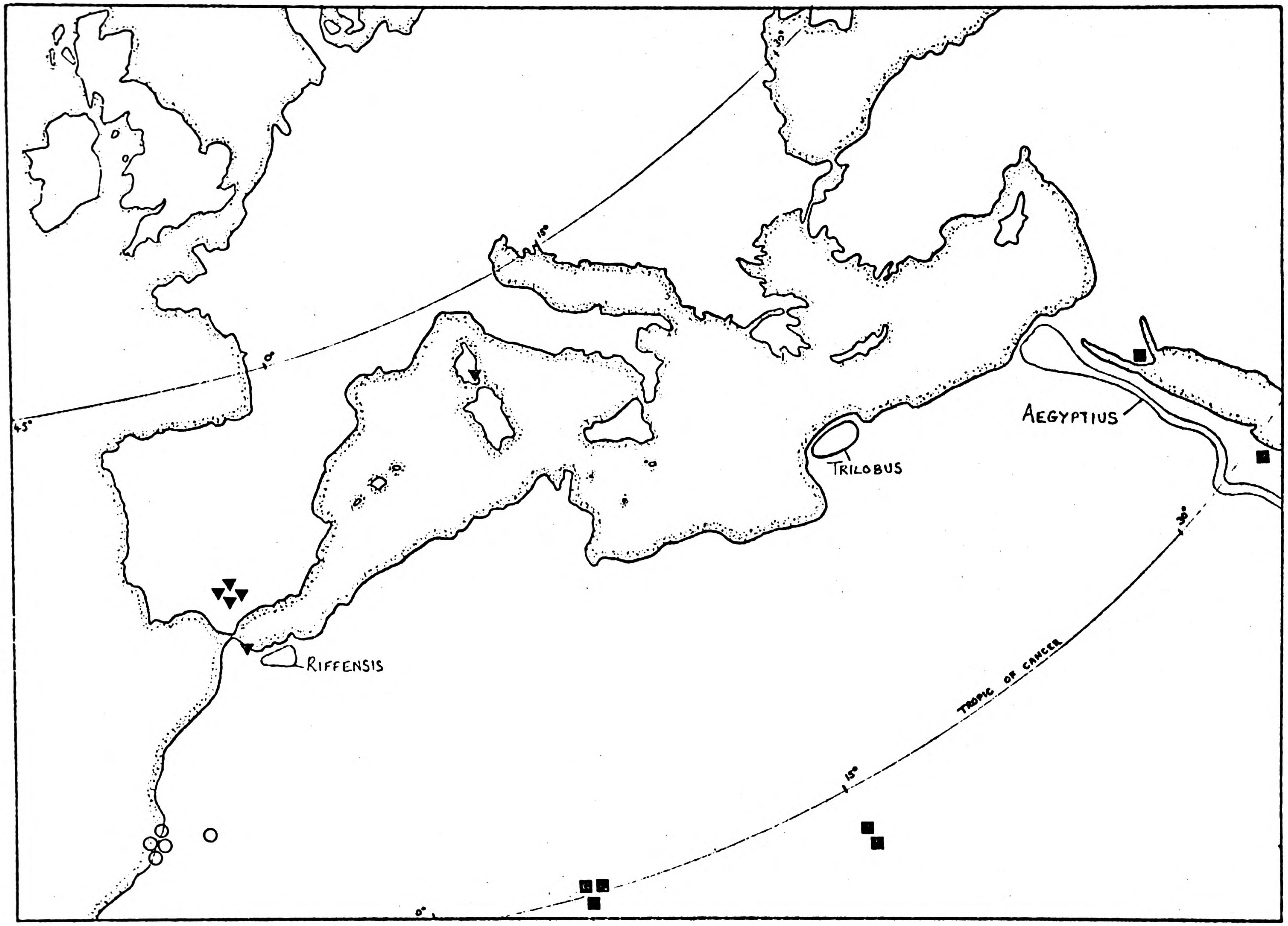


FIG. 43 Distribution of *S. riffensis*, *S. massaicus* ○ , *S. hoggariensis* ■ , *S. petraeus* ▼ , *S. aegyptius* and *S. trilobus*.

Algeria; Hoggar Mts: Tamanrasset, Maire 9.iii.1933 (MPU)! Hassi Dehine, Hunting Services 48(U2), (E)! Sinai: Gebel Qasar Abbas Pasha (nr. G. Katharina), Danin 24.iii.1968 (E, HUJ)!

Accession 45 (Fig. 64).

Distribution: S. Algeria (Hoggar Mts), N. Chad (Tibesti Mts), S.E. Egypt (G. Elba), Sinai (G. Katharina). (Map. Fig. 43).

A distinct species both morphologically and cytogenetically. Most crosses involving S. hoggariensis failed to produce viable achenes. When it was crossed with Scottish S. vulgaris, the resulting hybrids had 7% stainable pollen; the only other cross to produce viable seed was that made reciprocally with S. massaicus when the hybrids either produced no pollen or 0% stainable pollen.

19. S. petraeus Boiss. & Reuter, Pugillus: 59 (1852)
non Klatt., Abh. Naturf. Ges. Halle, 15: 330 (1882)
non Muschler in Bot. Jahrb. 43: 70 (1909)
non (R.E. Fries) R.E. Fries in Jacobsen, Handb. Sukkulent Pfl., 2: 1034 (1954)

Often described as similar to S. gallicus in lacking a calyculus (see remarks above). Differs from S. gallicus in having considerably larger glaucous capitula with phyllaries (6.0)7.0-10.0 mm, ligules 13-15, more than 10 mm and achenes 3 mm. Leaves much broader than S. gallicus, never more than shallowly sinuate lobed, leaf bases broad and amplexicaul, upper leaves cordate. 2n = 20.

Fl. 3-5. Limestone Mts. Spain.

Described from Grazalema, Spain.

Spain: Grazalema, Gibbs et al 69.1535 (E)! Sardinia: Giovannibono, San Vito, Sommier 20.iv.1872 (FI)! Morocco: Ceuta, Gandoger 78 n.v.

Accession 41 (Fig. 58).

Usually described as endemic to S. Spain (see Map. Fig. 43). The single specimen from Sardinia is a little shorter in involucre length than typical S. petraeus, but otherwise fits the description well.

When typical Spanish material was crossed with S. gallicus, the hybrids had an average of 87% stainable pollen. Despite this high interfertility, no intermediate wild gatherings have been seen and its morphological distinctness makes S. petraeus best kept as a separate species.

20. S. sylvaticus L., Sp. Pl. 2: 868 (1753)

Differs from no. 1, S. nebrodensis, in being an annual with small oblong capitula. Phyllaries 5.0-7.0 mm. Ligules 2.0-3.5 mm. Achenes strigulose. Slightly glandular, at least in inflorescence, not viscid. Leaves green.

Described from Europe. Hb. Linn. 996.21!

Distribution: North and central Europe, Balkan Peninsula.
Not used experimentally.

21. S. viscosus L., Sp. Pl. 2: 868 (1753)
Syn: S. calverti Boiss., Diagn. Ser. 2(3): 32 (1856)
S. tymphresteus Boiss. & Heldr., Ser. 2(6): 99 (1859)

Differs from no. 1, S. nebrodensis, in being an annual with oblong capitula. Phyllaries 7.0-10.0 mm. Ligules less than 5 mm. Achenes glabrous. Viscid in all parts. Leaves green.

Described from Europe. Hb. Linn. 996.19!

Distribution: Widespread throughout Europe, eastwards to Turkey and central Russia.

Not used experimentally.

22. S. lividus L., Sp. Pl. 2: 867 (1753)

Syn: S. auriculatus Desf., Fl. Atl. 2: 272 (1799)
S. auritus Willd., Sp. Pl. 3: 1982 (1803)
S. foeniculaceus Ten., Prodr. Fl. Nap. 2: 216 (1820)

Differs from no. 1, S. nebrodensis, in being an annual with oblong capitula. Leaves unlobed, sinuate or sometimes pinnatifid, brownish-green, often purple below. Phyllaries 8.0-10.0 mm, Ligules 1.0-1.5 mm. Achenes strigulose.

Described from Spain. Hb. Linn. 996.14!

Distribution: West and Central Mediterranean.

Not used experimentally.

23. S. aegyptius L., Sp. Pl. 867 (1753)

Glabrous to pubescent annual, 15-50 cm. Stems unbranched or branching above, less often from the base; indurated below. Basal and mid-cauline leaves elliptic to rhomboid in outline, pinnatifid, the lobes rounded or acute, antrorse; upper cauline leaves narrower in outline, more distantly and narrowly lobed or toothed, about 4 times longer than broad; branch leaves usually deeply pinnatipartite or bipinnatipartite, the lobes overlapping. Capitula 3-4 mm diam. at anthesis, oblong to urceolate in profile, borne in dense corymbs. Phyllaries c. 21, 3.0-4.0 mm, not reflexed in fruit. Calyculus of 4 to 10 linear-lanceolate bracts, up to 2 mm. Ray flowers absent or if present scarcely showing. Ligules 8-13, 1.0-2.0 mm. Achenes 1.5-2.0 mm, cylindric, sparsely strigulose. Pappus hairs c. 2 mm. $2n = 40$.

Fl. 12-3. Banks of R. Nile and associated waterways; desert oases. Egypt and Sudan. Also recorded from Cyprus and Port-Juvenal, nr. Montpellier, France. (Map. Fig. 43)

1. Ray flowers present .... var. aegyptius
1. Ray flowers absent .... var. discoideus

var. aegyptius

Syn: S. triflorus L., Sp. Pl. 867 (1753), Hb. Linn. 996.12!

Type: Habitat in Aegypt. Hb. Linn. 996.13!

Egypt: Giza, Davis 8232 (E)! Asswan, Davis 6048B (E)! Abu-Zabel, Schimper i.1835 (E)!

var. discoideus Boiss., Fl. Or. 3: 388 (1875)

Syn: S. arabicus L., Mant. 114 (1767) Hb. Linn. 996.9!
S. verbenaefolius Jacq., Hort. Vindob. 1: 2, t 3 (1770)
S. aegyptius var. verbenaefolius (Jacq.) Boiss., Fl. Or. 3: 386 (1875)

Differs from var. aegyptius only in the absence of ligules.

Syntypes: Egypt, Aucher-Eloy 3434 n.v., Cairo, Benisouef Kralik s.n., n.v.

Egypt, Thebes: Bornmüller 10704 (E)! Davis 6095B (E)! 2nd Cataract, Scott Elliot 3328 (E)! Accession 34 (Fig. 63).

Boissier (1875) noted that var. verbenaefolius, distinguished by having less dissected leaves, merged with the type variety. From the material examined it seems impossible to separate var. verbenaefolius satisfactorily, and as Jacquin's species is discoid I think it should be placed in var. discoideus. Jacquin's illustration of S. verbenaefolius and the Linnean type of S. aegyptius are very similar in leaf shape though the Linnean specimen is slightly more dissected, and is ligulate. As Jacquin's illustration was made from a cultivated specimen grown in Vienna, it might be expected to have less deeply dissected leaves.

S. aegyptius is a distinct species both morphologically and genetically. Most of the hybrid seed produced when it was used as a parent failed to develop, but hybrid plants with 7% stainable pollen were produced when *S. aegyptius* var. *aegyptius* was crossed with *S. leucanthemifolius* var. *fradinii* (*S. mauritanicus*), which is diploid. Crosses with other tetraploids resulted in poor seed or plants that failed to produce pollen. (Fig. 27).

S. belbeysius Del., Fl. Eg. Ill. 126, tab 45 (1814)

Syn: *S. belbeyticus* Poiret, Encyc. Suppl. 5: 129 (1817)
Acleia belbeysia DC., Prodr. 6: 340 (1838)

This name is frequently met in Egyptian Floras, but its status is not at all clear. It is usually diagnosed from *S. aegyptius* as having glabrous achenes and cup-shaped capitula. The illustration in Delille (1814) looks very similar to *S. aegyptius*. I have seen one specimen, named *S. belbeysius*, of a discoid plant with small round capitula and glabrous achenes. The leaves are not unlike those of *S. aegyptius*, but are narrower and less divided. Tackholm (1974) describes *S. belbeysius* as being similar to *S. vulgaris* apart from the glabrous achenes and rounded capitula; she describes it as being rare. It is possible that hybridisation is taking place between *S. aegyptius* and *S. vulgaris* as they are both tetraploid. The only other species in the area is *S. glaucus*, a diploid. Because of lack of material and uncertainty about its status, *S. belbeysius* has been omitted from the key.

24. S. flavus (Decne) Schulz Bip., in Webb & Berth., Phyt. Canar. 2: 319 (1845)

Syn: Crassocephalum flavum Decne in Ann. Sci. Nat. Ser. 2, 2: 265 (1834)

S. decaisnei DC., Prodr. 6: 342 (1838)

S. claviseta Pomel, Nouv. Mat. Fl. Atl. 60 (1874)

Erect glabrous, glaucous annual. Stems terete, finely ridged, usually much branched below. Leaves orbicular, triangular or cordiform, widely dentate, unlobed, auriculate, often purple below. Middle cauline leaves 2.0-5.0 x 0.7-3.0 cm. Capitula cylindrical in lax or dense corymbs. Calyculus of 1-5 bracts, often absent. Phyllaries c. 13, 6.0-9.0 mm. Ligules usually absent, sometimes c. 13, 1.5 mm, purplish or dull yellow with reddish veins on abaxial surface. Achenes 2.0-3.0 mm, subcylindrical, lanate. Pappus hairs c. 4 mm, fluked hairs present. $2n = 20$.

Fl. 3-5. Deserts and dry rocky and gravelly places. c. 1000 m.

Described from Sinai "Hab: le desert du Sinai".

Morocco: Tafraoute, Davis 53853 (E)! Algeria: Metlili, Cosson 11-14.v.1853 (E)! Egypt: Dchebel Ataka, Bornmüller 10703 (E)! Jordan: El Inab, Hunting Survey 73b (E)! Accession 7 (Fig. 58).

Distribution: Canary Isles, N. Africa, Arabia, Israel.

A distinct species morphologically. Poorly developed seed resulted from using S. flavus in crosses with all ploidy levels. The accession cultivated at Edinburgh had very short yellowish rays with red lines on the abaxial surface. Other rayed material has been seen, all from the eastern end of the range of this species.

25. S. trilobus L., Sp. Pl. 2: 868 (1753)

Erect, glabrous to sparsely arachnoid annual. Stems terete, ridged, branching mostly in upper half, sometimes from below, 20-110 cm. Leaves elliptic to oblong, broadest apically, regularly and closely dentate, divided in the upper half into three broad oblong lobes with rounded tips; the lateral lobes at about 45° to the midrib. Middle cauline leaves 4.0-6.0 x 2.0-4.0 cm. Capitula cup-shaped, small, clustered in dense corymbs. Peduncles arachnoid. Calyculus of 14-25 lacerate, rhomboid bracts, divided down to half their length; largest bracts c. 3.0 x 1.5 mm, abruptly narrowing into a stalk, apical half black. Phyllaries 5.0-8.0 mm, glabrous, tips black in form of an inverted 'V'. Ligules 13-21, yellow, 6.0-8.0 x 2.0-3.5 mm. Achenes strigulose 2.0-3.0 mm. Pappus hairs c. 4.5 mm, fluked hairs not found.

Fl. 3-5. Limestone mountains at about 1000 m. (Fig. 44).

Lectotype (provisional) Hb. Linn. Stockholm 364.17, photograph!

Described from Spain, probably in error as never since recorded from there.

Libya, Cyrenaica: El Abrach, Pampanini 9545 (FI, K)! Jebel Akhdar, Sandwith 2281 (K)! Lamluda, Pampanini 9546 (FI)! Cirene, Pampanini 9547 (FI)!

Distribution: All specimens examined come from Jebel al Akhdar in Cyrenaica. (Map. Fig. 43).

Unique among all the species examined during this investigation in having lacerate calyculus bracts (Fig. 5). The trifid nature of the leaves is also very characteristic. The name S. trilobus has been almost totally neglected since Linnaeus. De Candolle (1838) placed S. trilobus in synonymy with a question mark under S. leucanthemifolius; he probably did not examine any specimens. Presumably this species has never occurred in Spain, which Linnaeus cites as the country

HERB. HORT. BOT. REG. KEW.

EXPEDITION TO LIBYA, 1939.

Senecio cyrenaicus (Dur. et Bar.) Borzi ex Pamp.

CYRENAICA: altipiano di Slonta; limestone pavement on bare open summit of Jebel Akhdar.

Date April 3rd. Alt. c. 830 m.
Descr. Fls. yellow.

(= S. leucanthemifolius var. cyrenaicus Dur. & Bar.)

Leg. N. Y. SANDWITH. No. 1281.
(= N. D. SIMPSON. No. 39,279.)

H.32/73
56

FIG. 44

XEROX COPY OF S. TRILOBUS

x 3/8

of origin. According to W.T. Stearn (in litt.), it is quite possible that Linneaus could have obtained specimens from Cyrenaica, though no reference to this has been found. It is strange that all specimens examined have been identified as S. leucanthemifolius var. cyrenaicus which was described as having large heads in lax corymbs. Authentic material of var. cyrenaicus has been examined and there should be no confusion between these two taxa.

From the microfiche, specimen 996.17 in the Linnean Herbarium in London, matches the Cyrenaican material well in leaf shape, but the capitula seem larger and the corymb less dense. Specimen 364.17 in the Linnean Herbarium in Stockholm, also only examined from photographs, matches the material much better and is provisionally designated as a lectotype.

Sect. DELPHINIFOLIUS Reichenb

Differs from Sect. Senecio in having elliptic-ovate, papillose achenes. Pappus hairs barbellate, all of one type. Phyllaries broad, sericeous or sparsely strigose.

26. S. delphinifolius Vahl, Symb. Bot. 2: 91 (1791)

Erect, 20-60 cm, branching only in inflorescence, stems leafy. Corymbs dense, flat-topped. Calyculus of 6-10 bracts. Phyllaries c. 21, sparsely strigose.

Described from Tunisia. "Habitat passim in agris Tunetanis".

Distribution: Italy, Sicily, Sardinia, Algeria and Morocco.
Not used experimentally.

27. S. minutus DC., Prodr. 6: 346 (1838)

Subacaulous and scapose, or erect and branching from the base, 5.0-25.0 cm.

Capitula solitary or in loose corymbs. Calyculus absent. Phyllaries c. 13, sericeous.

Described from Spain: based on several syntypes (n.v.)

Distribution: Central and S. Spain, Morocco.

Not used experimentally.

CHAPTER 10 EVOLUTIONARY SPECULATIONS

10.1 INTRODUCTION

In this chapter, some of the basic evolutionary trends operating in the group are considered, and possible examples are cited of various causes of speciation. The term speciation is used here to describe the process by which reproductively isolated gene-pools are formed, whether the units formed are regarded as species or other taxa (Davis & Heywood, 1963 p.418). Only a very small part of Senecio has been examined, and thus ideas on the origin and evolution of the genus as a whole are not discussed in detail. It is emphasised that the theories are conjectural, but it was thought worthwhile to speculate about evolutionary processes that might have operated or still be operating within the group. Further details of interfertility and morphology are given under the taxa in question in 9.2.3.

10.2 LIFE-FORM

Small (1919) presents a model of Composite evolution in which Senecio, which he believes to be the ancestral genus of the family, is derived as a shrubby montane perennial from an arborescent scrambling Lobeloid similar to Siphocampylus Pohl. His reasons for considering Senecio to be the oldest and therefore most primitive genus in the Compositae are based on the "Age and Area Hypothesis" of Willis (1916), since considerably modified (Walters, 1961). Small believed that Senecio appeared in late Cretaceous or early Eocene times in the Andes, which are now known not to have reached their present height until the Pleistocene (Kummel, 1970). Most recent authors, e.g. Cronquist (1955) incline to the view that the ancestral tribe of the Compositae is the Heliantheae rather than the Senecioneae, and that their closest relatives are to be found among the Rubiales. Cronquist maintains that the first Composites were herbaceous, the woody condition being always derived, but adds that woody forms have probably given rise to plants with a secondary herbaceous habit.

Among the annuals and perennials considered in this thesis, evidence from breeding systems and chromosome number discussed below, suggests strongly that the herbaceous annuals are derived from the suffrutescent perennials.

10.3 ENVIRONMENT

The effect of environmental factors upon evolution is of course paramount. It will suffice here to consider a few examples in which particular environmental conditions have influenced speciation.

10.3.1 LOCAL SELECTION FROM A WIDESPREAD SPECIES

S. glaucus subsp. coronopifolius (S. desfontainei) is widespread in subdesert conditions from the Canary Isles eastwards across N. Africa to Afghanistan and W. Pakistan. Morphological differentiation, and possibly speciation, appear to be taking place in two areas where it encounters maritime conditions. In W. Morocco, subsp. coronopifolius has given rise to the morphologically distinct S. hesperidium, from which it is not completely isolated geographically or genetically. Their artificial hybrids had 75% pollen fertility. At the eastern end of the Mediterranean, on the coast of Israel and Egypt, S. glaucus subsp. glaucus (S. joppensis), which is less distinct morphologically and genetically from subsp. coronopifolius, has been developed. In this case, the hybrids were 95% fertile.

10.3.2 CATASTROPHIC SELECTION

Lewis (1962), from observations on experimental planting of Clarkia species in various environments, found that where extreme conditions, such as drought, obliterated the vast majority of a particular population, mutations, which would have been suppressed by the size of normal populations, can become established. If these differences from the norm are non-adaptive, then the effect is rather similar to genetic drift. Collections of S. leucanthemifolius var. leucanthemifolius from the mouth of the Cheliff River in N. Algeria show a very characteristic leaf-shape and glaucousness (S. pinguiculus, Fig. 57). It is possible that sudden flooding of the river mouth after storms inland could have drastically reduced the numbers of a more typical population, allowing this particular form to multiply in isolation. Hybrids between these plants and typical var. leucanthemifolius had pollen fertility of 95%.

10.3.3 ARIDITY

Many of the species considered here grow in areas in which water is an important limiting factor. Stebbins (1952) suggests that evolution can be most rapid in habitats where one particular factor such as moisture availability is fluctuating, as this is inclined to give rise to fragmented populations which may occasionally meet when the conditions allow it. S. leucanthemifolius var. fradinii (S. mauritanicus) has very much this sort of geographical structure. More or less isolated populations are found in Algeria and Morocco which show very high inter-population variation. This population structure has been suggested by Wright (1940) as being conducive to rapid evolution.

10.4 HYBRIDISATION AND POLYPLOIDY

Hybridisation is widely held to be a very important factor in speciation. Genetic isolation between the species investigated has been shown to be fairly weak in several cases. Added to this, many species favour disturbed habitats, being agrestals or ruderals, another factor encouraging establishment of hybrids. Hybrids are more likely to become established if a 'hybrid' environment is available between the environments of the parents. It is easy to appreciate that hybridisation has probably been important in this group, but considerably more difficult to be sure of particular cases of hybridisation without experimental evidence such as synthesis of the hybrid species. Stebbins (1959) stresses that amphiploids may often have migrated thousands of miles away from their area of origin and their parent species. They may also survive long after their parents have become extinct. In this group, there are a few cases in which it is possible to detect characters in some species, which, in their similarity to other extant species, suggest a hybrid origin. Hybridity is also suggested by polyploidy, as established autoploids are rather rare, nearly always having low fertility, in contrast to alloploids.

S. massaicus, a discoid tetraploid, is endemic to a small area of S.W. Morocco. In leaf shape and lobing it is somewhat similar to the diploid *S. glaucus* subsp. *coronopifolius* (*S. desfontainei*), with which it is sympatric. The two taxa are quite distinct morphologically and autoploidy is not suspected. Assuming that subsp. *coronopifolius* is one of its parents, it is hard to imagine what the other parent could be. *S. leucanthemifolius*, *S. vulgaris* and *S. hesperidium* also occur in the area, but none of them seems a very likely parent. Intermediates between *S. leucanthemifolius* var. *fradinii* (*S. mauritanicus*) and *S. glaucus* subsp. *coronopifolius* (*S. desfontainei*) are found in the Atlas Mts., and were also synthesised during this investigation, but they do not resemble *S. massaicus*. *S. vulgaris*, also discoid, is a tetraploid and when crossed with subsp. *coronopifolius* produced hybrids of 18% pollen fertility. In this case one has to assume either that the other parent is now extinct or that *S. massaicus* has evolved very rapidly and no longer resembles its other parent.

S. hoggariensis, a hexaploid with purple ligules, also shows some similarity to *S. glaucus* subsp. *coronopifolius* (*S. desfontainei*) in leaf shape, though the lobes are generally shorter and broader. It has a very disjunct distribution (Map.Fig. 43) and was presumably more widespread and coherent before the Saharan area became arid, though it is now restricted to desert mountains. Again, from present day distributions, it is hard to imagine what its parents might be. It is likely to have resulted from hybridisation between a diploid and a tetraploid. A further puzzle is the origin of the purple ligules. Many S. African species such as *S. elegans* L. have purple ligules and pinnatifid leaves and could possibly have been in contact with the Saharan area via E. Africa. Purple ligules also occur occasionally in European and other N. African species, such as S. flavus which is generally discoid but does have some Israeli populations with very short purple rays. However, S. flavus is genetically isolated from all other species crossed with it, including S. hoggariensis. It is quite possible that the purple ligules could have arisen spontaneously in S. hoggariensis, and acquired a selective advantage.

A hybrid origin is also suggested for S. squalidus, (P. Crisp, in litt.). In this case, no increase in chromosome number would have taken place, as the probable parents, S. aethnensis and S. chrysanthemifolius, like S. squalidus, are diploids. Although most authors treat S. aethnensis and S. chrysanthemifolius as separate species because of their very different leaf shape, they seem likely to have had a fairly recent common origin. They both occur on Mt. Etna in Sicily where they occupy different altitudinal ranges. They overlap at about 800 m. From most specimens, S. squalidus can be conceived as a hybrid between S. aethnensis and S. chrysanthemifolius, though British plants are rather closer to S. chrysanthemifolius and are atypical of the species as a whole (see 9.2.3).

10.5 BREEDING SYSTEMS

The correlation of breeding system, ploidy and ligule length is discussed in 5.3.2 and 7.3.3. As all the perennials investigated are diploid and probably cross-pollinated in nature, it is likely that the annual outbreeders were derived from them, in turn giving rise to the inbreeding annual polyploids with reduced attractive parts. Grant (1956) has commented on the correlation between the inbreeding condition and allopolyploidy in other genera of the Compositae such as Layia , and in Clarkia. One of the perennials, S. chalureaui, can either have short ligules or be discoid; presumably it is an inbreeder. Its chromosome number is not known. It is endemic to peaks at the eastern end of the Gt. Atlas where pollinators may be scarce, a factor which Stebbins (1957) cites as conducive to the development of self-compatibility. Another advantage arising from the development of self-compatibility is high fitness for a particular type of environment. S. vulgaris is almost entirely inbreeding and therefore unchanging morphologically or physiologically for many generations. It is highly adapted as an agrestal weed and therefore has no need for a flexible genetic system as found in long life-cycle plants such as forest trees.

The fact that many of the inbreeders, e.g. S. flavus and S. hoggariensis possess attractive ligules, presumably associated with outbreeding, is further evidence that the inbreeding condition is derived (Stebbins, 1957).

10.6 CONCLUSIONS

From the above examples it is clear that the species studied during this investigation have been, and probably still are, actively evolving. The population structure of many of the species, e.g. S. leucanthemifolius, fits the model described by Wright (1940) as being the most effective for the promotion of rapid evolution. Reproductive isolation is seen to be developing by both gradual and abrupt speciation (Valentine, 1949).

The difficulties experienced in fitting this group into a formal taxonomic structure are largely due to a combination of phenotypic plasticity, inter-population variability and indistinct specific limits, which all indicate a fast rate of evolutionary change.

APPENDIX I

Provenance of cultivated accessions used in experimental and morphological studies.

Name changes resulting from this research are given in brackets.

ACC.No.	NAME	COUNTRY	LOCALITY	COLLECTOR
1.	joppensis (glaucus ssp. glaucus)	Egypt	Bahr Maryut, Alexandria	Tackholm
2.	" "	Libya	Sidi Misri, Tripoli	Boulos
3.	desfontainei (glaucus ssp. coronop.)	Israel	Beersheba	Danin
4.	joppensis (glaucus ssp. glaucus)	"	Ashklon	"
6.	vernalis	"	Jerusalem	"
7.	flavus	"	Ein Gedi, Dead Sea	"
9.	gallicus v. araneosus (riffensis)	Morocco	Above Oued Nahor	Davis 51374
10.	pinguiculus (leuc. v. leuc.)	Algeria	Mouth of Cheliff R. Mostaganem	" 51764
13.	mauritanicus (leuc. v. fradinii)	"	80 km Constantine to Setif	" 52077
14.	" "	"	J. Aures, 32 km Batna to Arris	" 52344
16.	balansae (squalidus v. aurasiacus)	"	Mansoniah to Barrage de Erraguene	" 52888
18.	" "	"	J. Djurdjura, Tala Guilef	" 53197
19.	mauritanicus (leuc. v. fradinii)	Morocco	Ain Defali, S. of Ouezzane	" 51185
21.	" "	Algeria	J. Chelia, Aures	" 52490
22.	" "	"	Cap Falcon, W. of Oran	" 51587

ACC.No.	NAME	COUNTRY	LOCALITY	COLLECTOR
24.	gallicus	Portugal	Caba-Raso, Guineho	Catarino
29.	"	Spain	Algaida, Cadiz	Allen 6886
30.	leucanthemifolius (leuc. v. leuc.)	Malta	Għar Lapsi, Hal Far	Lanfranco
31.	squalidus	England	Frinton Railway Stn.	Burtt
34.	aegyptius	Egypt	Ain Maroun, Baharia Oasis	Tackholm
40.	lividus	Spain	Not known	Allen 6827
41.	petraeus	"	"	" 7106
43.	vulgaris	Scotland	Edinburgh	Alexander
44.	vernalis	Turkey	Hirkakoy, 25 km N. of Kayseri	Baytop 20556
45.	hoggariensis	Sinai	J. Qasar Abbas Pasha	Danin
51.	lividus	Sardinia	From cultivation in Cambridge	Jardine
52.	hesperidium	Morocco	Sidi Moussa, Tiznit	Davis 53536
59.	vulgaris	"	40 km Fez to Taza	" 51254
63.	leucanthemifolius	Algeria	Above Annaba	" 52094
64.	lividus	Morocco	El Harcha, Oulmes	Pauners et al
66.	massaicus	"	Mouth of Sous R.	Davis 53902
68.	desfontainei (glaucus ssp. glaucus)	"	Nr. Tafraoute	" 53818
71.	hesperidium	"	Mouth of Massa R.	" 53762

ACC.No.	NAME	COUNTRY	LOCALITY	COLLECTOR
73.	desfontainei (glaucus ssp. glaucus)	Morocco	Mouth of Massa R.	Davis 53727
74.	leucanthemifolius v. major	"	Beni Hosmar, nr. Tetuan	Alexander & Kupicha 112
79.	gallicus v. araneosus (riffensis)	"	Tizi Ouzli, El Hoceima to Taza	Alexander & Kupicha 260

APPENDIX II

FIGS. 46-64 LEAF SPECTRA OF ACCESSIONS USED IN THE HYBRIDISATION EXPERIMENTS

The leaves, which are reduced to $\frac{5}{8}$ natural size, were taken from plants grown in standard greenhouse conditions under a 16 hour daylength. The plants had all recently come into flower when dissected, and are all more or less of the same physiological age, though of varying ages chronologically. Numbers under leaves refer to nodes. Full details of preparation of leaf spectra are given in 5.2. Names used in part III of this thesis are given in brackets (see 2.3). Numbers after names refer to accessions (see appendix I).

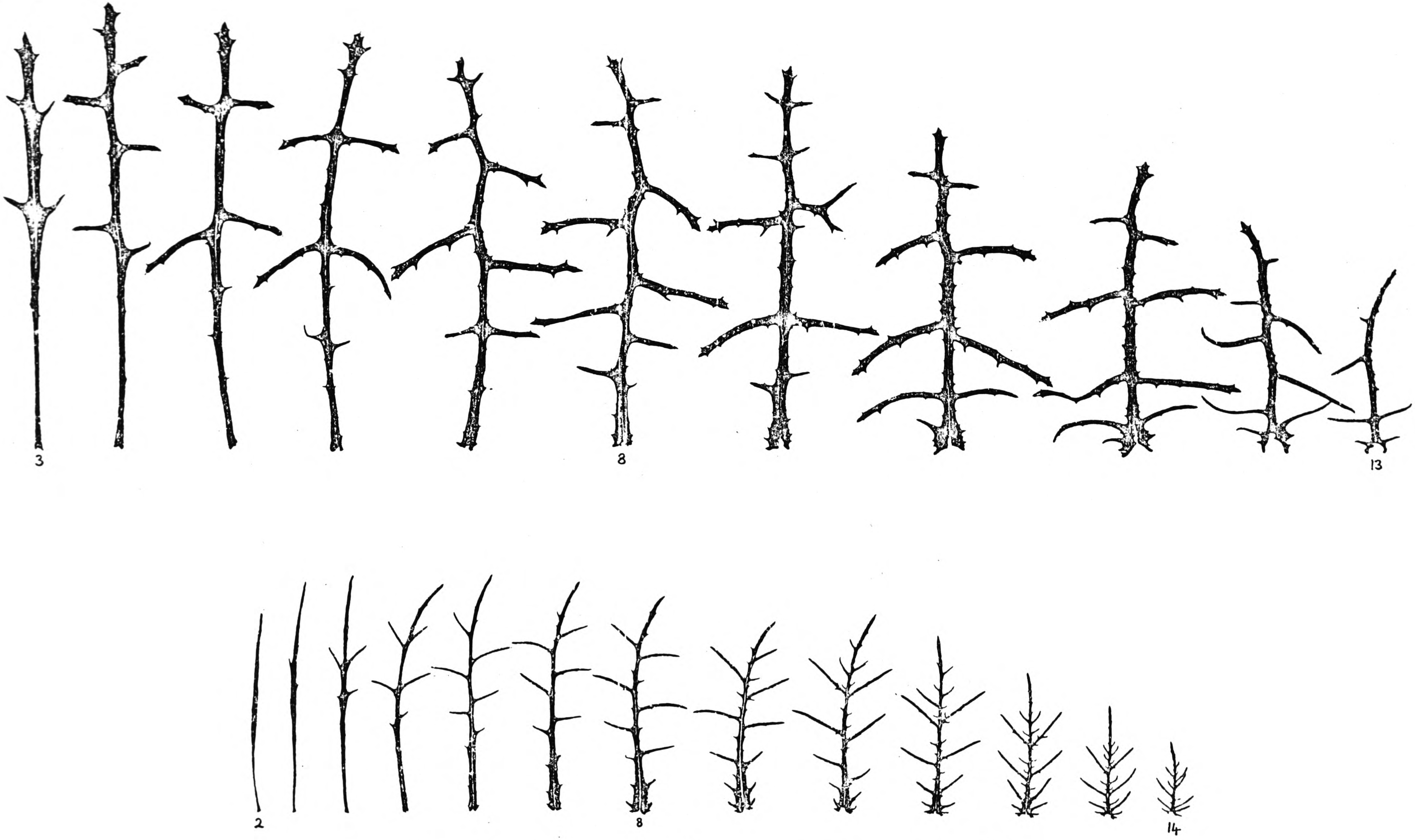


FIG. 46. S. joppensis (S. glaucus subsp. glaucus) 4

S. desfontainei (S. glaucus subsp. coronopifolius) 3

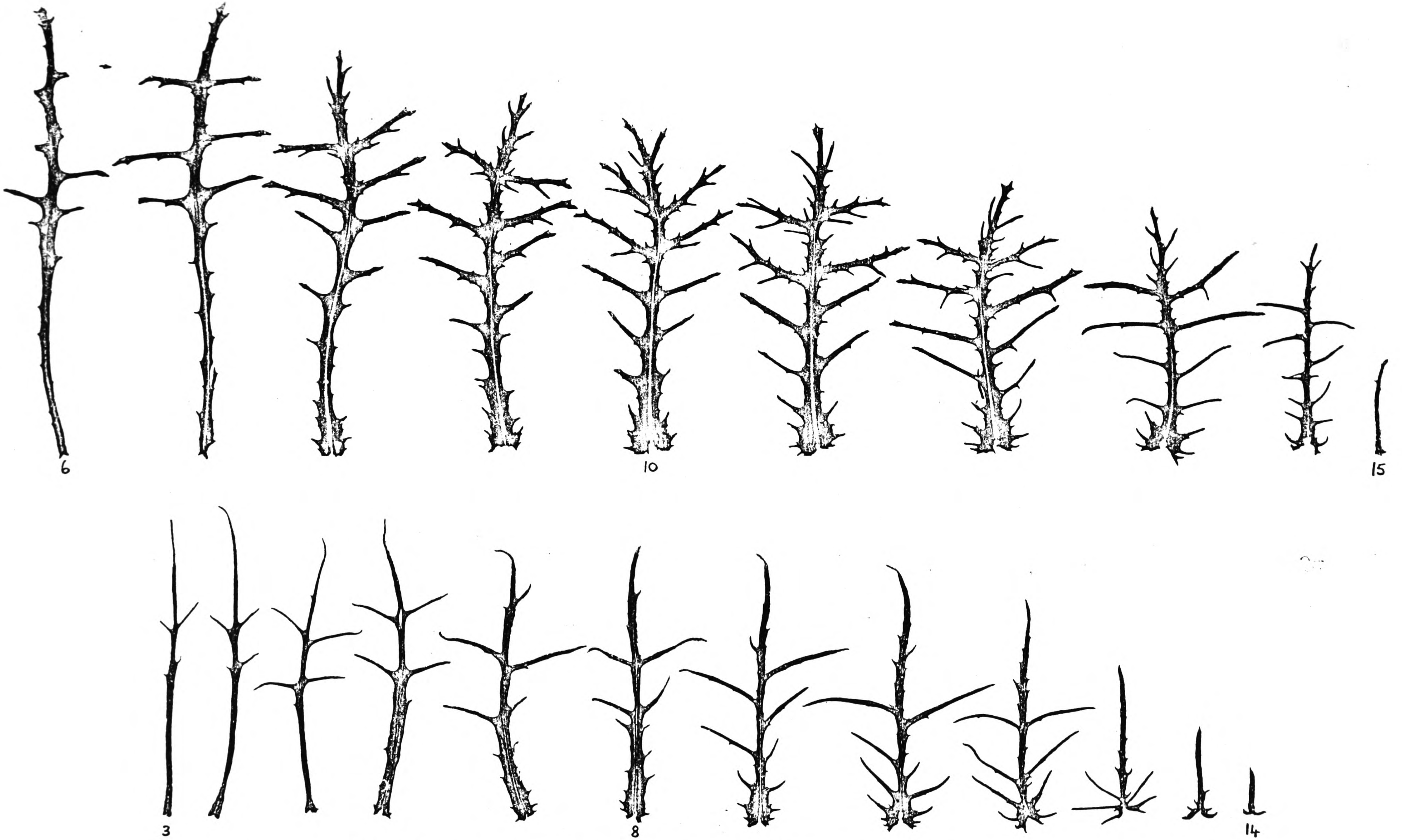


FIG. 47. S. joppensis (S. glaucus subsp. glaucus) 1

S. joppensis (S. glaucus subsp. glaucus) 2

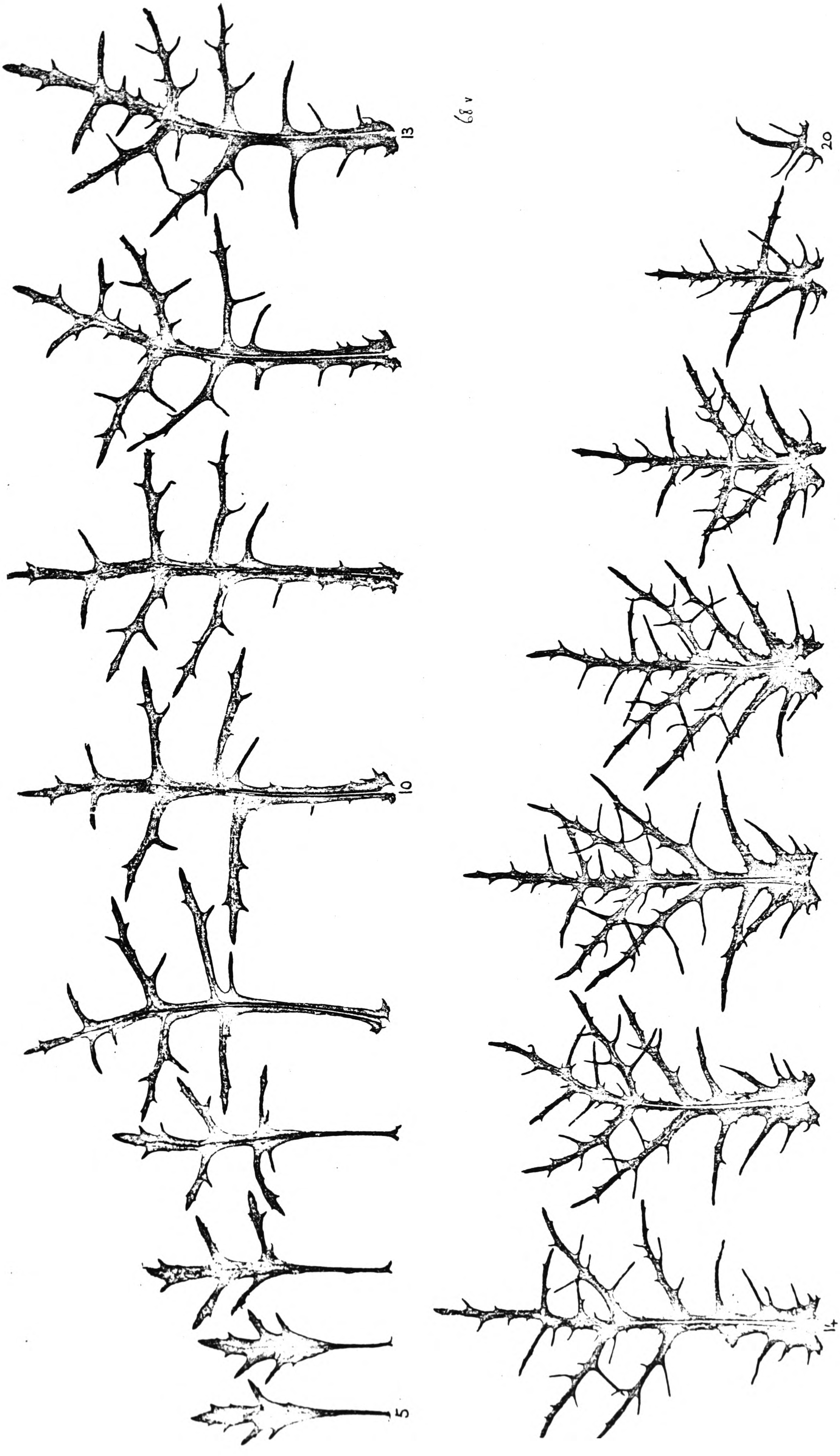


FIG. 48. S. desfontainei (S. glaucus subsp. coronopifolius) 68

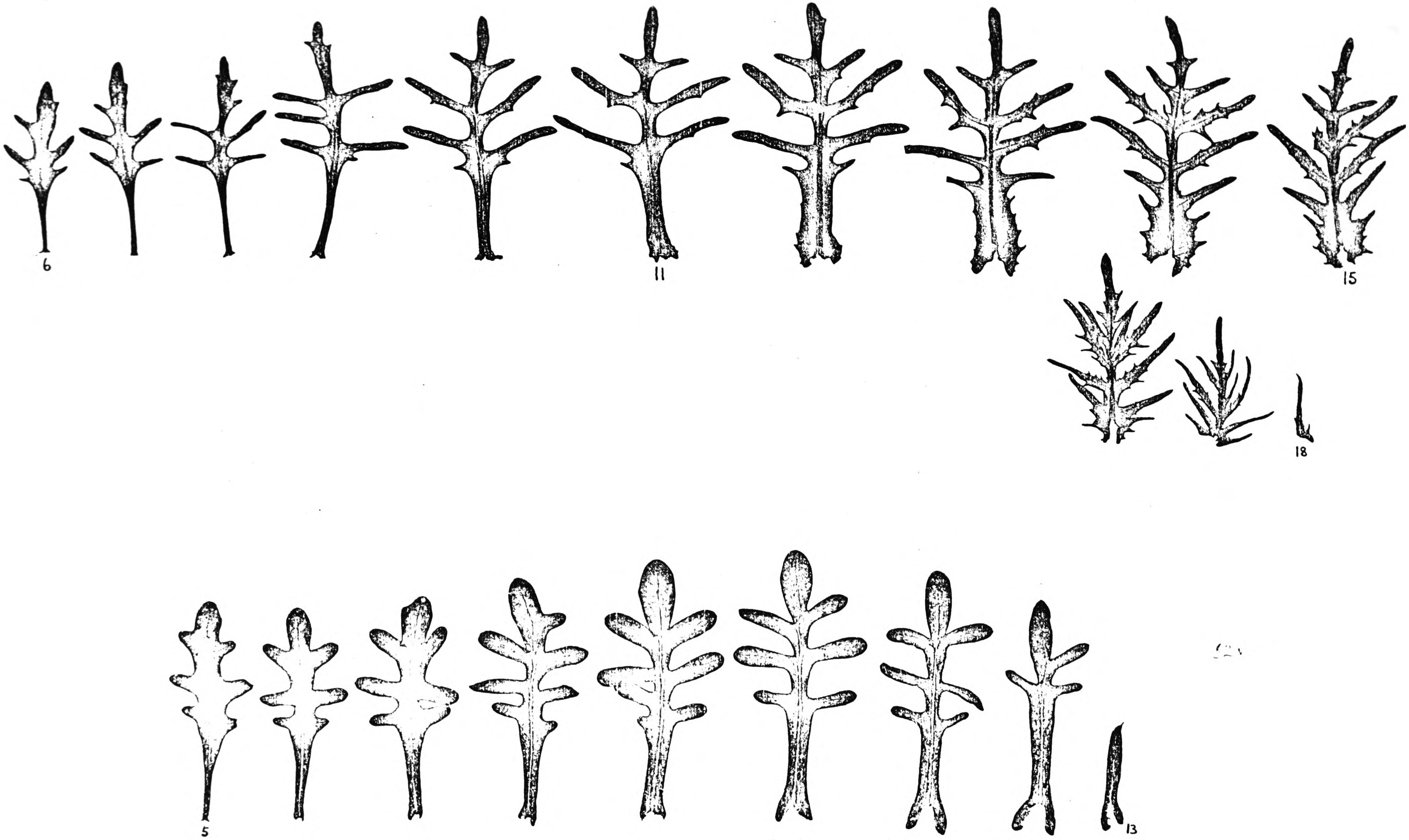


FIG. 49. S. desfontainei (S. glaucus subsp. coronopifolius) 73

S. hesperidium 52

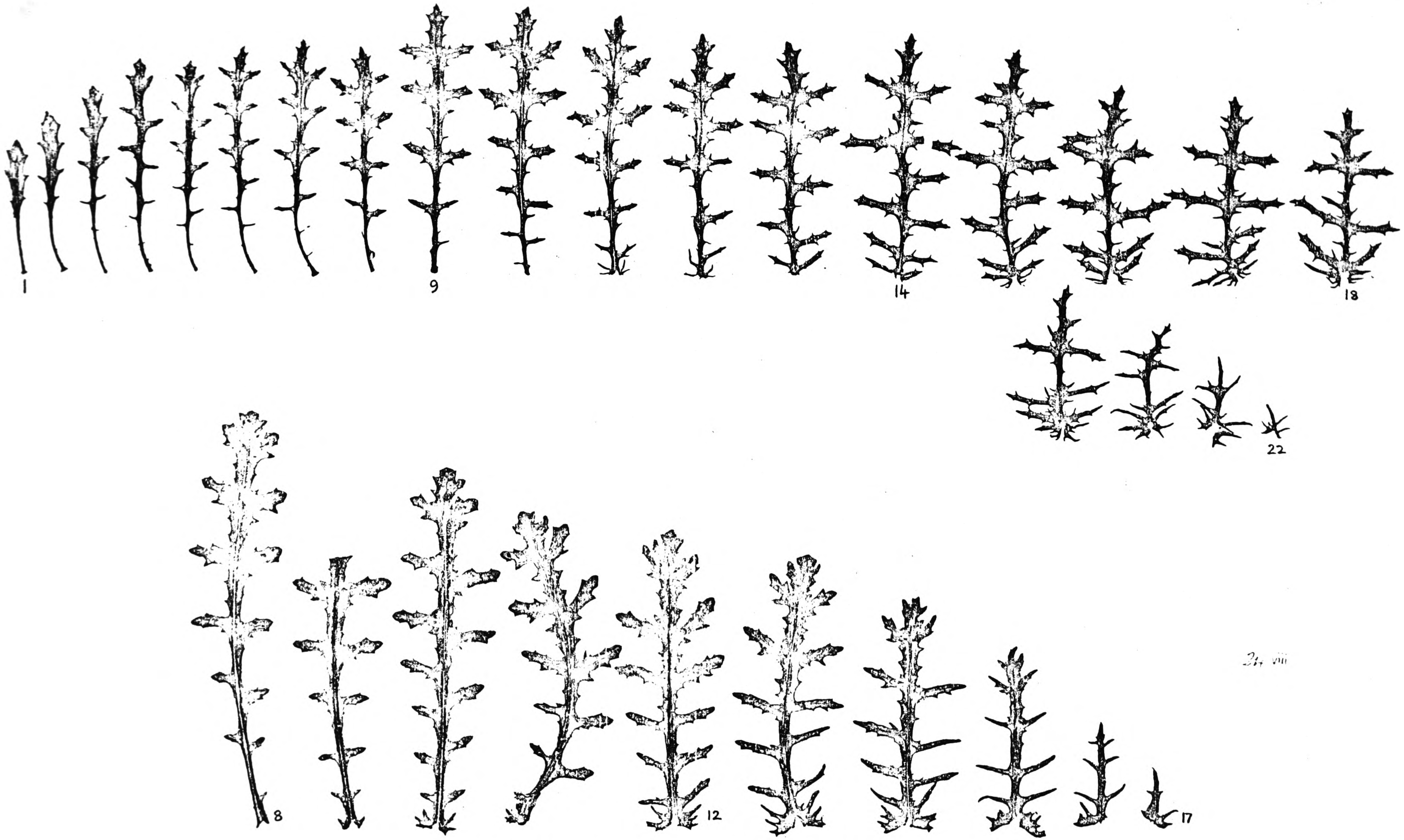


FIG. 50. S. gallicus 29, S. gallicus 24

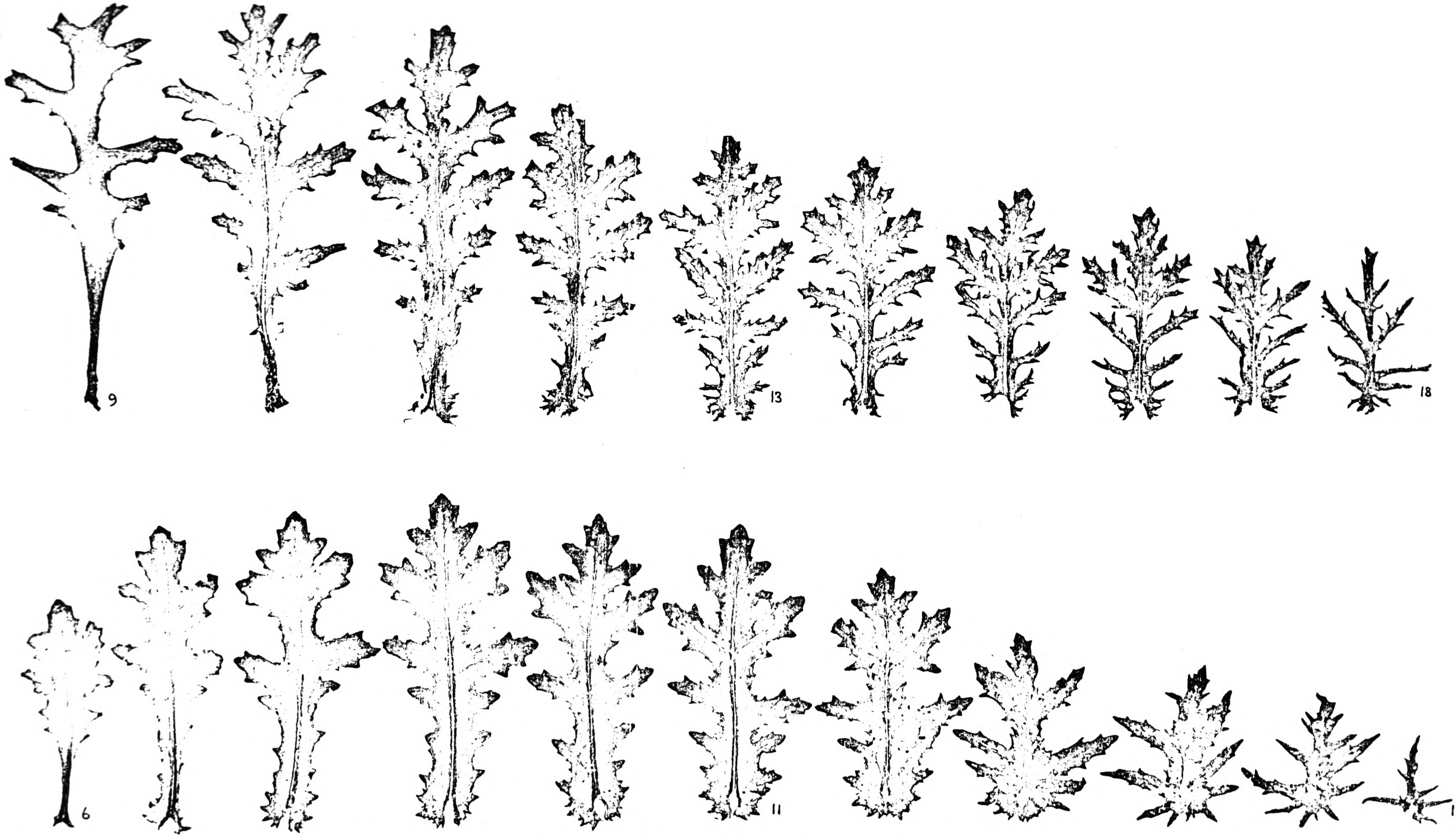


FIG. 51. Morphological intermediates between S. mauritanicus (S. leucanthemifolius var. fradinii) and S. desfontainei (S. glaucus subsp. coronopifolius) Accessions 76 and 77

FIG. 52. S. mauritanicus (S. leucanthemifolius var. fradinii) 22

S. leucanthemifolius (S. leucanthemifolius var. leucanthemifolius) 30

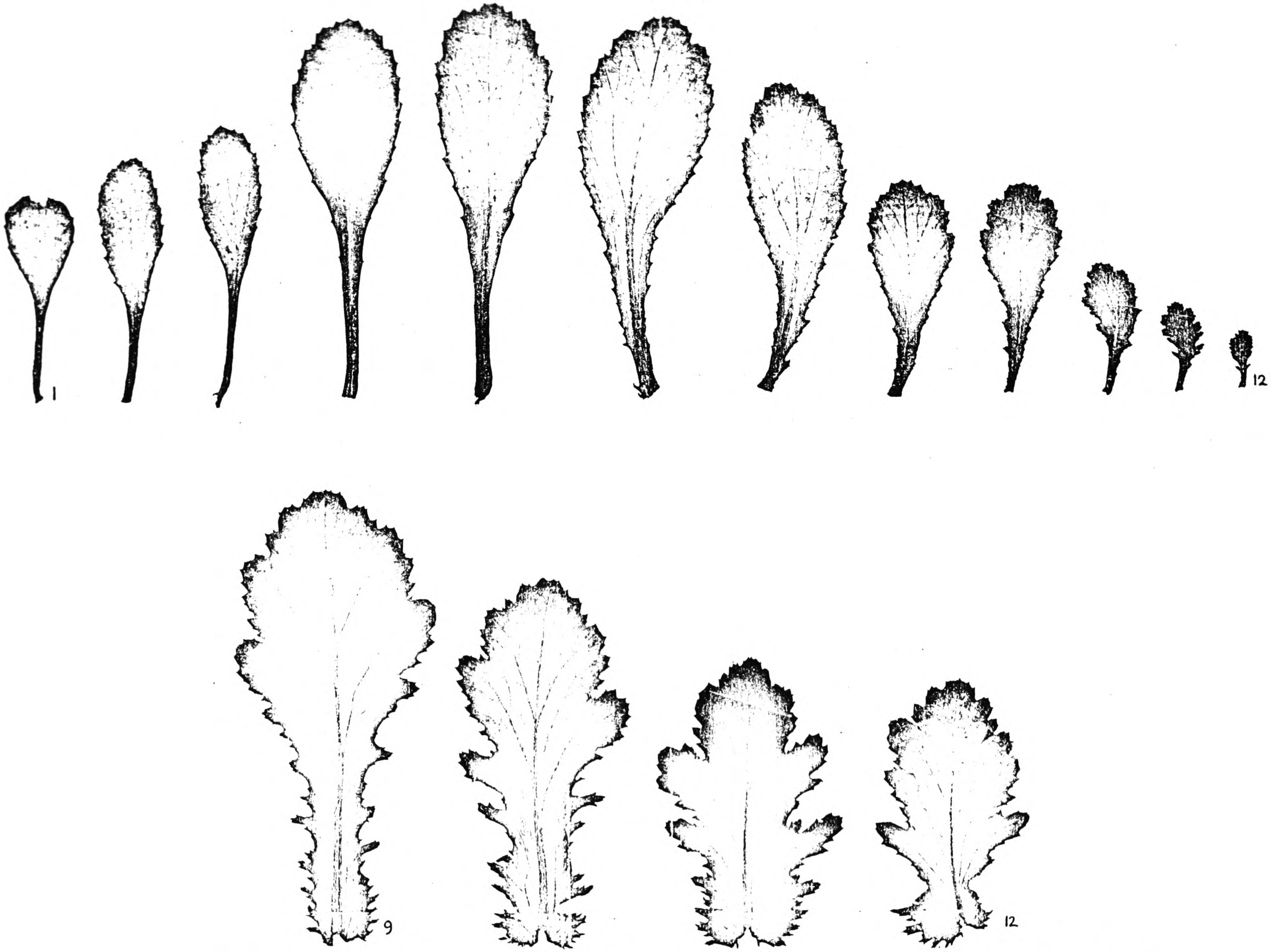


FIG. 53. S. leucanthemifolius (var. major) 74, young vegetative plant

S. leucanthemifolius (var. major) 74, plant in flower

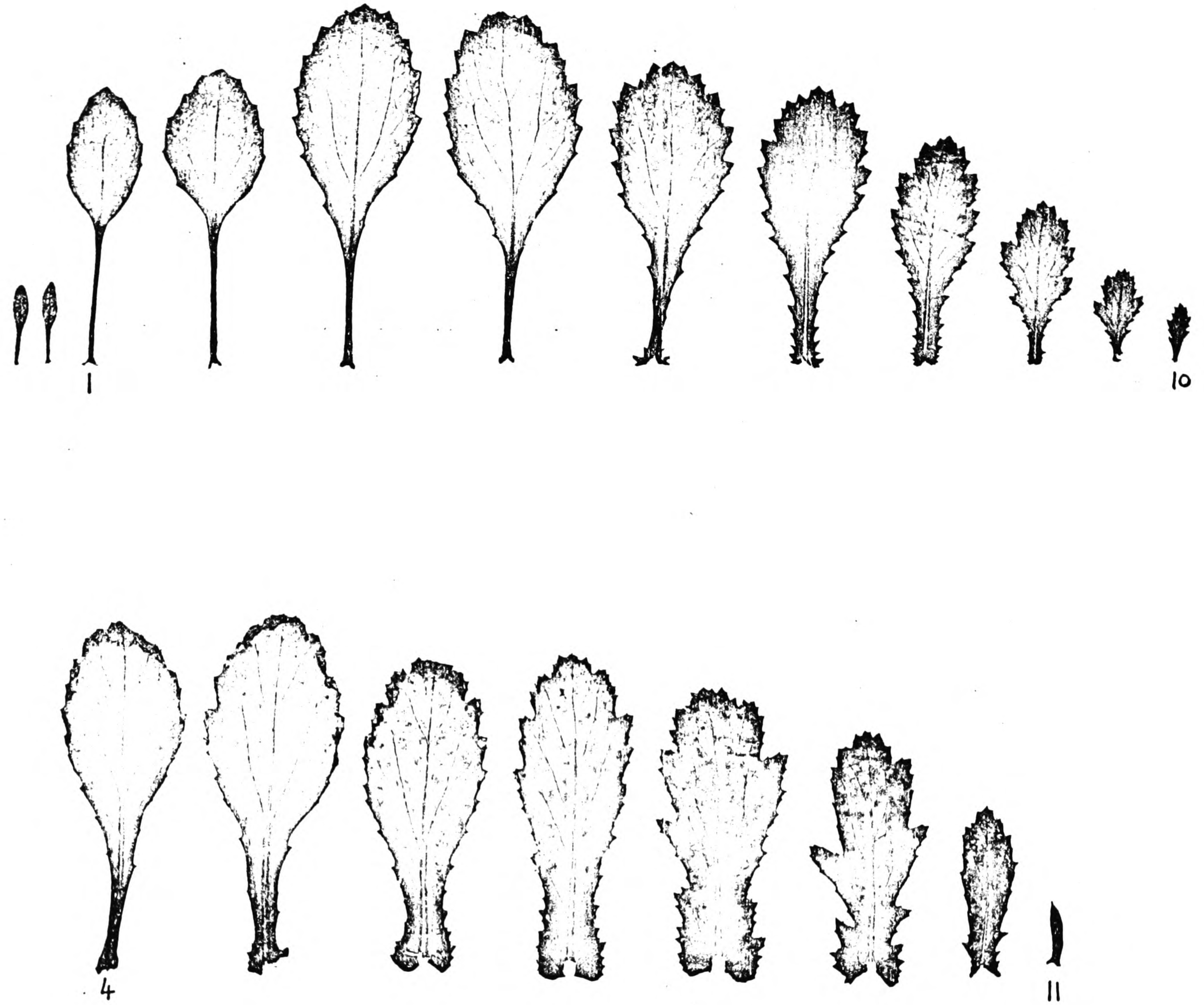


FIG. 54. S. leucanthemifolius (var. major) 63, young vegetative plant

S. leucanthemifolius (var. major) 63, plant in flower

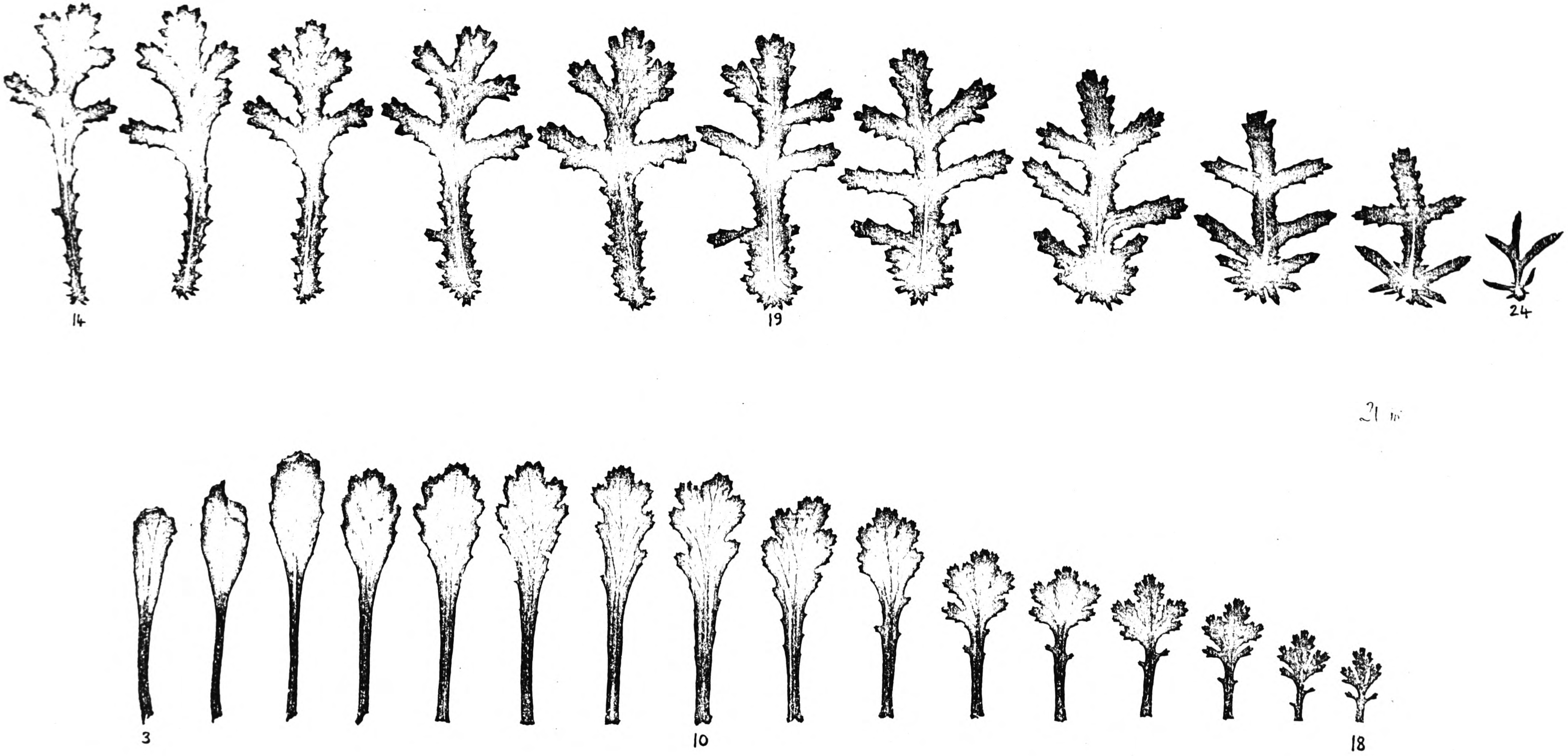


FIG. 55. S. mauritanicus (S. leucanthemifolius var. fradinii) 13

S. mauritanicus (S. leucanthemifolius var. fradinii) 21

FIG. 56. S. vernalis 44, young vegetative plant

S. vernalis 44, plant in flower

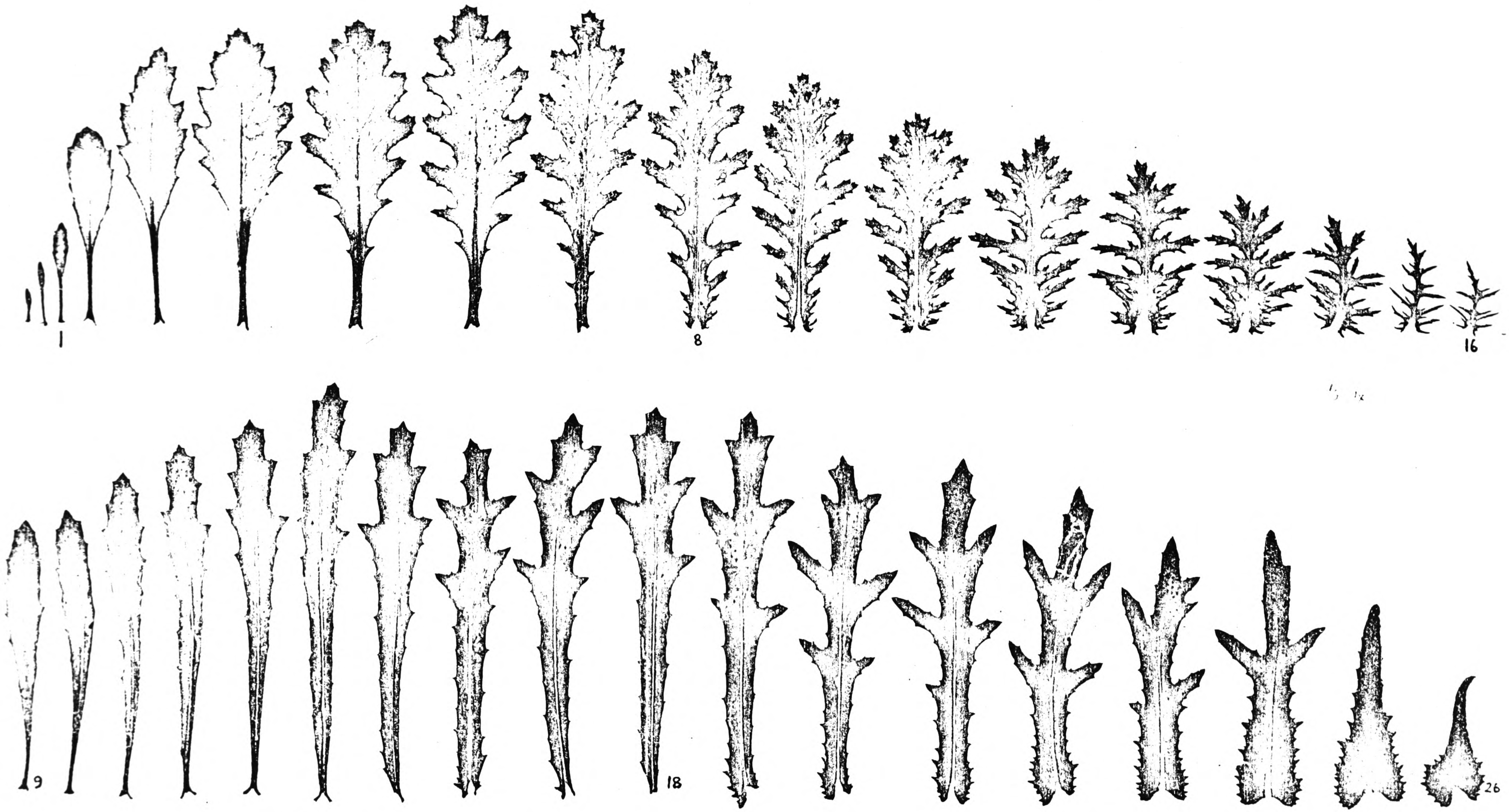


FIG. 57. S. vernalis 6

S. pinguiculus (S. leucanthemifolius var. leucanthemifolius) 10

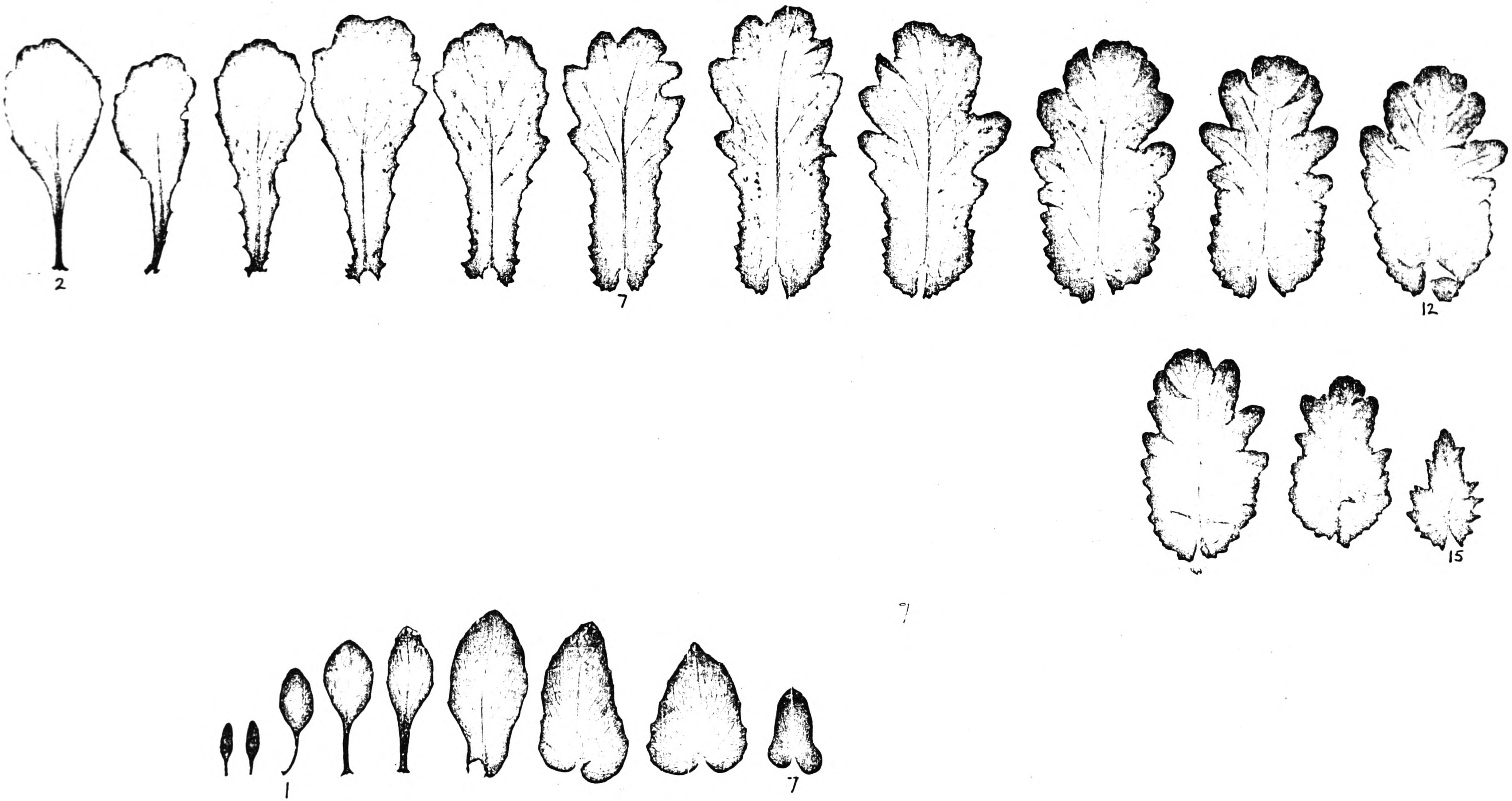


FIG. 58. <u>S. petraeus</u> 41, <u>S. flavus</u> 7

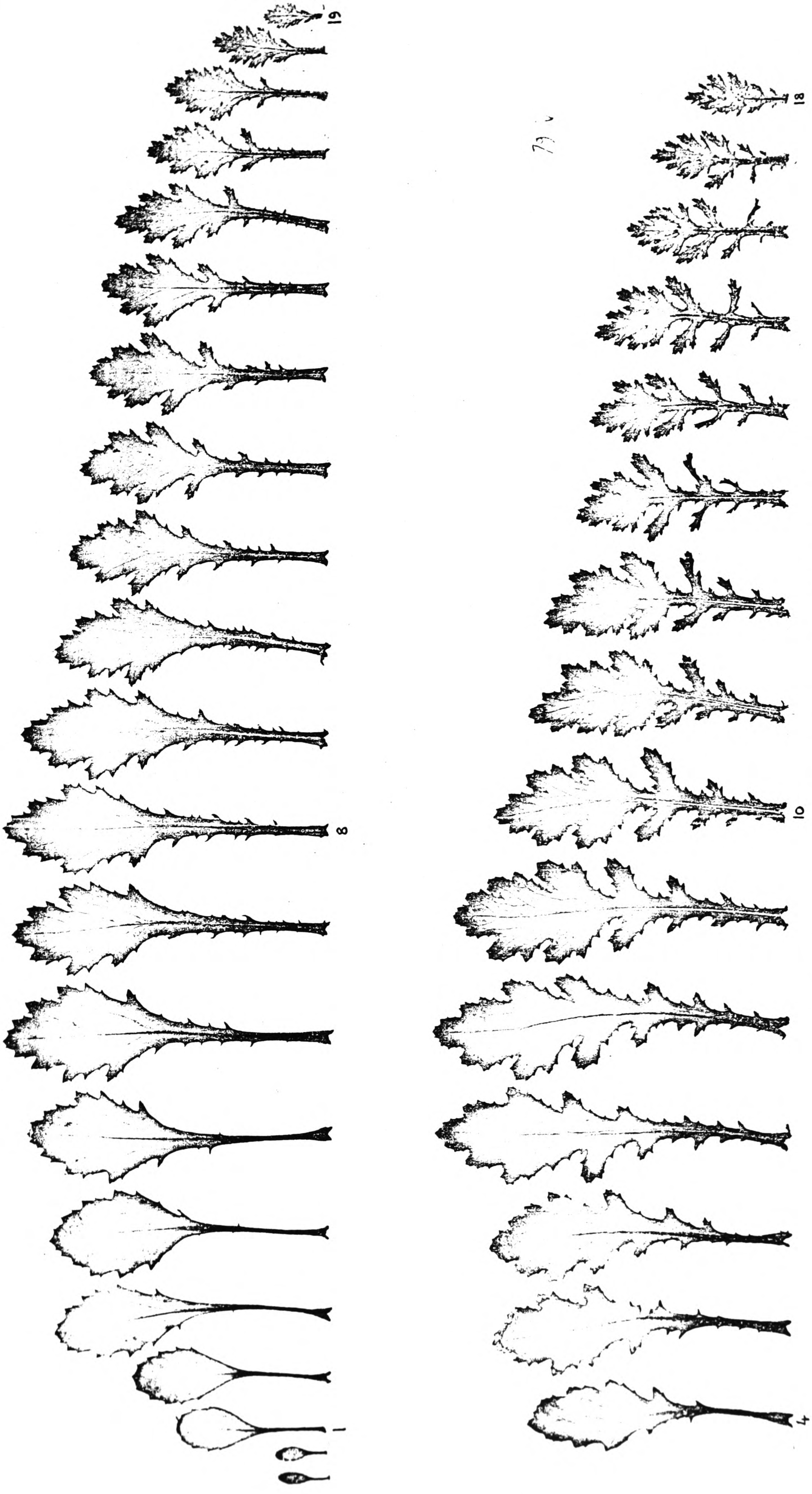


FIG. 59. *S. gallicus* var. *araneosus* (*S. riffensis*) 9

S. gallicus var. *araneosus* (*S. riffensis*) 79

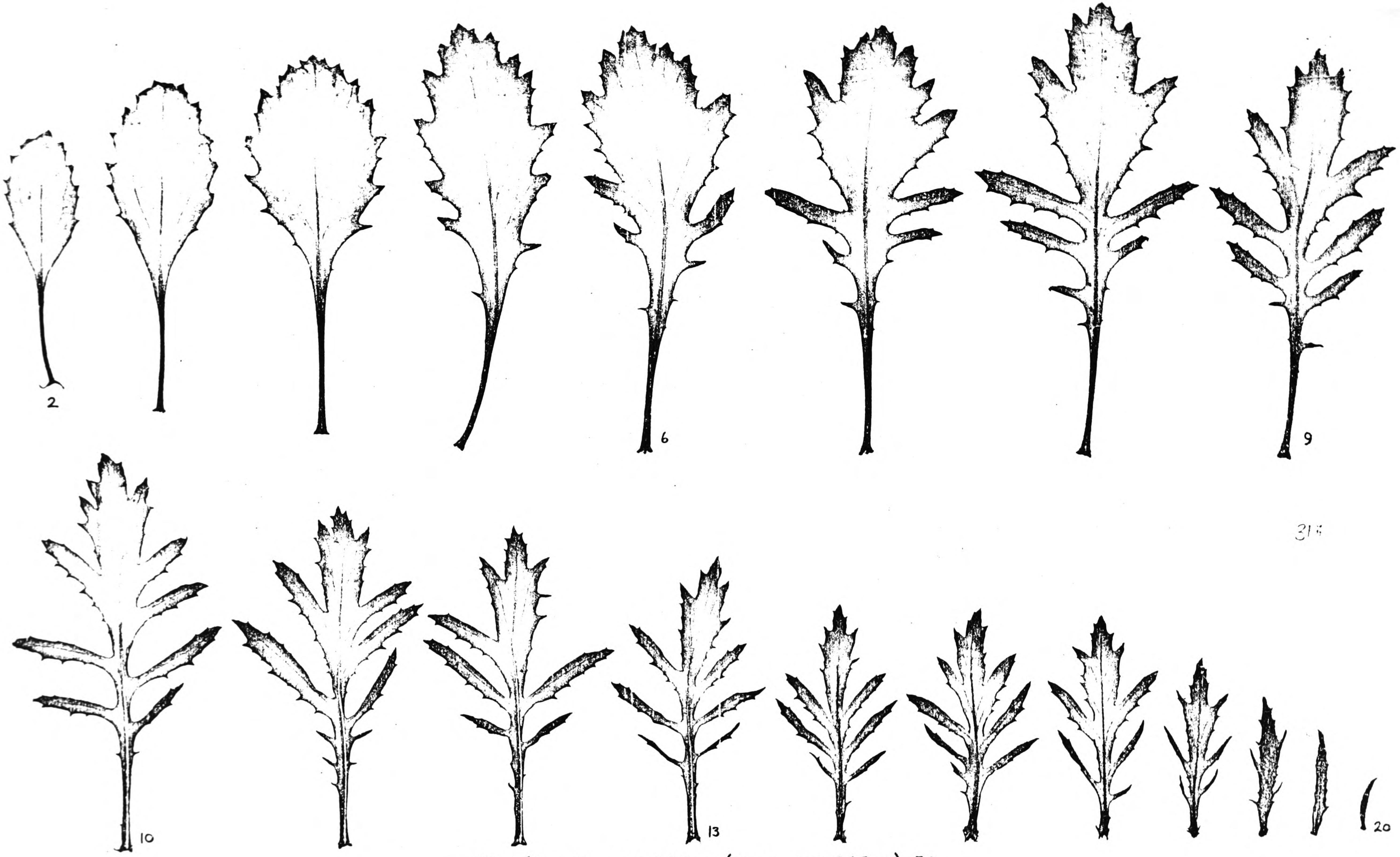


FIG. 60. S. squalidus (var. squalidus) 31

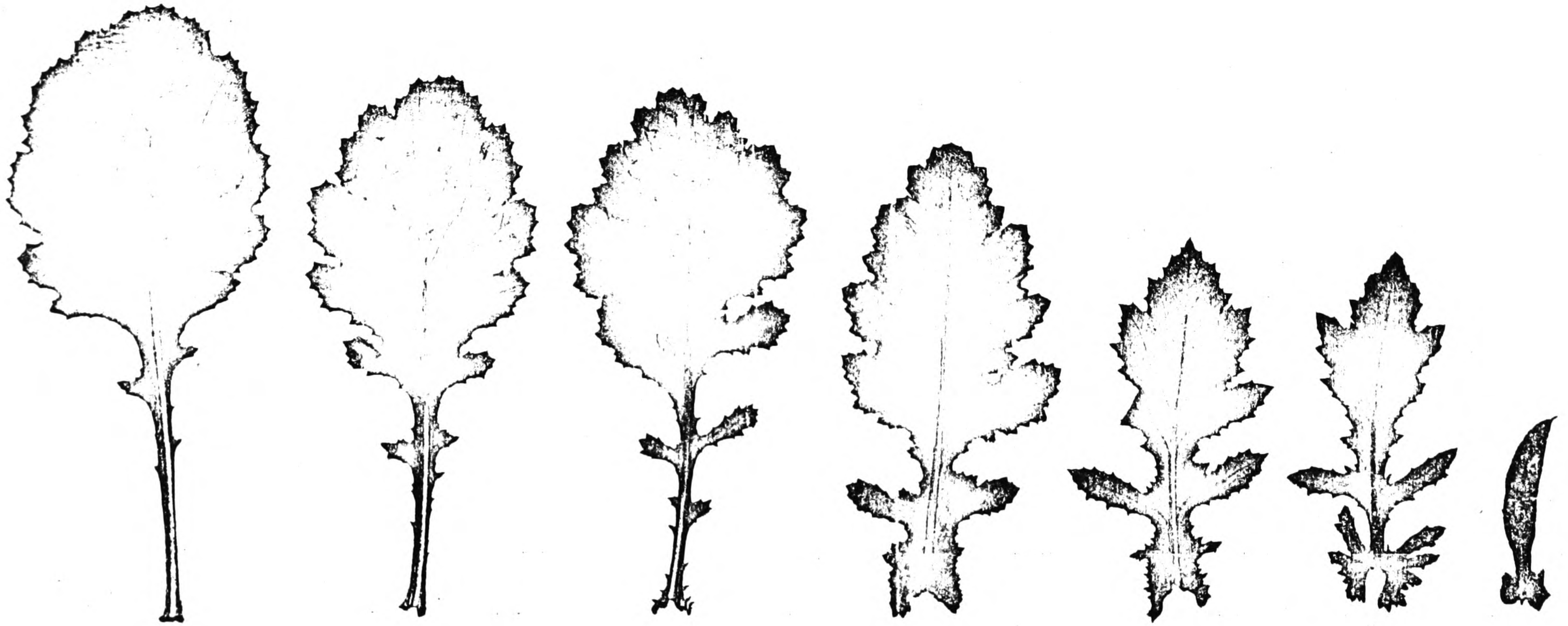
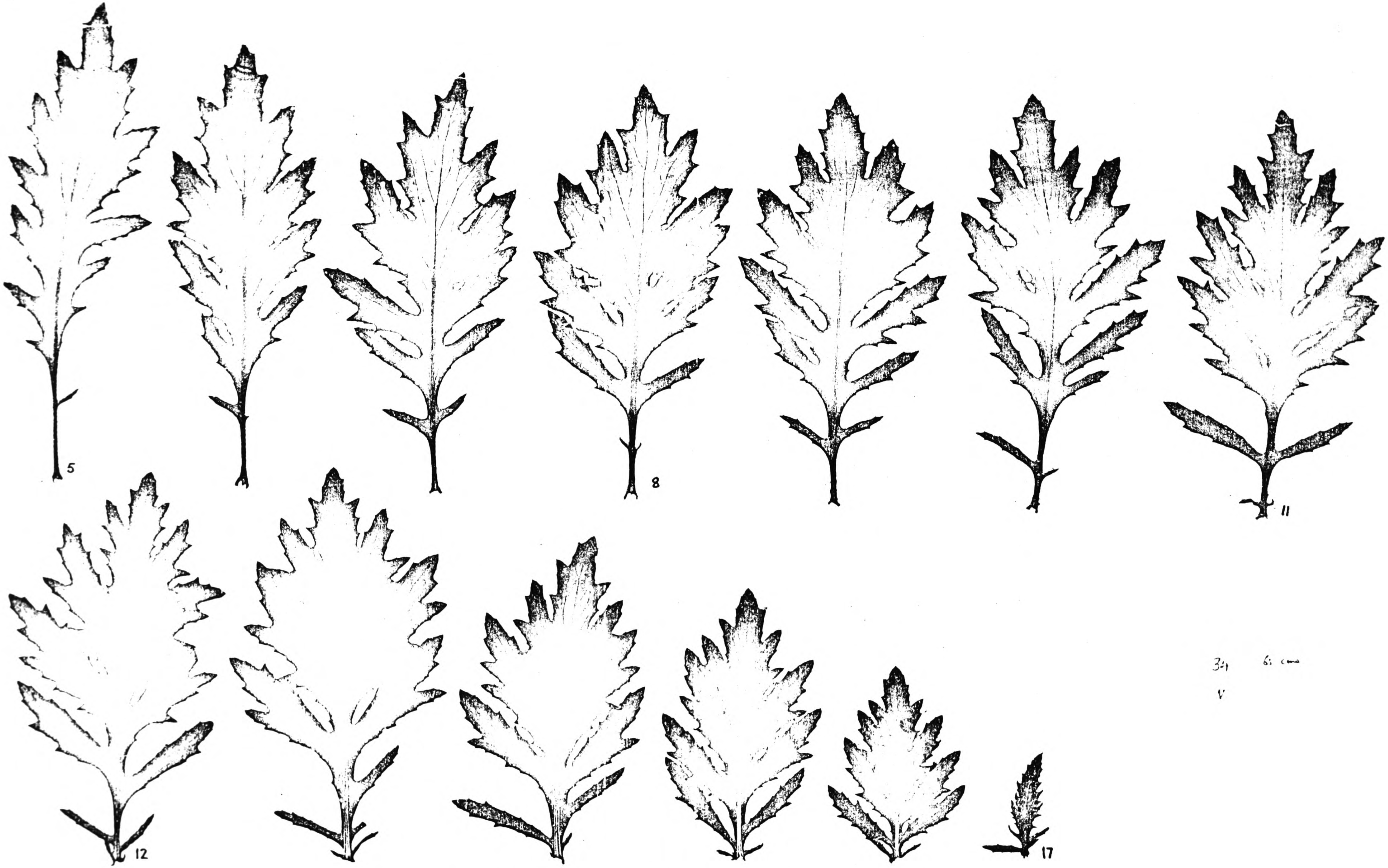


FIG. 61. S. balansae (S. squalidus var. aurasiacus) 16

FIG. 62. S. vulgaris 43, S. vulgaris 59



34 6 cm
V

FIG. 63. S. aegyptius (var. discoideus) 34

FIG. 64. <u>S. hoggariensis</u> 45, <u>S. massaicus</u> 66

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INDEX TO SPECIES DESCRIBED AND DIAGNOSED IN 9.2.3

Accepted names are underlined. Only the major reference for each name is given.