NOTES FROM THE
ROYAL BOTANIC GARDEN
EDINBURGH

VOLUME XXXVII · No. 3 · 1979

THE MEDITERRANEAN SPECIES OF SENECIO SECTIONS SENECIO AND DELPHINIFOLIUS

J. C. M. ALEXANDER*†

ABSTRACT. A revision is presented of the annual and related perennial species of *Senecio* L. (Compositae) from the Mediterranean area, based on morphological and experimental data. A key to 23 species is provided followed by descriptions, diagnoses and distribution maps. Section *Jacobaea* (Cassini) Dumortier is combined with the type section. The new variety *S. leucanthemifolius* Poiret var. *casablancae* Alexander is described and *S. vernalis* Waldst. & Kit. is treated as *S. leucanthemifolius* Poiret var. *vernalis* (Waldst. & Kit.) Alexander. Three other new combinations are made and the disused names *S. glaucus* L. and *S. trilobus* L. are reinstated. Chromosome counts of 2n = 20 are recorded for the following previously uncounted taxa: *S. squalidus* L. subspp. *araneosus* (Emb. & Maire) Alexander and *aurasiacus* (Batt. & Trab.) Alexander, *S. leucanthemifolius* Poiret vars. *leucanthemifolius*, *fradinii* (Pomel) Batt. and *major* Ball, *S. glaucus* L. subspp. *glaucus* and *coronopifolius* (Maire) Alexander, *S. hesperidium* Jahandiez, Maire & Weiller and *S. petraeus* Boiss. & Reut. The base number in the genus is discussed and techniques of emasculation and isolation described in an appendix.

CONTENTS

INTRODUCTION AND GENERAL COMMENTS

Problems have long been encountered in identifying certain species of *Senecio* L. from the Mediterranean area. The extensive synonymy found especially among some of the annuals is an indication of the difficulty

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* Cultivated Flora unit, University of Cambridge, at Royal Botanic Garden, Edinburgh.

† The material presented here is based on part of a thesis accepted in 1975 for the degree of Ph.D. in the University of Edinburgh.

experienced in setting satisfactory species limits. Walters (1964) remarked that the taxonomy of plants closely related to *S. squalidus* L. is extremely confused and commented that members of the group make excellent experimental material.

The investigation reported here started as an attempt to revise the annual species of *Senecio* from the countries bordering the Mediterranean, widening the scope geographically where dictated by distribution patterns. It soon became clear that some of the related biennials and perennials, especially those having pinnately divided leaves such as *S. squalidus*, are so close to the annuals morphologically and, as subsequently discovered, genetically, that any revision must include them. This strong affinity makes it unrealistic to maintain section *Jacobaea* (Cassini) Dumort. and it is here treated as part of section *Senecio* which contains the type species of the genus, *S. vulgaris* L. In this account a number of distinct and thus more easily identified perennials and biennials are not described, but have been included in the index for completeness.

The treatment described here is based on a synthesis of morphological, geographical and experimental data. Recent experimental work on the species in this group has been mainly concerned with mechanisms of introgression between species on different ploidy levels rather than with elucidating taxonomy. Particular attention has been paid to the relationship between *S. squalidus* ($2n = 20$) and *S. vulgaris* ($2n = 40$), following the observation that rayed plants of *S. vulgaris* appeared to be becoming more frequent in areas into which *S. squalidus* had recently spread (Crisp and Jones, 1970; Hull, 1974 a & b & 75; Ingram, 1977 & 78). It was known previously that the sterile triploid hybrid between these two species, *S. x baxteri* Druce (Ellis, 1944) had given rise to the fertile allohexaploid *S. cambrensis* Rosser (Rosser, 1955). The relationship between these two species is discussed further in the systematic account of *S. vulgaris* (p. 409). Crisp and Jones (1978) have also investigated the relationship between *S. squalidus* and *S. viscosus* ($2n = 40$) where the F_1 hybrids had a very low fertility. However, by the F_4 generation some progenies had more or less stabilised at the tetraploid ($2n = 40$) level and might therefore be interfertile with *S. viscosus*.

Intensive work has been done on the complex around *S. lautus* [Forst. ex] Willd. in Australasia (Ali, 1964a & b, 66 & 69; Ornduff, 1960 & 64). This group has many similarities to the pinnatifid annuals from around the Mediterranean, both in morphology and taxonomic problems.

The experimental data used in this account are based on small samples and thus have not been analysed statistically. Plants were raised under glass in Edinburgh from seed collected in southern Europe, north Africa, and south-west Asia. Experiments were performed to determine the breeding systems and a series of intra- and interspecific crosses carried out. Methods for emasculating and isolating capitula are described in the appendix. 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, whereas outbreeders tend to have long ligules and are diploid. This correlation has also been observed by Gibbs, Milne & Vargas Carrillo (1975) who found that the outbreeders have relatively low recombination indices. 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).

About 140 crosses were made. The resulting seed was sown and a study made of the morphology and pollen stainability of the viable F_1 hybrids. In general, interspecific fertility was found to be high even between morphologically dissimilar species.

Among the taxonomically "difficult" species floral morphology is unhelpfully uniform and emphasis has often been placed on vegetative characters. A limited series of cultivation experiments in controlled contrasting conditions showed that habit and leaf shape in several species are highly susceptible to environmental modification. Voucher specimens of plants involved in the hybridisation and cultivation experiments are stored in the herbarium of the Royal Botanic Garden, Edinburgh.

For all but the most distinct species, distribution maps were compiled solely from herbarium specimens, as literature records were felt to be too unreliable, particularly among those taxa with a history of misidentification. Several of the species described or diagnosed were not investigated experimentally; their systematic status has been determined purely from morphological and geographical data. Only selected specimens are recorded in the citation lists for each taxon.

CHROMOSOME NUMBERS

THE BASE NUMBER OF SENECIO

There is some disagreement in the literature about the base chromosome number of *Senecio*. Afzelius (1949) concluded that the base number for the tribe Senecioneae is five, and remarked that up to that time *S. discifolius* Oliver was the only member of the tribe recorded as a diploid of that number. However, in a previous paper, he recorded counts of $n = 5$ for two species of *Emilia* (Afzelius, 1924), and certainly regarded *Emilia* as a member of the Senecioneae. In this he followed Hoffmann [*Die Natürlichen Pflanzenfamilien* 4(5):297, 1894] who treated *Emilia* as a subgenus of *Senecio*. As in many of the other splits made in *Senecio*, the morphological boundary between *Emilia* and *Senecio* is rather vague. Since the publications of Afzelius, a further three species of *Senecio* and four species of *Emilia* have been recorded as $n = 5$ (Federov, 1969).

Prior to the discovery of *Senecio* species other than *S. discifolius* with $n = 5$, Ornduff et al. (1963) considered the absence of any species with haploid numbers which are higher multiples of five rather than ten as evidence for the latter as the base number of the genus. They suggested that the chromosome number of *S. discifolius* must have been derived by aneuploid loss although no counts are known in the genus between $n = 5$ and $n = 10$. They, however, accepted five as the base number of the morphologically closely related *Emilia*.

Turner & Lewis (1965), who recorded two new counts of $n = 5$ in *Senecio* species from east and central Africa, accepted this as the base number of the genus and accounted for the absence of species having $n = 25$, 35, etc. on the basis that 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 nine, has species with n = 27 and n = 45.

On the available data it seems likely that five is the original base number for *Senecio*. The absence of species with odd multiples of five suggests that fairly early in the history of the genus, the mechanisms of chromosome repatterning caused a diploidisation of the existing tetraploids. Such repatterning could have caused two structurally identical, or a least little differentiated, sets of five chromosomes to become one set of 10 different chromosomes. Since the establishment of n = 10, species with n = 5 do not appear to have been involved in the mainstream of evolution of the genus, although according to Nordenstam (1975) they are phylogenetically advanced. In the present work n = 10 is regarded as a secondary base number and species with this number are referred to as diploids.

NEW CHROMOSOME COUNTS

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 1:3 acetic alcohol. Before squashing, they were hydrolysed in 1N hydrochloric acid to aid spreading.

Table 1 shows the numbers counted, together with those recorded in Cave (1959–65), Moore (1965–77), Federov (1969) and Löve (1971–78).

TABLE 1

CHROMOSOME NUMBERS (2n)

	IPCN 1959–77	Federov 1969	Löve 1971–78	Alexander 1979
aegyptius		40		40
flavus	20			20
gallicus	20	20		20, 20
glaucus				
subsp. *glaucus*				20, 20
subsp. *coronopifolius*	40		20	20, 20
hesperidium				20
hoggariensis	60	60		60
leucanthemifolius	20, 20	20		
var. *leucanthemifolius*				20
var. *fradinii*				20, 20, 20
var. *major*				20
var. *vernalis*	40	20, 20	20, 20, 20	20, 20
massaicus		40		40
petraeus				20
squalidus				
subsp. *squalidus*	20	20		20, 20
subsp. *aurasiacus*				20, 20
subsp. *araneosus*				20
vulgaris	40 (many)	40 (many), 38		40

IPCN—*Index to Plant Chromosome Numbers* edited by Cave and later by Moore. Each figure represents a different report. Several counts in the first three columns were published under names which are treated as synonyms in this work.

Two of the numbers recorded in Moore disagree both with my counts and with those recorded in Federov and Löve. The single count of 2n = 40 for *S. leucanthemifolius* var. *vernalis* (*S. vernalis*) was published by Majovsky et al. (1970) from Czechoslovakian material, however, as counts of 2n = 20 have been recorded widely throughout its range, this variety must be regarded as predominantly diploid. The record of 2n = 40 for *S. glaucus* subsp. *coronopifolius* (*S. coronopifolius*) was published by Mehra & Remanandan (1969) from Western Himalayan material: a subsequent count of 2n = 20 using Egyptian material (Nordenstam, 1972) corresponds to my own results for two stocks of this subspecies. Caution is necessary in accepting counts for some taxa: misidentification is rife and provenance cannot always be relied on.

KEY TO THE SPECIES

1a.	Ray flowers absent	2
1b.	Ray flowers present	8
2a.	Leaves pinnatifid or pinnatipartite	3
2b.	Leaves entire or shallowly lobed	6
3a.	Lanate perennial; capitulum diam. more than 7 mm	2. *chalureaui*
3b.	Glabrous to pubescent annual; capitulum diam. less than 6 mm	4
4a.	Phyllary length more than 6 mm; calyculus bracts 10–20, black-tipped	9. *vulgaris*
4b.	Phyllary length less than 6 mm; calyculus bracts 4–10 brown-tipped	5
5a.	Pappus c. 2 mm; capitulum diam. 3–4 mm; corymbs dense	21. *aegyptius*
5b.	Pappus c. 5mm; capitulum diam. 5–6 mm; corymbs lax	15. *massaicus*
6a.	Basal leaves linear, distantly toothed or lobed	15. *massaicus*
6b.	Basal leaves ovate-spathulate or orbicular, crenate or shallowly lobed	7
7a.	Plant glaucous; middle cauline leaves triangular, auriculate, crenate; phyllaries 6–9 mm	23. *flavus*
7b.	Plant not glaucous; middle cauline leaves lanceolate to ovate-spathulate, entire or sinuately lobed: phyllaries less than 5 mm	7. *leucanthemifolius*
8a.	Ligules less than 3 mm	9
8b.	Ligules more than 3 mm	15
9a.	Plant glandular, at least in inflorescence	10
9b.	Plant not glandular	12
10a.	Achenes glabrous; plant viscid in all parts	19. *viscosus*
10b.	Achenes at least strigulose; plant glandular in inflorescence	11

11a. Phyllaries 8–10 mm; middle cauline leaves toothed, crenate or pinnatifid, upper cauline leaves broadly auriculate; capitula in lax corymbs . . . . 20. *lividus*
11b. Phyllaries 5–7 mm; middle cauline leaves pinnatipartite, upper cauline leaves narrowly auriculate; capitula in dense corymbs 18. *sylvaticus*

12a. Phyllaries more than 6 mm 13
12b. Phyllaries less than 5 mm 14

13a. Plant glaucous; middle cauline leaves triangular, auriculate, crenate; calyculus bracts 0–5 . . . . . . 23. *flavus*
13b. Plant not glaucous; middle cauline leaves ovate to oblong; calyculus bracts 10–20 . . . . 9. *vulgaris*

14a. Middle cauline leaves more than 4 cm, pinnatifid or pinnatipartite; phyllaries more than 15 . . . . 21. *aegyptius*
14b. Middle cauline leaves less than 4 cm, entire, sinuately lobed or shallowly pinnatifid; phyllaries fewer than 10 . . . . 7. *leucanthemifolius*

15a. Leaves unlobed, sinuate or trifid, not pinnatifid 16
15b. Leaves pinnatifid to pinnatisect 23

16a. Ligules purple or lilac 17
16b. Ligules yellow 18

17a. Disc flowers purple, ligules lilac . . . . 8. *rodriguezii*
17b. Disc flowers yellow, ligules purple . . . 7. *leucanthemifolius*

18a. Perennial, stems woody at base 19
18b. Annual, stems not woody at base 20

19a. Plant glaucous, fleshy; leaves lanceolate to elliptic, entire, occasionally distantly toothed . . . . . 6. *aethnensis*
19b. Plant green, not or slightly fleshy; leaves elliptic to oblong, dentate . . . . 4. *squalidus*

20a. Ligules more than 10 mm 21
20b. Ligules less than 8 mm 22

21a. Calyculus of 8–20 bracts . . . . . 7. *leucanthemifolius*
21b. Calyculus absent . . . . 17. *petraeus*

22a. Calyculus lacerate; peduncles arachnoid . . 24. *trilobus*
22b. Calyculus entire; peduncles glabrous . . 7. *leucanthemifolius*

23a. Achenes glabrous, ridged or papillose 24
23b. Achenes strigulose 28

24a. Phyllaries glabrous 25
24b. Phyllaries glandular or sericeous or with a few short scattered hairs 26

25a. Lanate perennial; calyculus of 6 or more bracts . 2. *chalureaui*
25b. Glabrous or pubescent biennial; calyculus of 5 or fewer bracts 3. *erraticus*

26a. Plant viscid; achenes subcylindrical, ridged, 3–4 mm . 19. *viscosus*
26b. Plant glabrous or pubescent; achenes elliptic to ovate, papillose 1–2 mm 27

27a. Calyculus absent; phyllaries c. 13, sericeous; stem less than 25 cm . . . . 26. *minutus*
27b. Calyculus of 6–10 bracts; phyllaries c. 21, sparsely strigose; stems 20–60 cm . . . . 25. *delphinifolius*

28a. Plant glandular at least in inflorescence 29
28b. Plant eglandular 30

29a. Perennial; phyllaries c. 10 mm, calyculus of 1–5 bracts; ligules 6–9 mm . . . . 1. *nebrodensis*
29b. Annual; phyllaries 5–7 mm; calyculus of 5–13 bracts; ligules 2–3·5 mm . . . . 18. *sylvaticus*

30a. Ligules purple . . . . 16. *hoggariensis*
30b. Ligules yellow 31

31a. Middle cauline leaves narrowly lobed; lobes linear, not triangular or denticulate, at least 3·5 × longer than broad, sinuses at least 3·5 × lobe width. If lobes closer and broader then fleshy and rounded, and ligules more than 8 mm . . 32
31b. Middle cauline leaves more broadly and closely lobed; lobes oblong to elliptic, sometimes denticulate, if narrow and distant then triangular 35

32a. Erect perennial, usually over 35 cm, stems densely leafy, branching in inflorescence . . . 5. *chrysanthemifolius*
32b. Decumbent or erect annual, usually under 35 cm, stems not densely leafy, branching above and below 33

33a. Calyculus of 0–3 bracts; leaves rarely more than 5 cm, lobes patent . . . . 10. *gallicus*
33b. Calyculus of 3 or more bracts; leaf lobes antrorse, if patent then leaves fleshy and some more than 5 cm 34

34a. Ligule breadth more than 4 mm; leaf lobes rounded; phyllaries 6–8 mm; plant not glacous . . . . 14. *hesperidium*
34b. Ligule breadth less than 4 mm; leaf lobes dentate or acute-tipped; phyllaries 4–6 mm; plant often glaucous . 11. *glaucus*

35a. Perennial, stems woody below; some basal and middle cauline leaves more than 6 cm, if less then leaves closely lobed, lobes tapering towards the midrib; ligules usually more than 2·5 mm broad . . . . 4. *squalidus*
35b. 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 36

36a. Calyculus of 4 or more bracts . . . 7. *leucanthemifolius*
36b. Calyculus of 0–3 bracts . . . . . . 10. *gallicus*

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).

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 subcylindrical, glabrous, strigulose or lanate. Pappus of shortly toothed hairs, usually a few fluked or clavate hairs present in outer pappus whorl.

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. sér. 2. 6:346 (1836).

Erect viscous perennial, 20–80 cm, 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, 6–9 mm. Achenes c. 3·5 mm, subcylindrical, sparsely strigulose. Pappus c. 6 mm.

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

Described, probably in error, from Sicily. Hb. Linn. 996.23

SPAIN. Granada, Sierra Nevada, *Heywood & Davis* 697(E); Above Capileira, Alpujarra, 7 vi 1969, *Allen* (E).

Distribution: restricted to mountains in C & S Spain. (Fig. 1).

Described by Linneaus (1763) as an annual from Sicily, Spain and the Pyrenees. Since then, plants matching his specimen have only been recorded from southern Spain. Countless other collections from central and southern Europe, Sicily and north Africa have been misnamed as *S. nebrodensis* when they are clearly referable to *S. squalidus* L.

A chromosome count of 2n = 20 is recorded for this species (Afzelius, 1924) but should be treated with reserve because of past misuse of the specific name.

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

Differs from *S. squalidus* (below) 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.

Type. Morocco, Ari Ayachi, Grand Atlas Oriental, éboulis calcaires de la croupe culminante et des pentes voisines, 3000–3500 m, *Humbert* 1055 (iso. MPU).

Distribution: endemic to the eastern end of the Gt Atlas Mts, Morocco.

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

Distinguished from *S. squalidus* (below) by having leaves lyrate-pinnatisect with narrow pointed lobes. Phyllaries broad with two prominent longitudinal ridges, c. 4 × 1·5 mm. Achenes glabrous. Biennial.

2n = 40 (Kuzmanov and Kozuharov, 1970).

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

In recently published floras, this species is considered to be a subspecies of *S. aquaticus* Hill. The *Flora of Turkey and the East Aegean Islands*, vol. 5, (Matthews, 1975) describes it as *S. aquaticus* subsp. *erraticus* (Bertol.) Matthews. Chater and Walters (1976) treat it as *S. aquaticus* subsp. *barbaraefolius* (Wimmer & Grab.) Walters, using the earlier varietal name var. *barbaraefolius* as the basionym.

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

Erect glabrous to densely arachnoid perennial, occasionally annual. Stems terete, ridged, 20–80 cm, sometimes suffrutescent below and arising from a woody perennating rootstock, or from old stem-bases. Lower cauline leaves elliptic, petiolate, entire and dentate or shallowly pinnatifid into oblong or elliptic lobes. Middle and upper cauline leaves 3·5–15 × 1·5–6·5 cm, elliptic to oblong, pinnatifid to pinnatipartite, rarely unlobed and dentate, sometimes lyrate-pinnatifid. Lobes oblong or elliptic, antrorse and acutely toothed. Leaf tips acute or rounded. Capitula in lax or dense corymbs. Calyculus of 4–20 bracts, 1–3·5 mm. Phyllaries 21–27, 5–10 mm. Calyculus and phyllaries often black-tipped. Ligules yellow, 13–21, 7–17 mm. Achenes 2–3·5 mm, sparsely strigulose. Pappus 4·5–7 mm.

Key to subspecies:

1a. Sparsely to densely arachnoid, branching mostly in upper half; leaf tips obtuse, not rounded, leaves never lyrate-pinnatifid; pappus 6–7 mm . . . . . . iii. subsp. *araneosus*
1b. Glabrous or sparsely arachnoid, branching above and below; leaf tips acute or if rounded than leaves lyrate-pinnatifid and closely toothed; pappus 4·5–6·5 mm 2
2a. Middle cauline leaves pinnatipartite, distantly toothed, leaf tips acute; plant glabrous or sparsely arachnoid . . . . i. subsp. *squalidus*
2b. Middle cauline leaves lyrate-pinnatifid, closely toothed, leaf tips rounded; plant usually arachnoid . ii. subsp. *aurasiacus*

i. subsp. **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 var. *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).

2n = 20, voucher: C 11745 (E), cultivated material from England.
Fl. 5–10. Ruderal of open sandy and rocky places; hillsides, wasteground and railway-sidings. 0–2200 m.
Described from S Europe. Hb. Linn. 996.33
AUSTRIA. Gailthal, 11 ix 1900, *Krebs* s.n. (E).
GREECE. Lakonia, *Heldreich* 1547 (E).
ITALY. Mt. Grigna, 24 ix 1890, *Lacaita* s.n. (BM).
JUGOSLAVIA. Cattaro, Dalmatia, 5 ix 1896, *Krebs* s.n. (E)
ROMANIA. Transilvania, *Gurtler et al.* 831 (BM).
SICILY. Rocca Busambra, Ficuzza, *Davis* 40005 (E).
SWITZERLAND. Silva Plana, Engadin, vii 1910, *Browning* s.n. (E).
ALGERIA. Djebel Mahmel, 30 vi 1920, *Maire* s.n. (MPU); Palestro, *Davis* 51968 (E); Above Tlemcen, *Davis* 58887 (E).
Distribution: S and E Europe, N Africa. Introduced to Britain and apparently spreading from there to N W Europe (Fig. 1).

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., 1973) has suggested that *S. squalidus* arose on Mt Etna in Sicily as a result of hybridisation between *S. chrysanthemifolius* and *S. aethnensis*, both of which have been described as varieties of *S. squalidus*.

Material of subsp. *squalidus* was used in a few experimental crosses. When crossed with *S. gallicus*, the resulting hybrids had 39% stainable pollen. On morphological grounds it seems likely that among the annuals, *S. leucanthemifolius* is most closely allied to subsp. *squalidus*.

Many specimens referable to *S. squalidus* from north Africa and southern 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, Spain and the Pyrenees. 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 plants clearly referable to *S. squalidus* are given in many European and north African floras under *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.

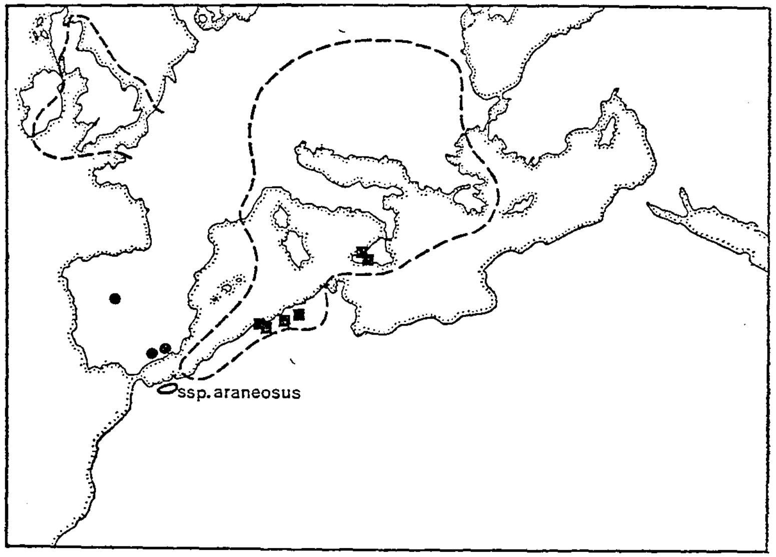

FIG. 1. Distribution of ● *S. nebrodensis*, and *S. squalidus* subspp. ■ *aurasiacus*, *squalidus* (broken line) and *araneosus* (continuous line).

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.

ii. subsp. **aurasiacus** (Batt. & Trab.) Alexander, **comb. et stat. nov.**

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

Distinguished from subspp. *squalidus* and *araneosus* by having lyrate-pinnatifid leaves with rounded apices. Whole plant often arachnoid.
2n = 20, voucher C 11746 (E), cultivated material of *Davis* 52888 from Algeria.
Fl. 4–6. Cliffs and rocky hillsides on limestone. 500–1500 m.
Described from Algeria: in declivitate boreali montis Gebel Tougour, prov. Constantine, 1853, *Balansa* s.n., *n.v.*
SICILY. Palermo, Ficuzza, *Ross* 546 (E).
ALGERIA. Djebel Djurdjura, *Davis* 53197 (E); *ibid.*, 9 vi 1930, *Maire* s.n. (MPU); Tlemcen mts, *Davis* 58965 (E).
Distribution: restricted to Algeria and Sicily (Fig. 1).

Although quite distinct morphologically from all the annual species, subsp. *aurasiacus*, when crossed with *S. leucanthemifolius* var. *leucanthemifolius*, produced hybrids with 97% stainable pollen. In spite of this close genetic affinity, it seems useful to maintain *S. squalidus* as a separate species.

Morphologically, subsp. *aurasiacus* merges with subsp. *squalidus*, both being present in Algeria and Sicily. However, crosses between the two produced non-germinable seed.

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 subspecies as described here.

iii. subsp. **araneosus** (Emb. & Maire) Alexander, **comb. et stat. nov.**

Syn.: *S. gallicus* var. *araneosus* Emb. & Maire in Mém. Soc. Sci. Nat. Maroc 18:54 (1927), *n.v.*

Distinguished from subsp. *squalidus* by its denser indumentum and more closely toothed leaves with obtuse apices, which are never lyrate-pinnatifid as in subsp. *aurasiacus*.

2n = 20, voucher: C 11747 (E), cultivated material of *Davis* 51374 from Morocco.

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

Described from Morocco: In Callietretis et Quercetis, solo margaceo, schistaceo, Aknoul, in monte Nador, Boured 800–1400 m, 19 vi 1926, *Maire* (iso. MPU).

MOROCCO. 70 km Talamerhait to Taza, *Alexander & Kupicha* 253 (E, BM); Above Oued Nador, *Davis* 51374 (E); Pass N. of Aknoul, *Davis* 51279 (E); Jbel Tazaote, Riff, *Sauvage* 15604 (RAB); *ibid., Alexander & Kupicha* 260 (E, BM and MO).

Distribution: endemic to the eastern end of the Riff Mts, N Morocco (Fig. 1).

Although originally described as a variety of *S. gallicus*, this plant is much closer to *S. squalidus* on both morphological and breeding criteria. Its most fertile hybrids produced by crossing with *S. squalidus* subsp. *squalidus* had 95% stainable pollen. Its morphological distinctness, however, justifies subspecific status.

Unfortunately the isotype 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 (1927).

5. S. chrysanthemifolius Poiret, Encycl. Meth. Bot. 7:96 (1806).

Distinguished from *S. squalidus* (p. 395) 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.

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

Distinguished from *S. squalidus*, (p. 395) 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.

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

Decumbent to erect, glabrous to pubescent or arachnoid annual, 2–60 cm., stems terete, shallowly ridged; sometimes plant subacaulous. Basal leaves spathulate to elliptic or rhomboid. Middle and upper cauline leaves elliptic to oblong, unlobed, sinuate, pinnatifid or pinnatipartite, sometimes unlobed above, 3–10 × 1–4 cm. Lobes isodiametric, oblong or triangular, usually forward-pointing and more than half the width of the sinuses; if patent or narrower, then always dentate or denticulate, but not themselves pinnatifid or pinnatisect. Capitula cylindrical to cup-shaped in lax or congested corymbs, pedicels 0·5–9 cm, bracteate. Calyculus of 4–20 bracts, 0·5–3 mm. Phyllaries 6–21, 4–8 mm. Phyllaries and calyculus often black-tipped. Ligules yellow, very rarely purple, 1·5–15 mm, spreading or revolute, sometimes absent. Achenes 1·5–3 mm, subcylindrical, sparsely or densely strigulose. Pappus hairs 2·5–7 mm.

It is difficult to make satisfactory infra-specific groups in this extremely variable species. Several characteristic facies are discernable, but in most cases there is continuous variation inter-connecting them. 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 here into varieties. Group A consists of fleshy, subacaulous, 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 six varieties are recognised, including the plant hitherto known as *S. vernalis* Waldst. & Kit. Group A consists of two varieties, one of which, var. *leucanthemifolius*, has probably been developed repeatedly from inland varieties whenever the latter encounter maritime conditions, and thus has little genetic unity. The other variety in group A, var. *pygmaeus*, appears to be a sporadic variant developed from var. *leucanthemifolius*. The two groups could have been treated as subspecies, but the probably polyphyletic origin and widespread distribution of the maritime group makes this inadvisable, and recognition of the inland group as subsp. *mauritanicus* would entail erecting subsp. *leucanthemifolius* as an autonym, according to article 19.4 in the International Code of Botanical Nomenclature (1978).

Key to varieties

1a. Plant fleshy, subacaulous, decumbent or short-stemmed with unlobed or shallowly lobed leaves, lobes simple (Group A) . 2

1b. 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

2a. Ligules more than 4 mm; phyllaries 13–21, more than 5 mm i. var. *leucanthemifolius*

2b. Ligules less than 4 mm; phyllaries fewer than 12, less than 5 mm ii. var. *pygmaeus*

3a. Phyllaries 7–9 mm, ligules 10–15 mm . . viii. var. *cyrenaicus*
3b. Phyllaries 6 mm or less, ligules less than 10 mm . . . 4
4a. Upper cauline leaves ± unlobed; auricles denticulate, or leaves regularly serrate or crenate 5
4b. Upper cauline leaves trifid or pinnatifid to pinnatipartite . 6
5a. Middle cauline leaves spathulate; auricles denticulate . . v. var. *major*
5b. Middle cauline leaves triangular, regularly serrate or crenate vi. var. *casablancae*
6a. Middle cauline leaves ± orbicular, attenuate; upper cauline leaves trifid, lobes rounded . . . . . vii. var. *vernus*
6b. Middle and upper cauline leaves pinnatifid to pinnatipartite . 7
7a. Lobes of middle cauline leaves forward-pointing and oblong, if denticulate then teeth obtuse. Plant branching from the base. iii. var. *fradinii*
7b. Lobes of middle cauline leaves patent and rounded, if forward-pointing then narrowly triangular and acutely denticulate. Plants unbranched or with a few ascending branches above . iv. var. *vernalis*

Group A (*vars. i & ii*)

i. var. **leucanthemifolius**

Syn.: *S. humilis* Desf., Fl. Atl. 2:271 (1799).
S. crassifolius Willd., Sp. Pl. 3:1982 (1803).
S. marmorae Moris, Stirp. Sard. Elench. 2:6 (1827).
S. apulus Tenore, Syll. Pl. Neap. 432 (1831).
S. humilis var. *pedunculosus* DC., Prodr. 6:345 (1838).
S. incrassatus Guss., Fl. Sic. 28 (1826).
S. leucanthemifolius var. *pectinatus* Guss., Fl. Sic. 28 (1826).
S. salisii Gay, MS. nomen (1838).
S. pinguiculus Pomel, Nouv. Mat. Fl. Atl. 62 (1874).
S. crassifolius var. *pinguiculus* (Pomel) Batt. & Trab., Fl. de. l'Alg. 473 (1889).
S. leucanthemifolius var. *pedunculosus* Fiori, Fl. Anal. d'It. 3:211 (1903).
S. leucanthemifolius var. *typicus* Fiori, Fl. Anal. d'It. 3:211 (1903).
S. leucanthemifolius var. *reichenbachii* Fiori, Fl. Anal. d'It. 3:211 (1903).
S. salzmannii Rouy, Fl. France 8:340 (1903), of uncertain status.
S. crassifolius var. *giganteus* Caballero (?) in Mem. R. Soc. Esp. Hist. Nat. 8:288 (1915).
S. leucanthemifolius subsp. *poiretianus* Maire, Cat. Pl. Maroc. 3:783 (1934), *p.p.*
S. leucanthemifolius subsp. *crassifolius* (Willd.) Batt. (citation of combination not found).

Subacaulous to decumbent or erect fleshy annual, 5–30 cm, glabrous or sparsely arachnoid. Basal leaves spathulate or elliptic, unlobed or distantly dentate to shallowly lobed, 2–5 × 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 cylindrical to cup-shaped, borne in lax corymbs or singly on bracteate peduncles up to 7 cm. Phyllaries 13–21, 4–6·5 mm, glabrous, often black-tipped. Calyculus of 4–20 bracts, 1–3 × 0·5–2 mm, often black-tipped. Ligules yellow, very rarely purple, 4–8·5 × 1–2·5 mm. Achenes subcylindrical, sparsely strigulose, 1·5–2 mm. Pappus hairs 2·5–5 mm.

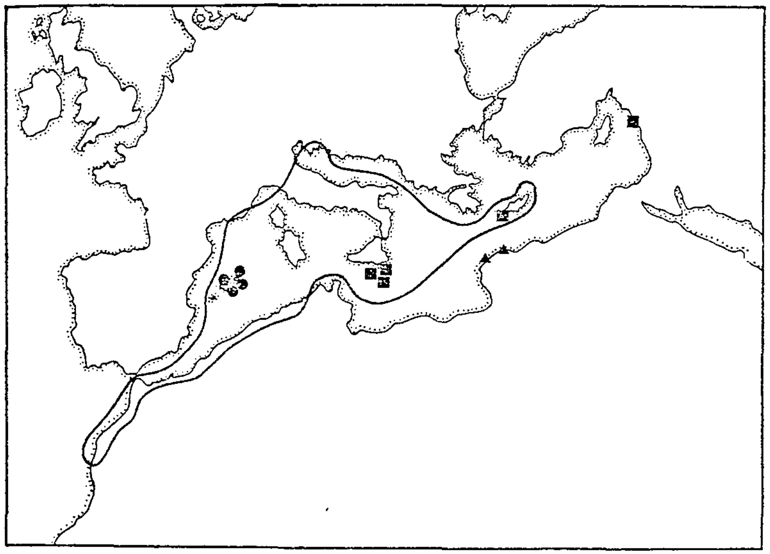

FIG. 2. Distribution of ● *S. rodriguezii* and *S. leucanthemifolius* vars. *leucanthemifolius* (continuous line), ■ *pygmaeus*, and ▲ *cyrenaicus*.

$2n = 20$, vouchers: C 11731 (E) and C 11732 (E), cultivated material of *Davis* 51764 from Algeria and *Lanfranco* s.n. from Malta respectively.

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

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

CORSICA. Porto Vecchio, *Mabile* 143 (FI); Calvi, iii–iv 1962, *Archibald* s.n. (E).
FRANCE. Iles de Porquerolles, *Bourgeau* 239 (K).
GREECE. Crete, Mavromuri, iii 1954, *Goulimy* s.n. (K); Karpathos, v 1883, *Pichler* s.n. (BM).
ITALY. Calabria, *Fiori* 970 (K,E).
JUGOSLAVIA. Pelagosa I., iii 1882, *Marchesetti* s.n. (K).
LAMPEDUSA. 8–14 iii 1906, *Sommier* s.n. (FI).
SARDINIA. Tempio, *Reverchon* 177 (E, K, FI).
SICILY. Balestrate, 21 ii 1906, *Fiori* s.n. (FI).
ALGERIA. Mostaganem, *Battandier* s.n. (MPU); *ibid.*, *Balansa* 177 (BM).

MOROCCO. Oualidia, *Davis* 54252 (E); Fedhala, ii 1930, *Trethewy* s.n. (BM).
TUNISIA. Ain Sebaa to Jebbara, *Davis* 57734 (E).
Distribution: W and C Mediterranean, eastwards to Crete and Karpathos (Fig. 2).

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-specific and do not represent distinct enough forms to warrant formal taxonomic recognition. 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* (p. 408).

ii. var. **pygmaeus** (DC.) Fiori, Fl. Anal. d'It. 3:211 (1903).
Syn.: *S. pygmaeus* DC., Prodr. 6:341 (1838).
S. caroli-malyi Horvatić in Biol. Glasn. Zagreb 8:37 (1956).

Differs from var. *leucanthemifolius* in being smaller in all its parts, though sometimes up to 20 cm tall. 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, 1–3 cm.
Fl. 2–6. Maritime rocks and sand 0–50 m.
Described from Sicily: "In Sicilia prope Capo-Pojato". Microfiche seen.
CRETE. Palaiokhora, *Davis* 1186 (E).
MALTA. Gozo, *Fiori & Béguinot* 1148 (BM).
SARDINIA. Isola Maddalena, vi 1893, *Vaccari* s.n. (FI).
LEBANON. Beirut, 12 v 1871, *Herb. Postian* (E).
Distribution: sporadic in C and E Mediterranean. (Fig. 2).

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 up to 3·5 mm. All collections are similar in the striking smallness of their capitula. It is probable that var. *pygmaeus* is of polyphyletic origin from var. *leucanthemifolius*, as there is some variation in habit and leaf-shape, and its distribution appears to be disjunct.

Group B (*vars. iii–viii*)
iii var. **fradinii** (Pomel) Batt., Fl. de l'Alg. 1:472 (1889).
Syn.: *S. mauritanicus* Pomel, Nouv. Mat. Fl. Atl. 62 (1874).
S. fradinii Pomel, Nouv. Mat. Fl. Atl. 61 (1874).
S. leucanthemifolius var. *pinnatifidus* Fiori, Fl. Anal. d'It. 3:212 (1903).
S. leucanthemifolius var. *lanigerus* Batt., Suppl. Fl. Alg. 55 (1910).
S. gallicus subsp. *mauritanicus* (Pomel) Maire in Mém. Soc. Nat. Maroc 17:54 (1927).
S. gallicus var. *mauritanicus* (Pomel) Pau, in sched. (1927).
S. leucanthemifolius var. *paui* Maire in Cavanillesia 2:173 (1929).

S. leucanthemifolius subsp. *crassifolius* var. *latisectus* Pau & Font Quer, in sched. (1929).
S. gallicus subsp. *mauritanicus* var. *eu-mauritanicus* Maire in Jah. & Maire, Cat. Pl. Maroc 3:784 (1934).
S. gallicus subsp. *mauritanicus* var. *lanigerus* (Batt.) Maire in Bull. Soc. Hist. Nat. Afr. Nord 25:304 (1934).
S. kebdanicus Maire & Sennen (?).

Erect glabrous, pubescent or arachnoid annual, 10–50 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 2–8 × 0·7–3 cm, lobes less than 3·5 times longer than broad, sinuses less than 3·5 times the lobe width. Cylindrical to cup-shaped capitula borne in lax corymbs. Phyllaries 13–21, 4–6·5 mm, glabrous, often black-tipped. Calyculus of 4–20 bracts, 1–3 × 0·5–2 mm, often black-tipped. Ligules yellow, 4–8·5 × 1–2·5 mm. Achenes subcylindrical, sparsely strigulose, 1·5–2 mm. Pappus hairs 3–5 mm.
$2n = 20$, vouchers: C 11735 and C 11738 (E), both from Algeria, cultivated material of *Davis* 52077 and 52490 respectively.
Fl. 12–6. Agrestal and ruderal of forest clearings, roadsides and hillsides mostly on calcareous soils, occasionally on sandy soils. 50–2250 m.
Type. Algeria, Environs d'Alger, *Fradin* s.n. (iso. MPU).
SARDINIA. Cagliari, *Cavara* s.n. (FI).
SICILY. Panormum, *Todaro* 521 (FI); Palermo, 2–3 iv 1947, *Parlatore* s.n. (K).
ALGERIA. Guelma, *Davis* 52305 (E); Djurdjura, *Davis* 59416 (E).
LIBYA. Cyrenaica, Tolmetta, *Pampanini* 9550 (FI); Baiada, *Davis* 49961 (E).
MOROCCO. Bab Bou Idir, Fez, *Alexander & Kupicha* 281 (E, BM, MO); Mischliffen, *Alexander & Kupicha* 345 (E, BM, MO); Fez, *Weiller* 316·21 (MPU).
Distribution: Morocco, N Algeria, Sardinia, Sicily and Cyrenaica. (Fig. 3).

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, non-fleshy leaves, with lobes usually dentate or secondarily lobed. The range of indumentum density found made it impracticable to maintain var. *lanigerus* Batt. as a separate variety. As European and north African work has mostly proceeded independently, European plants acceptable in var. *fradinii* have previously been referred to var. *pinnatifidus* Fiori.

iv. var **vernalis** (Waldst. & Kit.) Alexander, **comb. et stat. nov.**
Syn.: *S. vernalis* Waldst. & Kit., Pl. Rar. Hung. 1:23, t. 24 (1802).
S. rapistroides DC., Prodr. 6:346 (1838).
S. polycephalus Ledeb., (?) Fl. Ross. 2:630 (1845).
S. peduncularis Griseb., (?) Spicil. Fl. Rumel. 2:224 (1846).

Differs from var. *fradinii* in having stems unbranched or with a few ascending branches above and leaf lobes rounded to triangular, usually denticulate. Whole plant sparsely to densely arachnoid, rarely glabrous. Calyculus bracts 0·5–2 mm. Ligules 5–10 mm. Achenes 2–3 mm. Pappus 4–6 mm.

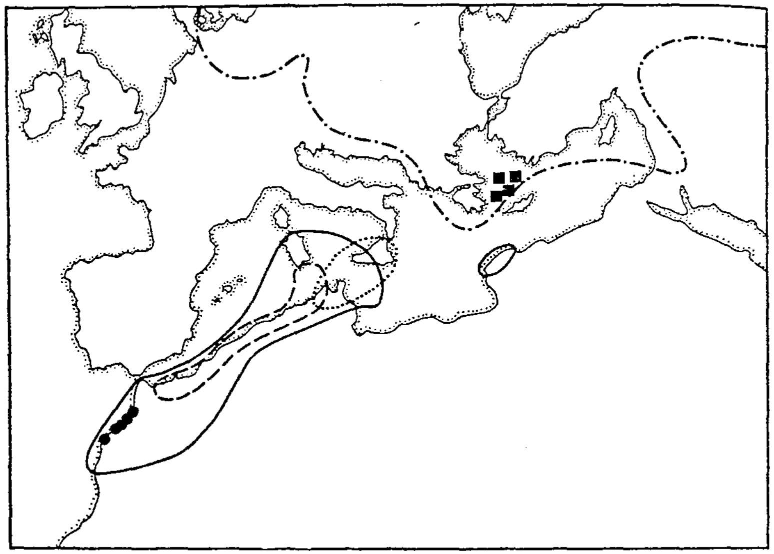

FIG. 3. Distribution of *S. leucanthemifolius* vars. *vernalis* (line of dashes and dots), *fradinii* (continuous line), *major* (broken line), *vernus* (dotted line), and ● *casablancae*. ■ Intermediates between *S. leucanthemifolius* var. *vernalis* and *S. glaucus*.

2n = 20, vouchers: C 11733 (E) from Israel and C 11734 (E) from Turkey (the latter cultivated material of *Baytop* 20556); Czechoslovakia (Vachova and Ferakova, 1978). n = 10, Iran (Aryavand, 1977).
2n = 40, Czechoslovakia (Majovsky et al., 1970).
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).
BULGARIA. Mt Vitosa, *Stojanov* 199 (E).
CYPRUS. Stavros valley, *Foggie* 93 (E).
DENMARK. Zealand, *Jacobsen* 97 (E).
GERMANY. Berlin, 11 iv 1901, *Lackowitz* s.n. (E).
GREECE. Kalimnos, *Major* 364 (E); Rhodos, *Bourgeau* 90 (BM).
JUGOSLAVIA. Vranje, v 1895, *Krebs* s.n. (E).
ROMANIA. Deva, 17 iv 1887, *Tauscher* s.n. (E).
SWEDEN. Oland, 6 vi 1922, *Kohler* s.n. (E).
SYRIA. Nebk, *Davis* 5531 (E).
IRAN. Sanandag, Kurdistan, *Archibald* 2000 (E).
IRAQ. Amadia, *Polunin* 5120 (E).
ISRAEL. Sharon Plain, Qeisari, *Marder* 07024 (HUJ).
JORDAN. Wadi Musa, Ma'an, *Davis* 8686 (E).
LEBANON. Harissa, *Polunin* 5273 (E).
TURKEY. Antalya, iii 1849, *Heldreich* s.n. (BM).
Distribution: N E and C Europe, SW Asia, S Russia and Afghanistan. Apparently spreading into W Europe. (Fig. 3).

Artificial hybrids between var. *vernalis* and other varieties of *S. leucanthemifolius* showed pollen stainability of up to 80%. As there are also no reliable morphological characters for separating *S. vernalis* from the rest of *S. leucanthemifolius*, especially var. *fradinii*, it seems reasonable to treat it under this species. The arguments against giving it subspecific rank are discussed on p. 399. This variety 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 sub-entire triangular lobes. Many infra-specific taxa have been described under *S. vernalis*, but these cannot be sustained if it is now treated as a variety of *S. leucanthemifolius*. Many other names are given as synonyms for *S. vernalis* in *Index Kewensis* and other sources. In most cases no specimens are cited in the descriptions accompanying the publication of these names, and the descriptions alone are inadequate to justify listing them as synonyms.

Discrepancies among the chromosome counts for this variety are discussed on p. 391.

v. var. **major** Ball in J. Linn. Soc. Bot. 16:514 (1878).
Syn.: *S. atlanticus* Boiss. & Reut., Pugillus 58 (1879) non Coss. (1856).
S. nebrodensis var. *sardous* Fiori, Fl. Anal. d'It. 3:212 (1903).

Differs from var. *fradinii* in having all leaves broadly spathulate to oblong, sinuate to shallowly lobed, dentate, amplexicaul; auricles large and denticulate to lacerate.
2n = 20, voucher: C 11740 (E), cultivated material of *Alexander & Kupicha* 112 from Morocco.
Fl. 3–6. Calcareous cliffs and rocky hillsides. 200–1000 m.
Described from Algeria: "Hab. in Atlante Algeriensi supra Blidah ascendendo ad Ain Telazid in faucibus fluminis Chiffa", 1849, *Reuter*, *Boisser* s.n., *n.v.*
SARDINIA. Capoterra, *Fiori* 1767 (BM); Monte Santo, 7 v 1879, *Biondi* s.n. (FI).
ALGERIA. Nr. Constantine, *Bourgeau* s.n. (BM).
MOROCCO. Chauen, *Font Quer* 406 (BM, MPU); Beni Hosmar, above Tetuan, *Davis* 432 (K, E).
Distribution: N Morocco, N Algeria and Sardinia. (Fig. 3).

This variety is morphologically closest to var. *fradinii* with which it intergrades, though its most fertile hybrids were produced with var. *leucanthemifolius*. It showed higher fertility when crossed with *S. glaucus* than did other accessions of *S. leucanthemifolius*.

vi. var. **casablancae** Alexander, **var. nov.**

Similis var *majori* sed statura robusta, foliis nunquam spathulatis distinguitur. Differt a var. *fradinii* foliis infima et mesocaulina nunquam pinnatifidis vel pinnatisectis; marginibus regulariter serratus vel lobis non profundis rotundatis imbricantibus.

Erect glabrous or very sparsely pubescent annual, often a little fleshy, 10–60 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 4–8 × 1·5–4 cm. Upper cauline leaves triangular, often long and narrow, serrate, occasionally lobed at the base,

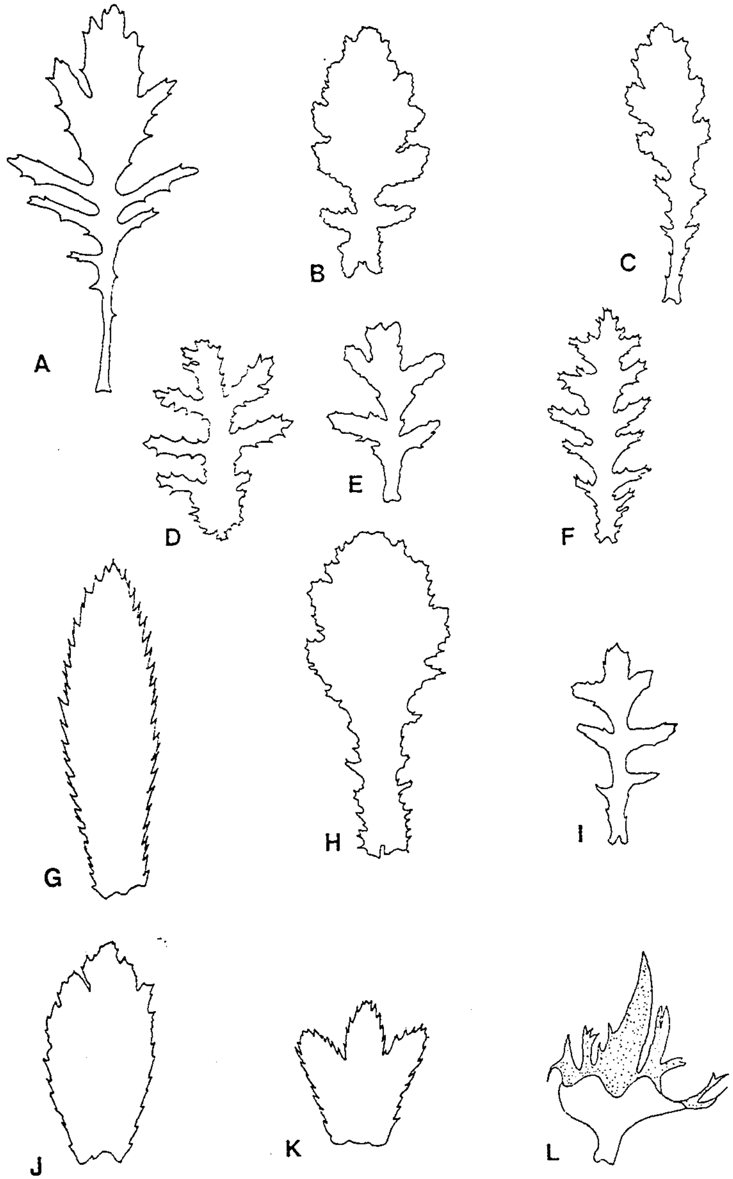

FIG. 4. A–K, Leaf silhouettes. A–C, *S. squalidus*: A, subsp. *squalidus*; B, subsp. *aurasiacus*; C, subsp. *araneosus*. D–J, *S. leucanthemifolius*: D, var. *fradinii*; E, var. *vernus*; F, var *vernalis*; G, var. *casablancae*; H, var. *major*; I, var. *leucanthemifolius*; J, var. *cyrenaicus*. K, *S. trilobus*. L, cayculus scale of *S. trilobus*. A–D, F, H & I × ½; E, G & J × ⅔; K × ½; L × 10. A–D, F, H & I from cultivated specimens, the rest from wild collections.

2·5–6 × 0·8–2 cm. Capitula in dense corymbs, pedicels bracteate, 0·5–5 cm. Capitula cylindrical to cup-shaped, phyllaries 13–21, 5–6 mm. Calyculus of 5–10 bracts, 1–2 × 0·5 mm. Phyllaries and calyculus bracts usually black-tipped. Ligules yellow, 6–10 × 1·5–3 mm. Achenes strigulose, 1·5–2 mm. Pappus hairs 4–5 mm.
Fl. 1–5. Sand dunes, rocky calcareous slopes and cliffs by the sea. 0–50 m. (Fig. 3).
Type. Morocco, Casablanca, iii 1931, *Trethewy* 157 (holo. K).
MOROCCO. Cap Blanc, *Davis* 54260 (E); Casablanca and Chaouia, *Gentil* 1909 (MPU); Rabat, 27 i 1924, ?*Zhuby*, Institut Cherifien 40640, (RAB); Salé, v 1888, *Grant* s.n. (E); Fedhala, *Trethewy* 175 (K).
Distribution: restricted to about 300 km of the W Moroccan coast from Beddouza to Salé. (Fig. 3).

Distinguished from var. *fradinii* by having large, oblong rhomboid or triangular leaves and 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. Var. *casablancae* is the only variety in Group B with a purely coastal distribution.

vii. 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* 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.
Fl. 12–6. Maritime sands and sandy fields near the sea. No information on altitudinal range, but probably below 150 m. (Fig. 4).
Type. Sicily, *Bivona* s.n., (iso. BM).
SICILY. Palermo, 1855, *Todaro* s.n. (FI); Taormina, ii 1902, *Higgins* s.n. (E).
ALGERIA. Bône, 17 v 1875, *Meyer* s.n. (MPU).
TUNISIA. Cap Bon, *Davis* 56913 (E).
Distribution: C Mediterranean. (Fig. 3).

viii. var. **cyrenaicus** Dur. & Barr., Fl. Lib. Prodr. 135 (1910).
Syn.: *S. cyrenaicus* (Dur. & Barr.) Borzi, Min. Aff. Esteri, Monogr. Rapp. Col. 7:9 (1912).

Differs from var. *fradinii* in being more robust and larger in all its parts. Phyllaries 7–9 mm, ligules 10–15 mm, achenes 2–2·5 mm. Large capitula held in lax or more crowded corymbs. Leaves 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), Dernam Kenissié, *Taubert* 603, *n.v.*
LIBYA (Cyrenaica). Tolmetta, *Vaccari* 209 (FI); *ibid.*, *Vaccari* 1087 (E, FI, BM).
Distribution: restricted to Cyrenaica (Fig. 2).

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 smaller head size and unique calyculus morphology (Fig. 4) the latter are clearly referable to *S. trilobus* L. (p. 420). Being easily distinguishable on the size of its capitula, var. *cyrenaicus* might warrant subspecific rank; however, only two gatherings have been examined and no material was available for experimental work.

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

Differs from *S. leucanthemifolius* var. *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.
2n = 20 (Afzelius, 1967).
Fl. 3–5. Rocky sea-shores.
Described from the Balearic Is.
BALEARIC IS. Majorca, C. Formentor, *Kennedy* 25 (E). Minorca, C. Mesquieda, 23 iv 1903, *Bucknall & White* s.n. (E).
Distribution: restricted to the Balearic Is. (Fig. 2).

This species is unique among annual species of *Senecio* from Europe and north Africa in having purple disc flowers. In spite of this distinction, it is treated in *Flora Europaea* (Chater and Walters, 1976) under *S. leucanthemifolius* without formal rank. Purple or lilac rays are also found in *S. hoggariensis* and very occasionally in *S. leucanthemifolius*.

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

Differs from *S. leucanthemifolius* var. *vernalis* (p. 403) in having a longer, always cylindrical, capitulum, and phyllaries 6–8 mm.

Calyculus of 10–20 triangular, overlapping bracts, often with large black tips. Ray flowers usually absent; occasionally 6–12, ligules 1·5–4 mm, yellow. Leaves elliptic to oblong, denticulate, pinnatifid to pinnatipartite; lobes oblong to triangular, patent, with denticulate or lacerate auricles.
2n = 40, vouchers: C 11750 (E), cultivated material from Scotland and C 11751 (E), cultivated material of *Davis* 51254 from Morocco.
Fl. 1–12. Ruderal and agrestal of waste places, fields, disturbed habitats and rocky hillsides. 0–2000 m.
Described from Europe. Hb. Linn. 996.7.
BALEARIC IS. Soller, *Bianor* 704 (E).
CYPRUS. Yaila, *Davis* 2838 (E).
FRANCE. Iles d'Hyeres, *Herb. Ball* s.n. (E).
ITALY. Mandusia, v 1874, *Groves* s.n. (E).
PORTUGAL. Coimbra, *Moller* 275 (E).
SICILY. Roca Busambra, *Davis* 40045 (E).
SPAIN. Barcelona, 2 iv 1911, *Sennen* s.n. (E).
ALGERIA. Oran, 12 ii 1936, *Fauré* (E).
EGYPT. Giza, *Davis* 8327 (E).

MOROCCO. Tizi-n-Tichka, *Alexander & Kupicha* 489 (E).
IRAN. Jahrum, *Koelz* 14672 (E).
IRAQ. Baghdad, 2 iii 1955, *Wheeler Haines* s.n. (E).
ISRAEL. Jerusalem, *Meyers & Dinsmore* B1038 (E).
LEBANON. Harissa, *Polunin* 5312 (E).
TURKEY. Edirne, *Davis* 41901 (E).
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 gave surprisingly high percentages of stainable pollen, reaching over 10% in four cases. Other crosses showed that isolation between *S. vulgaris* and other polyploid species seems to be stronger; this was also shown by Gibbs (1971) who found that experimental crossing of *S. vulgaris* with *S. viscosus*, also a tetraploid, produced infertile seed. Morphologically, *S. vulgaris* is one of the more distinct species: the capitula are quite characteristic. The leaf shape remotely resembles *S. gallicus* and *S. leucanthemifolius* var. *vernalis*. Populations of *S. vulgaris* from different parts of its range are very similar morphologically when grown under standard conditions.

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 (1974a, 1974b and 1975), Richards (1975) and Benoit et al. (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 possibly back-cross repeatedly with *S. vulgaris*, giving rise to rayed forms of *S. vulgaris*, known as *S. vulgaris* forma *radiatus* Hegi. However, the occurrence of forma *radiatus* 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. Unreduced gametes, however, are known to have been formed in a triploid F_1 hybrid resulting from artificially crossing *S. vulgaris* with *S. squalidus* (Ingram, 1978), when chance selfing among the F_1 generation produced, among other infertile plants, a single highly fertile hexaploid in the F_2. Biochemical support for the introgression theory is provided by Hull (1974b) who found greater similarity in esterase patterns between *S. squalidus* and *S. vulgaris* forma *radiatus* than between rayed and discoid *S. vulgaris*, when all three were growing in the same area. Additional evidence is provided by Richards (1975) who has observed that forma *radiatus* 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 could 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. Crisp and Jones (1978) showed that, after several generations of selfing the progeny resulting from crossing *S. squalidus* and *S. viscosus*, the F_4 generation contained some individuals with chromosome numbers at or near the tetraploid level. If this were also the case in crosses between *S. vulgaris* and *S. squalidus*, introgression could then occur from *S. squalidus* via the F_4 generation into *S. vulgaris*, without necessarily involving the formation of unreduced gametes in the parental species. However, if introgression from *S. squalidus* into *S. vulgaris* really is taking place, it is surprising that other morphological characters from *S. squalidus* are not found in populations of *S. vulgaris* which are thought to have been introgressed.

10. S. gallicus Vill., Hist. Pl. Dauph. 1:371 (1786).
Syn.: *S. squalidus* sensu Willd., Sp. Pl. 3:1991 (1803), *p.p.*, 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. sér. 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 in upper half, less commonly below. Lower cauline leaves narrowly elliptic to oblong in outline, 2–5 × 1–2 cm, widely toothed or pinnatifid, attenuate; middle cauline leaves oblong with small auricles, up to 6 × 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 cylindrical to cup-shaped, calyculus usually absent, sometimes of up to 3(–10) subulate bracts, 1–2 mm. Phyllaries 13–21, glabrous, sometimes a little glaucous, 4·5–6 mm, reflexing in fruit. Ligules 8–13, 5–11 × 2–3 mm. Achenes 2–2·5 mm, subcylindrical sparsely strigulose. Pappus hairs 4–6 mm.

2n = 20, vouchers: C 11729 (E), cultivated material from Portugal, and C 11730 (E), cultivated material of *Allen* 6886 from Spain.

Fl. 3–7. Sand dunes, sandy fields and *Pinus* forests, river banks. Less commonly on schists and calcareous soils. 0–1000 m.

Type. Vapinci, in mureis, vineis. (Gap, Dauphiné, SE France), *Villars* s.n. (iso. BM).

FRANCE. Sarras, Ardéche, *Chabert* 2120 (K); Fontan les Bois, *Reverchon* 209 (E).

PORTUGAL. Aljezur, 15 v 1969, *Lousley* s.n. (BM); Carrapeteira, *Davis* 50873 (E).

SICILY. Herb. *U. Martelli* s.n. (FI).

SPAIN. La Rabida, Huelva, *Gibbs* 69.135 (E); Madrid, *Atchley* 434 (K).

ALGERIA. Oran, vii 1910, *Fauré* s.n. (E).

Distribution: SW Europe, Sicily, Algeria, Alboran Is. No specimens seen from Balearic Is, Corsica or Sardinia. (Fig. 5).

Intermediate with *S. glaucus* subsp. *coronopifolius*: 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 edition 4 of *Species Plantarum* (1803) Willdenow amplifies Linnaeus' description and places *S. gallicus* in synonymy. *S. squalidus* sensu Willd. is therefore only partly synonymous with *S. gallicus*. *S. uliginosus* was described by de Candolle (1838) as a perennial 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 distinct from *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* (Jahandiez & Maire, 1934; Chater & Walters, 1976). However the area in which intermediates occur is quite small, and crosses between them made during this investigation 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 distinct species on the basis of breeding experiments. In leaf shape, some populations approach *S. leucanthemifolius* var. *vernalis*. Hybrid seed produced by crossing these two taxa failed to germinate.

11. S. glaucus L., Sp. Pl. 868 (1753).

Decumbent or erect fleshy annual, 8–50 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, antrorse, patent or slightly retrorse, entire, dentate or secondarily lobed; tips of lobes acute, or rounded and bi- or trifurcate; sinuses at least 3–5 times the lobe width. Upper cauline leaves more finely and closely lobed, becoming unlobed and linear above. Capitula in lax corymbs. Phyllaries 13–21, 4·5–8 mm. Calyculus of (0–)1–12 bracts, 1–4 mm. Phyllaries and calyculus occasionally with small black tips. Ligules 10–17, yellow, 6–12 × 1·5–3 mm. Achenes 2–3·5 mm, sparsely strigulose. Pappus hairs 4–7 mm.

1a. Phyllaries 6–8 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 . . . i. subsp. *glaucus*

1b. Phyllaries 4·5–6 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 . . . . ii. subsp. *coronopifolius*

i. subsp. **glaucus**

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

2n = 20, vouchers: C 11723 (E), cultivated material from Egypt, C 11724 (E), cultivated from material from Libya, and C 11725 (E) cultivated material from Israel.

Fl. 12–6. Maritime sand and sandy places not far from the sea. 0–20 m.

Described from Egypt: "Hab. in Aegypto". Hb. Lin. 996. 24

EGYPT. Alexandria, *Bornmüller* 10707 (E).

ISRAEL. Shefalah, *Sheinkar* 07009 (HUJ); Even Yehuda, *Davis* 4069 (E).

Distribution: Israel and Egypt (Fig. 5).

Generally more robust and fleshier than subsp. *coronopifolius*. The large capitula are often indurated at the base in fruit. 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. leucanthemifolius* var. *vernalis* is taking place inland. Until these arachnoid inland plants are proved to be hybrid in origin, the manner of leaf lobing refers them to subsp. *glaucus*.

The Linnean name *S. glaucus* was adopted for this species (hitherto usually called *S. coronopifolius* Desf. or *S. desfontainei* Druce) on the evidence of cultivation experiments. An Egyptian accession of *S. joppensis* grown in Edinburgh produced upper cauline leaves which closely match specimen 996.24 (*S. glaucus*) 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 *S. glaucus*. As *S. joppensis* and *S. desfontainei* are best treated conspecifically on both morphological and breeding criteria, it seems appropriate to include them both as subspecies 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.

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

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

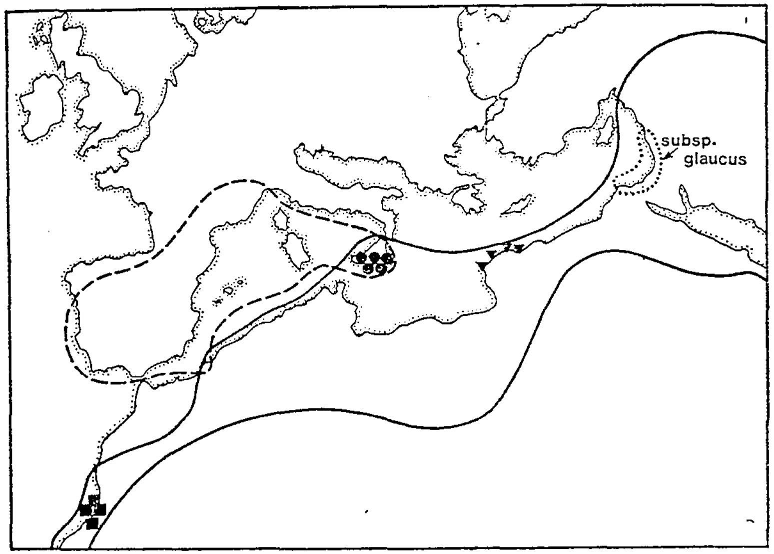

FIG. 5. Distribution of *S. gallicus* (broken line), *S. glaucus* subspp. *glaucus* (dotted line) and *coronopifolius* (continuous line). ● Intermediates between *S. gallicus* and *S. glaucus* subsp. *coronopifolius*. ▼ Intermediates between *S. leucanthemifolius* var. *fradinii* and *S. glaucus* subsp. *coronopifolius*. ■ *S. hesperidium*.

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. 16:154 (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).

2n = 20, vouchers: C 11726 (E), cultivated material from Israel, C 11727 and C 11728 (E), cultivated material from Morocco, of *Davis* 53818 and 53727 respectively. 2n = 40 (Mehra and Remanandan, 1969). Discrepancies among the chromosome counts are discussed on p. 391.

Fl. 1–7. Agrestal and ruderal of sandy fields, river banks, stony and rocky slopes and deserts. Also recorded from limestone. 0–2370 m.

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

CANARY IS. Teneriffe, *Burchard* 208 (E).

MOROCCO. Oued Massa, 7 iv 1922, *Maire* s.n. (RAB); Chichaoua, 5 iv 1921, *Maire* s.n. (MPU); Tafraoute to Tleta de Tasserirt, *Davis* 48796 (E).

ALGERIA. Ain Sefra, 12 v 1938, *Fauré* s.n. (E); Mzab, *Weiller* 867 (MPU).

TUNISIA. Gafsah, *Pitard* 413 (E).

SICILY. Licata, *Ross* 545 (FI); *ibid.*, *Lacino* (?) 588 (E, BM); Djebel Chambi, *Davis* 57467 (E).

LIBYA. Tripoli, *Davis* 49458 (E).
EGYPT. Almaza, 2 iv 1946, *Lupton* s.n. (BM).
ISRAEL. Rafiah, 5 v 1924, *Eig* s.n. (HUJ).
JORDAN. Wadi Ram, *Davis* 9095 (E).
SYRIA. Abu ed Duhur, 1946, *Rechinger* s.n. (E).
IRAQ. Arak, *Archibald* 1758 (E).
AFGHANISTAN. Ispoli, Kandahar, *Hedge & Ekberg* 7067 (E).
PAKISTAN. Surkhab Valley, Baluchistan, *Lace* 3710 (E).
Distribution: Canary Is, N Africa, Sicily, SW Asia and W Himalayas (Fig. 5).

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 tips. The capitula are never indurated at the base. Crosses between this subspecies and subsp. *glaucus* 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* also produced non-germinating achenes. 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*. 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 being a later homonym is illegitimate. A note under article 72 in the *International Code of Botanical Nomenclature* (1978, p. 57) 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.

Accounts of two other species, *S. krascheninnikovii* and *S. vulcanicus*, though removed geographically from the scope of this paper, are included here as they have some similarity to *S. glaucus* subsp. *coronopifolius*. They do not appear in the key.

12. S. krascheninnikovii Schischk. in Not. Syst. Herb. Inst. Bot. Acad. Sci. URSS 15:410 (1953).
Syn.: *S. pedunculatus* Edgew. in 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 the 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 Boisser (1888) and Komarov (1961).

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

Differs from *S. glaucus* subsp. *coronopifolius* in being a subacaulous alpine plant with narrow linear to lanceolate subpinnatifid leaves. Ligules c. 5 mm. Achenes glabrous.
Fl. 7–8. Volcanic rocks and soil. 3000–4000 m.
Types. Iran, Mt Demavend, *Kotschy* 667, *n.v.*; Elamout Mts, *Aucher* 4717, *n.v.*
IRAN. Mt Demavend, *Bornmüller* 7478 (E); *ibid.*, *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. 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 (1875) treated *S. lacerus* as *S. coronopifolius* var. *psilocarpus*.

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).

Differs from *S. glaucus* subsp. *coronopifolius* in having larger capitula with phyllaries 6·5–7·5 mm and c. 13 longer and broader ligules, 8–14 × 4–5 mm. The plant is fleshy and the leaves pinnatipartite or bipinnatipartite into rounded linear lobes which are entire, never dentate.
2n = 20, voucher: C 11743 (E), cultivated material of *Davis* 53536 from Morocco.
Fl. 3–4. Colonised sand dunes and sandy slopes by sea. 0–50 m.
Types. Morocco, Sidi Moussa, *Jahandiez* 81 (iso. RAB); *ibid.*, 22 iv 1931, *Maire* s.n. (iso. MPU).

MOROCCO. Sidi Moussa, *Davis* 53536 (E); *ibid.*, *Davis* 53545 (E).
Distribution: Sidi Moussa, SW Morocco, known only from the type locality (Fig. 5).

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* 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* produced hybrids with 99% stainable pollen. This is surprising as from leaf morphology one might have expected their parentage to have involved *S. glaucus* subsp. *coronopifolius* rather than *S. hesperidium*.

15. 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* subsp. *coronopifolius* in having smaller oblong rayless capitula, 5–6 mm in diameter. Leaves 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, vcucher: C 11755 (E), cultivated material of *Davis* 53902 from Morocco.
Fl. 3–5. Sandy and gravelly river terraces, often more or less saline. 0–1000 m.
Type. Morocco, shores of R. Massa, 8 iv 1922, *Maire* s.n. (iso. MPU).
MOROCCO. Mouth of R. Sous, *Davis* 53902 (E); Agdz, 14 v 1933, *Maire* s.n. (MPU).
Distribution: Morocco, mouths of R. Sous and R. Massa, Agdz on R. Draa (Fig. 6).

A distinct species both morphologically and genetically. Being a tetraploid, *S. massaicus* is effectively isolated from local populations of *S. glaucus* subsp. *coronopifolius*, 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 was produced. Hybrids of much lower fertility were produced when *S. massaicus* was crossed with *S. vulgaris*; they are both tetraploid.

The distribution of this species (Fig. 6) is rather curious, as the localities from which it was recorded are some way apart. Also the inland station is on a different river from the coastal ones. The population sizes 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 (Davis, pers. comm.). 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.

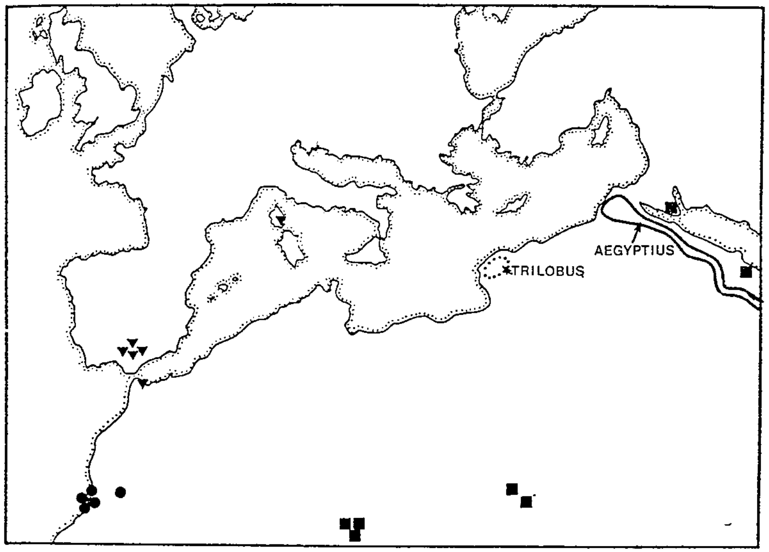

FIG. 6. Distribution of ● *S. massaicus*, ■ *S. hoggariensis*, ▼ *S. petraeus*, *S. aegyptius* (continuous line) and *S. trilobus* (dotted line).

16. 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, 4–5·5 × 1–1·5 mm. The capitula are narrowly cylindrical, phyllaries 6–8 mm. The leaves are more broadly and closely lobed than in subsp. *coronopifolius*.
2n = 60, voucher: C 11756 (E), cultivated material of *Danin* s.n. from Sinai.
Fl. 3 and "spring". Montane sandy river beds and fallow fields. 1400–2500 m.
Type: Algeria, Laperrine, Hoggar Mts, *Battendier* s.n. (iso. MPU).
ALGERIA. Hoggar Mts: Tamanrasset, 9 iii 1933, *Maire* s.n. (MPU); Hassi Dehine, *Hunting Services* 48(U2) (E).
SINAI. Gebel Qasar Abbas Pasha (nr. G. Katharina), 24 iii 1968, *Danin* s.n. (E, HUJ).
Distribution: S Algeria (Hoggar Mts), N Chad (Tibesti Mts), SE Egypt (G. Elba), Sinai (G. Katharina). (Fig. 6).

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 no stainable pollen.

17. 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 it in having larger glaucous capitula with phyllaries (6–)7–10 mm, ligules 13–15, more than 10 mm long, 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, voucher: C 11742 (E), cultivated material of *Allen* 7106 from Spain.
Fl. 3–5. Limestone mts. Spain.
Described from Grazalema, Spain, vi 1849, *Boissier & Reuter* s.n., *n.v.*
SARDINIA. Giovannibono, San Vito, 20 iv 1872, *Sommier* s.n. (FI).
SPAIN. Grazalema, *Gibbs et al.* 69.1535 (E).
MOROCCO. Ceuta, *Gandoger* 78, *n.v.*
Distribution: Usually described as endemic to S Spain (Fig. 6).

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.

18. S. sylvaticus L., Sp. Pl. 2:868 (1753).
Differs from *S. nebrodensis* (p. 393) in being an annual with small oblong capitula. Phyllaries 5–7 mm. Ligules 2–3·5 mm. Achenes strigulose. Slightly glandular, at least in the inflorescence, not viscid. Leaves green.
2n = 40 (Fernandes and Queiros, 1971).
Described from Europe. Hb. Linn. 966.21
Distribution: N and C Europe, Balkan Peninsula.

19. S. viscosus L., Sp. Pl. 2:868 (1753).
Syn.: *S. calverti* Boiss., Diagn. ser. 2(3):32 (1856).
S. tymphresteus Boiss. & Heldr., Diagn. ser. 2(6):99 (1859).
Differs from *S. nebrodensis* (p. 393) in being an annual or biennial with oblong capitula. Phyllaries 7–10 mm. Ligules less than 5 mm. Achenes glabrous. Viscid in all parts. Leaves green.
2n = 40 (Majovsky et al., 1970).
Described from Europe. Hb. Linn. 966.19
Distribution: widespread throughout Europe, eastwards to Turkey and C Russia.

20. 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 *S. nebrodensis* (p. 393) in being an annual with oblong capitula. Leaves unlobed, sinuate or sometimes pinnatifid, brownish-green, often purple below. Phyllaries 8–10 mm. Ligules 1–1·5 mm. Achenes strigulose.
2n = 40 (Fernandes and Queiros, 1971).
Described from Spain. Hb. Linn. 996.14
Distribution: W and C Mediterranean.

21. 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, 3–4 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, 1–2 mm. Achenes 1·5–2 mm, cylindrical, sparsely strigulose. Pappus hairs c. 2 mm.
2n = 40, voucher: C11752 (E), cultivated material from Egypt.
Fl. 12–3. Banks of R. Nile and associated waterways; desert oases. (Fig. 6).

1a. Ray flowers present . . . . . . i. var. *aegyptius*
1b. Ray flowers absent . . . . . . ii. var. *discoideus*

i. var. **aegyptius**
Syn.: *S. triflorus* L., Sp. Pl. 2:867 (1753).
Type. Habitat in Aegypt. Hb. Linn. 996.13
EGYPT. Giza, *Davis* 8232 (E); Asswan, *Davis* 6048B (E); Abu-Zabel, i 1835, *Schimper*, s.n. (E).
Distribution: Egypt and Sudan. Also recorded from Cyprus and Port-Juvenal, nr Montpellier, France.

ii. var. **discoideus** Boiss., Fl. Or. 3:388 (1875).
Syn.: *S. arabicus* L., Mant. 114 (1767).
S. verbenaefolius Jacq., Hort. Vindob. 1:2, t. 3 (1770).
S. aegyptius var. *verbenaefolius* (Jacq.) Boiss., Fl. Or. 3:386 (1875).
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).
Distribution: as for var. *aegyptius*.
Differs from var. *aegyptius* only in the absence of ligules.

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*, which is diploid. Crosses with other tetraploids gave poor seed or plants that failed to produce pollen.

22. S. belbeysius Del., Fl. Eg. III. 126, t. 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. Täckholm (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.

23. S. flavus (Decne.) Sch. Bip. in Webb & Berth., Phyt. Canar. 2:319 (1845).
Syn.: *Crassocephalum flavum* Decne. in Ann. Sci. Nat. sér. 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 2–5 × 0·7–3 cm. Capitula cylindrical in lax or dense corymbs. Calyculus of 1–5 bracts, often absent. Phyllaries c. 13, 6–9 mm. Ligules usually absent, sometimes c. 13, 1·5 mm, purplish or dull yellow with reddish veins on abaxial surface. Achenes 2–3 mm, subcylindrical, lanate. Pappus hairs c. 4 mm.
2n = 20, voucher: C11748 (E), cultivated material from Israel.
Fl. 3–5. Deserts and dry rocky and gravelly places. c. 1000 m.
Described from Sinai: "Hab: le desert du Sinai".
ALGERIA. Metlili, 11–14 v 1853, *Cosson* s.n. (E).
EGYPT. Dchebel Ataka, *Bornmüller* 10703 (E).
MOROCCO. Tafraoute, *Davis* 53853 (E).
JORDAN. El Inab, *Hunting Survey* 73b (E).
Distribution: Canary Is, N Africa, Arabia, Israel.

A distinct species morphologically. Poorly developed seed resulted from using *S. flavus* in crosses with other species at 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.

24. 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 4–6 × 2–4 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 × 1·5 mm, abruptly narrowing into a stalk, apical half black. Phyllaries 5–8 mm, glabrous, tips black in form of an inverted "V", Ligules 13–21, yellow, 6–8 × 2–3·5 mm. Achenes strigulose 2·0–3·0 mm. Pappus hairs c. 4·5 mm.
Fl. 3–5. Limestone mountains at about 1000 m.
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. (Fig. 6).

Unique among the species examined in having lacerate calyculus bracts (Fig. 4). 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 of origin. According to W. T. Stearn (in litt.), it is quite possible that Linnaeus could have obtained specimens from Cyrenaica, though no reference to this has been found. It is strange that all specimens examined had previously 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.

Judging 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.

25. S. delphinifolius Vahl, Symb. Bot. 2:91 (1971).

Erect annual, 20–60 cm, branching only in inflorescence, stems leafy. Corymbs dense, flat-topped. Calyculus of 6–10 bracts. Phyllaries c. 21, sparsely strigose.
2n = 40 (Afzelius, 1949).
Described from Tunisia: "Habitat passim in agris Tunetanis".
Distribution: Italy, Sicily, Sardinia, Algeria and Morocco.

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

Subacaulous and scapose annual, or erect and branching from the base, 5–25 cm. Capitula solitary or in loose corymbs. Calyculus absent. Phyllaries c. 13, sericeous.

Described from Spain based on several syntypes, microfiche seen.

Distribution: C & S Spain, Morocco.

INDEX OF TAXA

Accepted names are in Roman, synonyms in italics. An asterisk indicates a species probably not closely related to the pinnatifid annuals and thus not treated in this account.

ACKNOWLEDGMENTS

I would like to thank my supervisors, Dr P. H. Davis and Dr P. M. Smith of Edinburgh University Botany Department for advice and encouragement; Dr Davis also provided numerous accessions of seed collected in the field. This research would not have been possible without use of the herbarium, library and glasshouse space kindly provided by the Regius Keeper of the Royal Botanic Garden, Edinburgh, Mr D. M. Henderson. Many members of his staff have given help and advice. Seeds were kindly provided by many individuals. The Directors of the following herbaria lent specimens: BM, FI, HUJ, K, MPU, RAB. Field Work in Morocco was made possible by a grant from the Weir Fund of Edinburgh University.

REFERENCES

AFZELIUS, K. (1924). Embryologische und zytologische Studien in Senecio und verwandten Gattungen. *Acta Horti Berg.* 8:123–219.

——(1949). On chromosome numbers in Senecio and some allied genera. *Ibid.* 15:65–77.

——(1967). Chromosome numbers in some Senecioneae. *Svensk. Bot. Tidskr.* 61:1–9.

ALEXANDER, J. C. M. (1975). *Experimental Taxonomy in some annual species of Senecio from the Mediterranean area.* Ph.D. thesis, University of Edinburgh.

ALI, S. I. (1964a). Senecio lautus complex in Australia I. Taxonomic considerations and discussion of some of the related taxa from New Zealand. *Austr. J. Bot.* 12:282–291.

——(1964b). *Op. cit.* II. Cultural studies of populations. *Ibid.* 12:292–316.

——(1966). *Op. cit.* III. The genetic system. *Ibid.* 14:317–327.

——(1968). *Op. cit.* IV. The biology of the complex. *Phyton* 13:53–62.

——(1969). *Op. cit.* V. Taxonomic interpretations. *Austr. J. Bot.* 17:161–176.

ARYAVAND, A. (1977) in LÖVE A. (Ed.). IOPB chromosome number reports LVII. *Taxon* 26:444.

BALL, J. (1878). Spicil. Florae Maroc. *J. Linn. Soc. Bot.* 16:281–742.

BENOIT, P. M., CRISP, P. C. & JONES, B. M. G. (1975) in STACE, C. A. (Ed.). *Hybridisation and the flora of the British Isles.* London.

BOISSIER, P. E. (1849). *Diagnoses Plantarum Orientalium Novarum*, ser. 1(11).

——(1875). *Flora Orientalis* 3:385–392.

——(1888). *Flora Orientalis Supplementum* 301–302.

CANDOLLE, A. P. de (1838). *Prodromus Systematis Naturalis Regni Vegetabilis* 6:341–351.

CAVE, M. S. (1959–65). *Index to plant chromosome numbers*, 1 & 2. Univ. N. Carol. Press.

CHATER, A. O. & WALTERS, S. M. (1976) in TUTIN, T. G. et al. (Ed.). *Flora Europaea.* 4:191–205. Cambridge.

CLARKE, C. B. (1876). *Compositae Indicae.* Calcutta.

CRISP, P. & JONES, B. M. G. (1970). Senecio squalidus L., S. vulgaris L. and S. cambrensis Rosser. *Watsonia* 8:47–48.

——(1978). Hybridisation of Senecio squalidus and S. viscosus and introgression of genes from diploid into tetraploid Senecio species. *Ann. Bot.* 42:937.

DELILE, A. R. (1814). *Florae Aegyptiacae Illustratis.* Paris.

DUMORTIER, B. C. J. (1827). *Florula Belgica.* Tornaci Nerviorum.

DYER, A. F. (1963). The use of lacto-propionic orcein in rapid methods for chromosome preparation. *Stain. Tech.* 38:85–90.

ELLIS, E. A. (1944). Senecio x baxteri Druce. *Trans. Norf. Norw. Nat. Soc.* 15:424–425.

EMBERGER, L. & MAIRE, R. (1927). Spicilegium rifanum. *Mém. Soc. Sci. Nat. Maroc.* 17:1–58.

FEDEROV, A. (1969). *Chromosome numbers of flowering plants.* Leningrad.

FERNANDES, A. & QUEIROS, M. (1971). Contribution à la connaissance cytotaxonomique des Spermatophyta du Portugal, II. Compositae. *Bol. Soc. Brot.* 45:5–122.

FIORI, A. & PAOLETTI, G. (1903). *Flora Analitica d'Italia.* Padua.

FRITSCH, R. M. (1973) in LÖVE, A. (Ed.). IOPB chromosome number reports XLI. *Taxon* 22:461.

GIBBS, P. E. (1971). Studies on synthetic hybrids of British species of Senecio, I. S. viscosus L. x S. vulgaris L. *Trans. Bot. Soc. Edinb.* 41:213–218.

——, MILNE, C. & VARGAS CARRILLO, M. (1975). Correlation between the breeding system and recombination index in five species of Senecio. *New Phytol.* 75:619–626.

GRANT, V. (1958). The regulation of recombination in plants. *Symposia on Quantitative Biology* 23:337–363.

——(1967). Linkage between morphology and viability in plant species. *Amer. Nat.* 101:125–139.

HOFFMANN, O. (1894). Compositae in ENGLER & PRANTL, *Die Natürlichen Pflanzenfamilien* 4(5):87–391.

HULL, P. (1974a). Self-fertilisation and the distribution of the radiate form of Senecio vulgaris in Central Scotland. *Watsonia* 10:69–75.

——(1974b). Differences in esterase distribution detected by electrophoresis as evidence of continuing interspecific hybridisation in the genus Senecio. *Ann. Bot.* 38:697–700.

——(1975). Selection and hybridisation as possible causes of changes in the frequency of alleles controlling capitulum type in Senecio vulgaris L. *Watsonia* 10:395–402.

INGRAM, R. (1977). Synthesis of the hybrid Senecio squalidus L. x S. vulgaris L. f. radiatus Hegi. *Heredity* 39:171–173.

——(1978). The genomic relationship of Senecio squalidus L. and S. vulgaris L. and the significance of genomic balance in their hybrid S. x baxteri Druce. *Ibid.* 40:459–462.

International Code of Botanical Nomenclature, (1978). *Regnum Vegetabile*, 97. Utrecht.

JAHANDIEZ, E. & MAIRE, R. (1934). *Catalogue des Plantes du Maroc* 3. Algiers.

KOMAROV, V. L. (1961). *Flora URSS* 26. Moscow & Leningrad.

KUZMANOV, B. A. & KOZUHAROV, S. I. (1970) in LÖVE, A. (Ed.). IOPB chromosome number reports XXVI. *Taxon* 19:264–269.

LEDEBOUR, C. F. von (1833). *Flora Altaica.* Berlin.

LINNAEUS, C. (1753). *Species Plantarum.* Stockholm.

LÖVE, A. (Ed.). (1972–78). IOPB chromosome number reports 35–61. *Taxon* 21–27.

MAJOVSKY, J. et al. (1970). Index of chromosome numbers of Slovakian flora, part 2. *Act. Fac. Rerum. Nat. Univ. Comen. Bot.* 18:45–60.

MATTHEWS, V. A. (1975) in DAVIS, P. H. (Ed.). *Flora of Turkey and East Aegean Islands* 5:145–168. Edinburgh.

MEHRA, P. N. & REMANANDAN, P. (1969) in LÖVE, A. (Ed.). IOPB chromosome number reports XXII. *Taxon* 18:437–439.

MOORE, R. J. (1965–1977). Index to plant chromosome numbers. *Regnum Vegetabile* 50, 55, 90, 96, IAPT.

NORDENSTAM, B. (1972). Chromosome numbers in some Compositae from Egypt. *Bot. Not.* 125:393–396.

——(1977) in HEYWOOD, V. H., HARBORNE, J. B. & TURNER, B. L. (Eds.). *The Biology & Chemistry of the Compositae.* New York.

ORNDUFF, R. (1960). An interpretation of the Senecio lautus complex in New Zealand. *Trans. Roy. Soc. NZ.* 88:63–77.

——(1962). Inter-subspecific hybridisations in Senecio glaucophyllus. *Trans. Roy. Soc. NZ Bot.* 1:225–229.

——(1964). Evolutionary pathways of the Senecio lautus alliance in New Zealand and Australia. *Evolution* 18:349–360.

——, RAVEN, P., KYHOS, D. & KRUCKEBERG, A. (1963). Chromosome numbers in Compositae III. Senecioneae. *Amer. J. Bot.* 50:131–139.

Palmblad, I. G. (1965). Chromosome numbers in Senecio, I. *Can. J. Bot.* 43:715–721.

Rosser, E. (1955). A new British species of Senecio. *Watsonia* 3:228–232.

Richards, A. J. (1975). The inheritance and behaviour of the rayed gene complex in Senecio vulgaris. *Heredity* 34:95–104.

Stebbins, G. L. (1975). Self-fertilisation and population variability in the higher plants. *Amer. Nat.* 91:337–354.

Tackholm, V. (1974). *Students' Flora of Egypt*, 2nd ed. Cairo.

Tischler, G. (1934). Die Bedeutungen der Polyploidie für die Verbreitung der Angiospermen, erläutert an den Arten Schleswig-Holsteins, mit Ausblicken auf andere Florengebiete. *Bot. Jahrb.* 67:1–36.

Trow, A. H. (1912). On the inheritance of certain characters in the common groundsel and its segregates. *J. Genet.* 2:239–276.

Turner, B. L. & Lewis, W. H. (1965). Chromosome numbers in the Compositae, IX. African species. *J. S. Afr. Bot.* 31:207–217.

Vachova, M. & Ferakova, V. (1978) in Löve, A. (Ed.). IOPB chromosome number reports LXI. *Taxon* 27:383.

Villars, M. (1786–1789). *Histoire des Plantes de Dauphine.* Grenoble, Lyon & Paris.

Walters, S. M. (1964). Senecio rupestris Waldst. & Kit. and S. squalidus L. *Proc. Bot. Soc. Brit. Is.* 5:382.

Willdenow, C. L. (1803). *Species Plantarum*, ed. 4, vol. 3(3).

Appendix: experimental 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 in this way by Gibbs produced a few achenes, though the average was only three to four achenes per capitulum.

During this investigation, it was necessary to determine 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 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. 7). However, this operation will damage the stigmas of the older flowers and leave some pollen in the younger flowers; but these unsatisfactory flowers can be removed from the capitulum with forceps. The blades of most fine forceps are too wide for this operation, but a pair with 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. Other workers in the Compositae have emasculated capitula by removing all the hermaphrodite disc flowers, leaving only the female ray flowers. In *Senecio*, I found this method unsatisfactory as very few achenes developed. Possibily 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 of *Chrysanthemum* spp. are covered with typewriting correction fluid which sets sufficiently firmly to prevent the disc flowers from opening until the ray flowers have been fertilised.

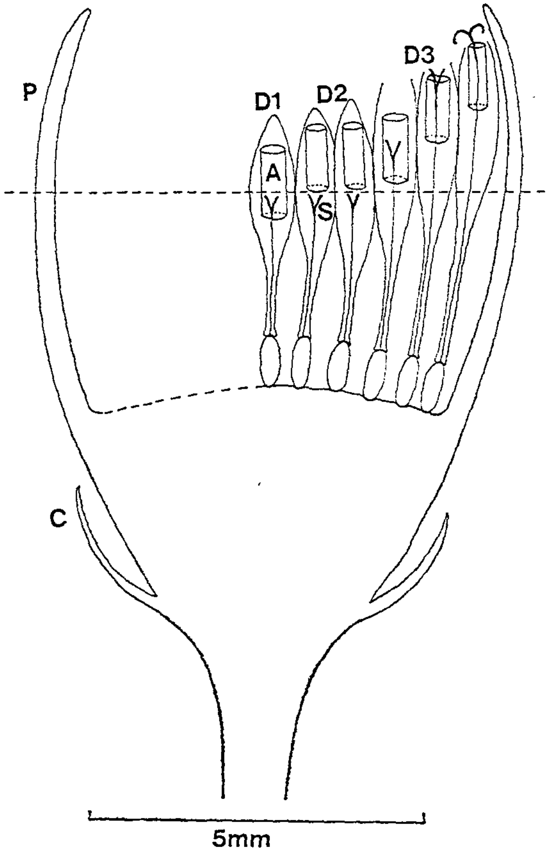

Fig. 7. Diagrammatic longitudinal section through discoid capitulum. A, anther tube; C, calyculus bract; D1, youngest disc flower; D2, disc flowers shortly before opening; D3, open disc flowers; P, phyllary; S, stigma. Pappus hairs and filaments omitted. Cutting at level indicated emasculates flowers D2 without damaging the stigmas.

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 fresh 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. Manilla 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. 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 and, if accidentally moistened 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 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.

Book Review

Tropical trees and forests. If any biologist did not read Hallé and Oldeman's work on the architecture and dynamics of growth of tropical trees or Oldeman's essay on the architecture of the Guianan forest, they now have no excuse (barring poverty, or, less probably, the inaccessibility of a library). *Tropical trees and forests**, subtitled *an architectural analysis*, is, however, more than these two books combined, and includes examples from temperate species and forests which suggest the wider application of the ideas discussed. Some points raised are treated in more detail in the recent *Tropical trees as living systems*, edited by P. B. Tomlinson & M. H. Zimmermann, which is also recommended reading.

The first two chapters include discussion of features like orthotropy, modular construction, etc., many of which are later used to characterize models. It is rightly emphasized that little is known about these characters, especially in tropical plants, and that this makes definitions difficult. Some of the many problems suggested need little more than patience and careful observation to solve, but it is a sad commentary on our knowledge that such basic questions can still be asked.

The next section deals with inherited tree architecture, "the visible, morphological expression of the genetic blueprint of a tree at any one time" (p. 74: elsewhere no time restriction is mentioned). This is done by describing models, "the growth programme that determines the successive architectural phases" (p. 75). The authors state that organizational diversity is greatest in the tropics, yet is not a continuum, and is less likely to be disturbed by exogenous, environmental factors in the understorey of the forest, and so is more accessible to the observer. The models are keyed out and described in detail; a section on the "strategy" of the model is usually added. The final sections of this part deal with vines, the connection between the architecture of trees and that of herbs, and fossil trees. The temptation to name new models has largely been resisted, although the variation within models like those of Troll and Tomlinson, and even Stone and Schoute, seem to be in characteristics that elsewhere define separate models.

The chapter on opportunistic architecture centres on reiteration, the modification of the tree's architecture not inherent in the definition of the model which results from environmental stimuli. This is important, since the shape of many mature trees is the result of reiteration superimposed on the basic architecture. Energetics and other aspects of the shape and size of crown and trunk are mentioned. The section on "strategy" treats a tree as a population of meristems. Trees of the future, present and past are defined and discussed. Although the tree is considered more from the point of view of its physiognomy and throughout its life cycle, the last section, curiously titled "a note on floristics", adopts a less flexible attitude.

The analysis of forest architecture begins with undisturbed forest, which is treated as horizontal sets of trees of the present (abundantly reiterated trees); the gradients of light, meristems, and humidity through the canopy are described. Discussion of the colonisation of gaps emphasises gaps of rather large size; colonisation proceeds through a series of homeostatic phases, each characterised by a set of trees of the present.

This outline does no justice to the diversity of topics covered. One can no longer consider a tree as a trunk, bundle of branches, and a rather larger bundle of twigs; as the authors happily put it, clouds of leaves, flowers and fruits, etc., do not hang in the air, but are parts of an organism. By examining the plant throughout its growth, they have clarified the action of some of the basic growth processes and shown that the way to understand pattern is through an appreciation of the process that produces it.

However, certain aspects of the argument, or lack of it, seem unsatisfactory, especially those concerning model delimitation and recognition, and these also affect other parts of the book. One can ask how the idea of tree growth conforming to a limited number of models might help us. Do models communicate the characters used to describe them? Do they show correlations with ecological or taxonomic patterns? Can concepts of tree architecture satisfactorily be integrated with ideas of forest growth?

To a considerable extent, of course, the answer to the first question determines the answers to the others, and I have had problems teaching tree architecture due to a number of interrelated reasons. The definitions of the characteristics used to recognize models are unsatisfactory and in some cases simply do not work; the problem is increased by

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* Tropical trees and forests by F. Hallé, R. A. A. Oldeman and P. B. Tomlinson. Springer-Verlag, Berlin, Heidelberg, and New York. 1978. xvii + 441 pages. $65.00 U.S.