Drawings of Scandinavian Plants 17–20

Rubus L. Subgen. Rubus

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INTRODUCTION

The genus *Rubus* is cosmopolitan, occurring on all five continents, while the subgenus *Rubus* occurs mainly in Europe and in North and South America (Fig. 1). This subgenus is represented in Europe by section *Rubus,* which was divided into six subsections by FOCKE (1914), of which *Suberecti, Senticosi, Glandulosi,* and *Caesii* occur in Europe. The last named is represented by *Rubus caesius* L. and the *Corylifolii* group. Owing to the presence of apomixis within section *Rubus,* this group is taxonomically one of the most difficult among the phanerogams. The number of named European blackberries was estimated to be 3000 by FOCKE (1914 p. 6).

All four European subsections are represented in Scandinavia. HYLANDER (1955) recognized 47 species, 14 varieties, 1 form, and 2 hybrids as members of subsections *Suberecti, Senticosi,* and *Glandulosi,* and 1 variety and 2 hybrids under *Rubus caesius,* and 30 species and 22 varieties as belonging to the *Corylifolii* group.

My own experience in the identification of blackberries is based on a frequency mapping in southern Sweden between 1959 and 1963, and on studies of Swedish collections in the botanical museums (herbaria) of Gothenburg, Lund, Stockholm, and Uppsala. As to the three first-mentioned subsections above, I have found the division into species by HYLANDER quite useful in Sweden; on the other hand, the *Corylifolii* group has had to be treated as a unit. It is probably not a mere coincidence that of the species HYLANDER has listed for Scandinavia as belonging to the *Corylifolii* group, nine-tenths of these have Scandinavian auctors, while this is the case for only one-fourth of the other blackberries. The Scandinavian contribution to the nomenclatural confusion within *Rubus* subgen. *Rubus* in Europe is restricted mainly to the *Corylifolii* group.

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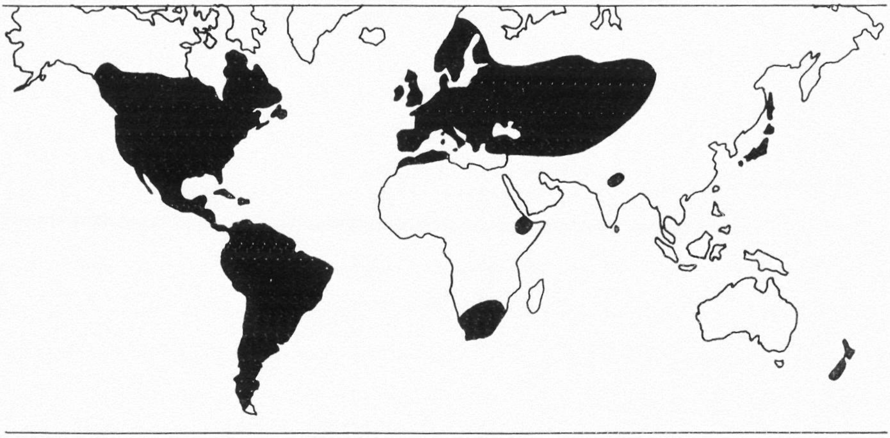


Fig. 1. World distribution of *Rubus* L. subgen. *Rubus*. After EICHWALD (1959 p. 25).

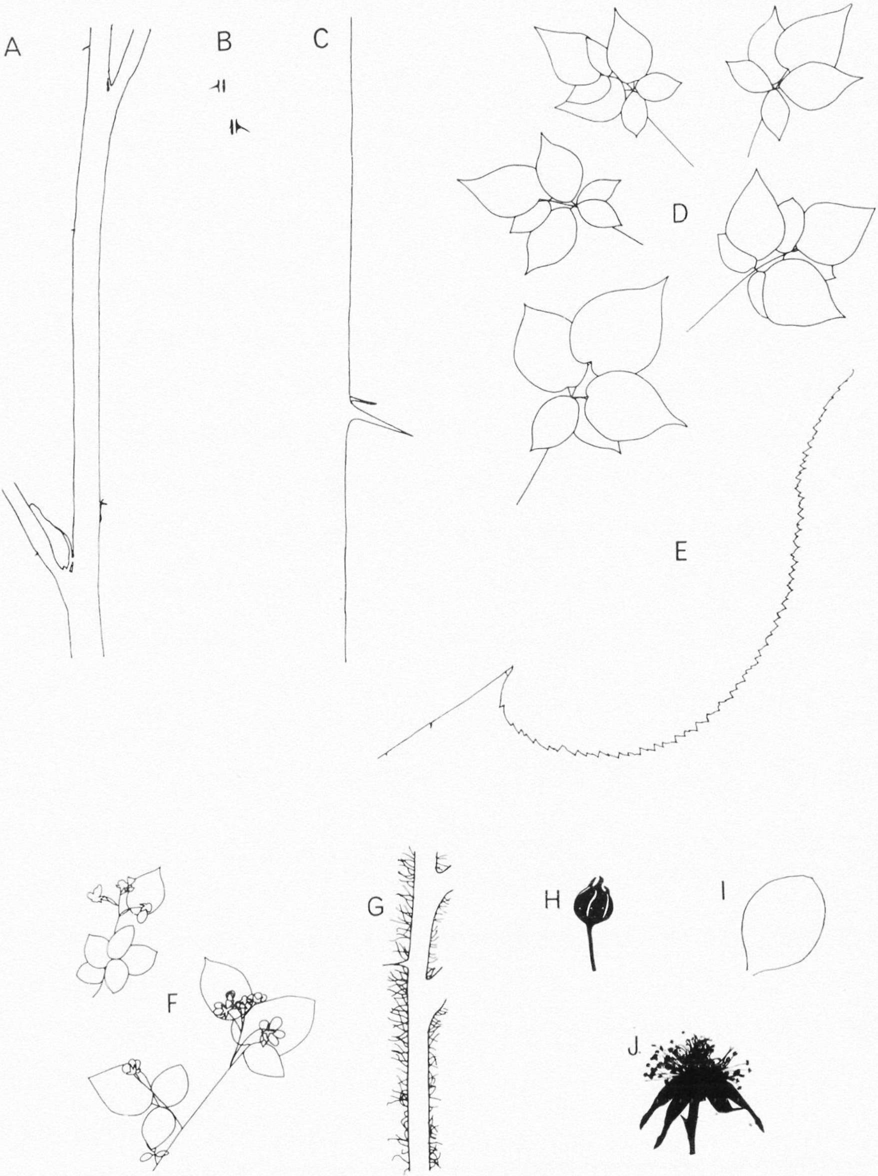
PURPOSE AND METHOD

This contribution to "Drawings of Scandinavian Plants" is not intended to give an exhaustive description of each selected taxon, but rather to show characteristic differences between taxa in order to facilitate the examination of blackberries both in the field and in the herbarium. The plate and the first part of the text depicts and presents the characters within a fixed order recurring for each selected taxon, while the remainder of the text deals with typical characters useful within smaller groups of taxa, noting, for example, varieties and briefer distributions. The drawings are copies of dried specimens made either directly, as from leaves (D) and inflorescences (F), or by means of a photographic enlarger. The drawings are exclusively silhouettes, except for the floral buds (H) on which the degree of hairiness has been indicated by free hand. Some characters that are illustrated are not described in the text; for example, the serration of the terminal leaflet.

GENERAL LEGEND FOR THE PLATES

First-year growth (*primocane*): A. Stem with prickles. 1 : 1. — B. Prickles, drawn from the side and from above. 1 : 1. — C. Stem with prickles, glands, and hairs. 4 : 1. — D. Leaves (without serration and petiole diameter shown). 1 : 8. — E. Margin of a terminal leaflet with a petiolule. 1 : 2. — *Second-year growth* (*floricane*): F. Inflorescences (without prickles, serration of the leaves, and axis diameters shown). 1 : 8. — G. Rachis with prickles, glands, and hairs. 4 : 1. — H. Floral bud with prickles. 1 : 1. — I. Petal (without hairs). 1 : 1. — J. Flower (without petals, glands, and hairs). 1 : 1.

XVII



Pl. XVII. *Rubus nessensis* W. HALL. — Remark: E refers to a 5-foliolate leaf.

Rubus nessensis W. HALL 1794 var. **nessensis**

(*R. suberectus* G. ANDERSSON ex SM.)

Stem erect, glabrous; *prickles* 2—3 mm long, straight, slender, base less than 1 mm long, narrow; *leaves* 5 (7)-foliolate, glabrescent; *terminal leaflet* from a 5-foliolate leaf, cordate; *inflorescence* short, leafy, glands absent; *flowers* usually over 2.5 cm across; *sepals* green with a white-felted border, prickles absent; *petals* white, broadly obovate; *filaments* 5—6 mm long.

Normally, the stem is 1—1.5 m long with a curving tip, green, thick and terete; the prickles are sparse; the leaves are large, thin, and non-plicate; the fruit is deep red, watery, relatively small, tasting somewhat like a raspberry. *R. nessensis* often grows in boggy areas associated with forests. This species has the most inland and northern distribution of all the Scandinavian blackberries (63° N lat. in Norway and 61° N lat. in Sweden). Pl. XVII.

Rubus nessensis W. HALL var. **armatus** (NEUM.) C. E. GUST.

Differs markedly from the typical variety by its straight or slightly bent, 3—5 mm long *prickles* with a broad, conical, purplish-black base; but also in other respects, for instance, in *leaf* serration. This variety may be up to 2 m or more in height in bogs, but can also be of more normal size. It is rare compared to the typical variety, and does not seem to have a separate distribution. Variety *armatus* may be confused with *R. plicatus* or the blackberry noted as a variety of *R. scissus*. Pl. XVIII.

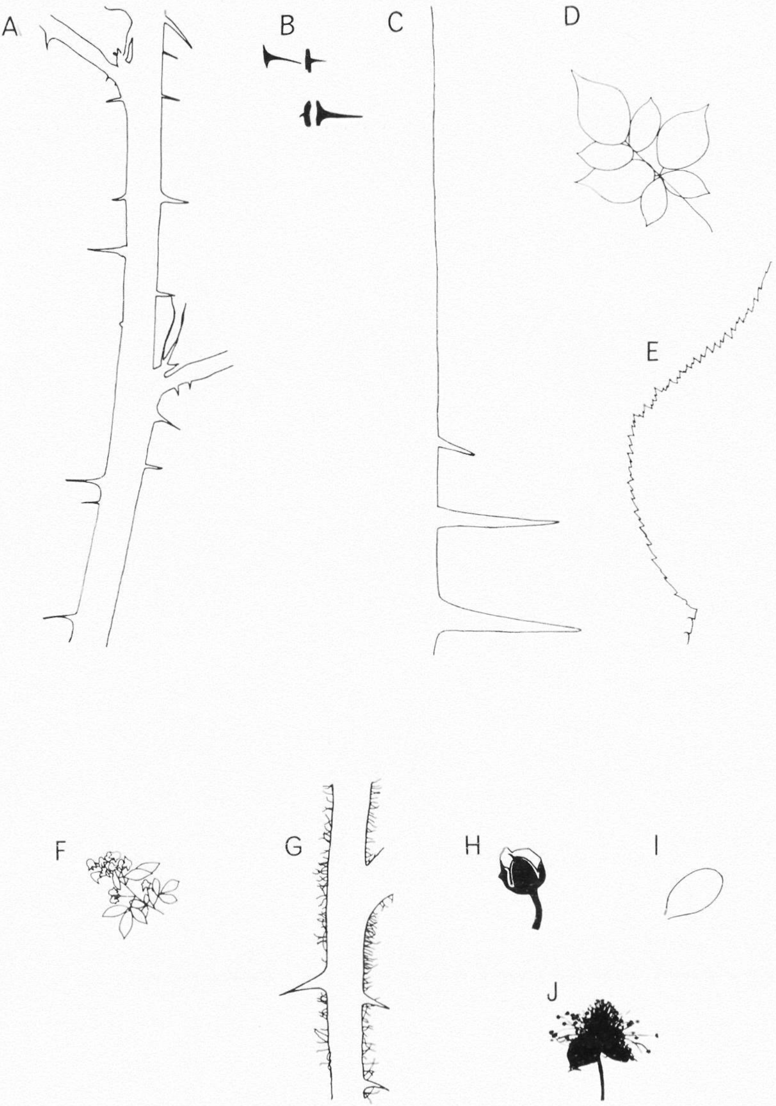
Rubus scissus W. C. R. WATSON 1937

(*R. fissus* auct. mult. non LINDLEY 1835)

Stem erect, glabrous; *prickles* numerous, 2.5—5 mm long, straight or slightly recurved, subulate, base 0.5—2 mm long, narrow; *leaves* 5—7-foliolate, densely pubescent below; *terminal leaflet* ovate; *inflorescence* short, leafy, glands absent; *flowers* less than 2 cm across; *sepals* green with a white-felted border, usually with some prickles; *petals* white, narrowly obovate; *filaments* 2—3 mm long.

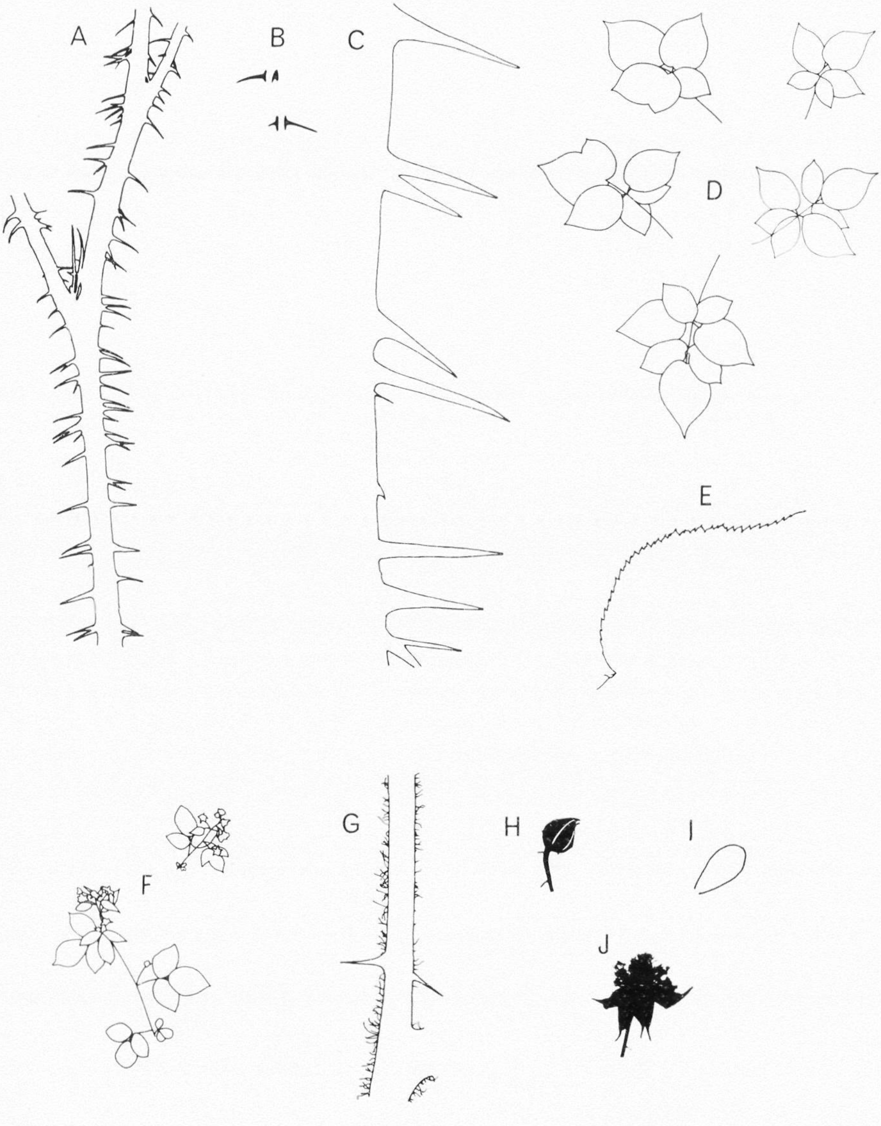
Normally, the stem is 0.5—1 m long, upright and arching, light brownish-red, with ca. 20 prickles per internode; the tips of the prickles are pale yellow; the leaves are plicate; the flowers are 4—10 in each inflorescence. *R. scissus* prefers poor soils. It is found in all three

XVIII



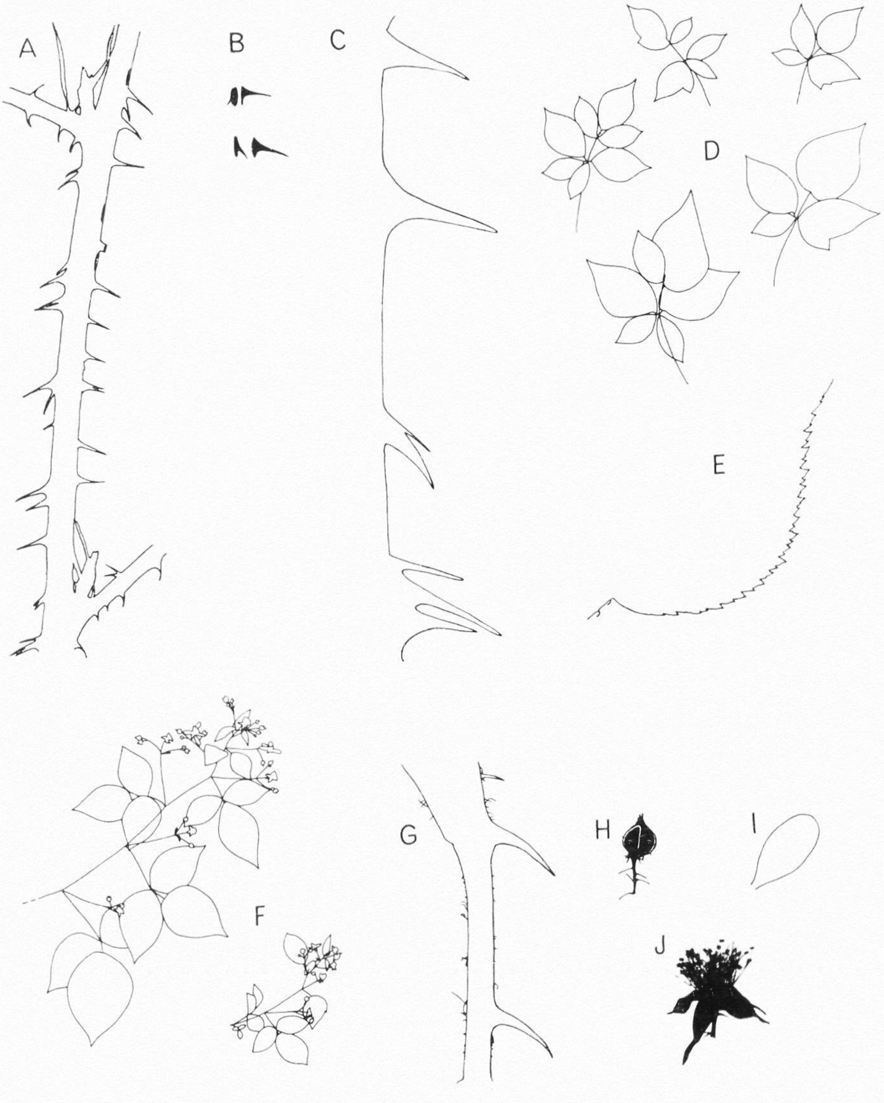
Pl. XVIII. *Rubus nessensis* W. Hall var. *armatus* (Neum.) C. E. Gust. — Remarks: The drawings all refer to a collection from Fjärås, Halland in SW Sweden. — D. Other collections also have leaves similar to the typical variety. — E refers to a 7-foliolate leaf. — I. Other collections have larger petals.

XIX



Pl. XIX. *Rubus scissus* W. C. R. Watson. — Remark: E refers to a 7-foliolate leaf.

XX



Pl. XX. A blackberry in southernmost Sweden (Åsljunga) that may be a variety of *Rubus scissus* W. WATSON. — Remarks: A. The three black spots at the top indicate lost prickles. — E refers to a 7-foliolate leaf. — F. The larger inflorescence type may be unusual. — J. Often the filaments are not so long.

Scandinavian countries, but in Norway and Sweden only within strictly limited areas in the south. Pl. XIX.

Within a restricted area with its center in Åsljunga, a village in southernmost Sweden, a blackberry occurs that may be a variety of *R. scissus*. It differs from this taxon in the following respects: The *stem* is usually 1—1.5 m long, branched, with a prolonged tip; the base of the *prickles* is 1—3 mm long, relatively broad, purplish-black; the *leaves* are often larger, the upper ones 3-foliolate; the *inflorescence* contains 6—20 flowers; the *flowers* are 2—2.5 cm across; the *petals* are broader; the *filaments* are 3—5 mm long. The geographical area of this blackberry is not overlapped by *R. scissus*, but this species occurs on two sides. This blackberry is also remindful of *R. nessensis*, especially its variety *armatus*. Pl. XX.

In the next paper, I shall deal with *R. sulcatus* VEST, *R. plicatus* W. & N., *R. nitidus* W. & N., and *R. affinis* W. & N.

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Variation in the Satellite Chromosomes of Nigella doerfleri (Ranunculaceae)

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ABSTRACT

Chromosome morphology in root-tip mitosis of thirteen *Nigella doerfleri* populations from different Aegean islands is described. Five pairs of nearly metacentric and one pair of nearly telocentric chromosomes were constantly found. Usually the telocentric pair and two of the metacentric pairs possess satellites. The secondary constrictions of the metacentric chromosomes vary in conspicuousness from one population to another. A maximum number of six nucleoli were found in all populations. Disappearance of the satellites on the telocentric chromosomes was recorded in one case. Instead, this population possessed another pair of metacentric satellite chromosomes. The possibility of a reciprocal interchange is considered.

In hybrids, the parental chromosome types were not changed under the influence of the new genotype.

Some of the literature on secondary constrictions and nucleolar organization is briefly reviewed.

INTRODUCTION

Secondary constrictions, that is, faintly staining regions other than the centromere, often are characteristic landmarks on individual chromosomes. They may vary in conspicuousness, and are not necessarily associated with the formation of nucleoli. Clearly visible secondary constrictions occupying a subterminal position usually arise in conjunction with nucleolus formation, whereas faint secondary constrictions in various positions along the chromosome may represent regions of differential spiralization or low DNA content (see Kaufmann 1948 pp. 68—74, Swanson 1965 pp. 131—134 for references). The term “satellite chromosome”, or “SAT-chromosome”, is generally applied when a distal portion of one arm is pinched off by a conspicuous secondary constriction.

Secondary constrictions that disclose the position of nucleolar organizers are usually constant structural components of particular chromosomes. Other secondary constrictions are less constant on the other hand, and may respond to factors in the cellular environment or the genetic make-up of the cell.

The number and morphology of satellite chromosomes are usually constant features of a particular individual or taxon. In certain cases, however, differences have been found between inbred lines (HENEEN 1962 a) or isolated populations (HENEEN & RUNEMARK 1962) of cross-fertilizing plants.

Alterations in chromosome morphology due to hybridization were reported by NAVASHIN (1934). Similar cases were investigated by HENEEN (1962 b, 1963). In the spontaneous hybrid *Elymus arenarius* × *Secale cereale,* enlargement of the rye chromosomes was observed, as well as disappearance of the nucleolar constriction of the rye complement. In certain *Nicotiana* hybrids individual chromosomes undergo enlargement that may be accompanied by changes in density and staining (MOAV, MOAV & ZOHARY 1968).

It may be assumed that the amount of change in chromosome morphology under influence of the hybrid genotype is a rough measure of the genetic diversity between the parental forms (REES 1961).

MATERIAL AND METHODS

Spontaneous material of the self-fertilizing annual *Nigella doerfleri* VIERH., a member of the family *Ranunculaceae,* was investigated. This species is endemic to the Greek islands; its total distribution is shown in Fig. 1. The Kikladhian islands and Kriti (Crete) are now rather well known floristically from the recent studies of H. RUNEMARK, W. GREUTER, and others.

Thirteen populations were studied in detail cytologically. The material was cultivated in the greenhouses of the Lund Botanical Garden. From a morphological point of view, *Nigella doerfleri* is a "rigid species", showing little variation.

The enlarged area of the map shows the Astipalaia area. The names Doma, Maltesana and Kounoupia indicate the origins of three populations whose chromosome morphologies were of particular interest. The investigated populations are indicated by arrows in Fig. 1. The numbers of the collections correspond to those below.

Material from the following collections was analysed cytologically (names of localities are in accordance with The Times Atlas and the Sea Charts of the British Admirality):

1. Kithnos: The small island of Piperi (SE Kithnos). Slopes facing N and NW, 160—180 m s.m. A. STRID, 30.6.1966.
2. Serifos: The small island of Serfopoula (NE Serifos), western part. Rocky slope facing N, 30—40 m s.m. A. STRID, 30.6.1966.

3. Serifos: The small island of Vous (NE Livadhy Bay, Serifos). Slope facing N, ca. 50 m s.m. A. STRID, 30.6.1966.
4. Folegandros: Ca. 0.5 km NW of the village of Karvostasi Bay, 10—40 m s.m. A. STRID, 6.7.1966.
5. Ios: Along a stonewall between fields, ca. 2 km N of the harbour of Ios, ca. 70 m s.m. A. STRID, 5.7.1966.
6. Skhoinousa (S Naxos): The small island of Agrilousa. Garigue on limestone. H. RUNEMARK & B. NORDENSTAM no. 15571, 9.6.1960.
7. Iraklia (S Naxos): The small island of Venetico, ca. 30 m s.m. Hard limestone. H. RUNEMARK & B. NORDENSTAM no. 15530, 9.6.1960.
8. Amorgos: Mt. Krikelas, 5—6 km NE Langada. Stony slope facing NW, garigue, 650—750 m s.m. R. v. BOTHMER, 4.8.1966.
9. Anafi: NW of the monastery of Kalamos. Garigue. H. RUNEMARK & B. NORDENSTAM no. 14967, 29.5.1960.
10. Kriti, Distr. Sitia: Ravine ca. 1 km N of Kato Zakros. Slope facing N, ca. 50 m s.m. A. STRID, 20.6.1966.
11. Astipalaia: The Doma peninsula (E of Panormos). Garigue. H. RUNEMARK & B. NORDENSTAM no. 15047, 30.5.1960.
12. Astipalaia: Between Maltesana and Vriseu Punda, 0—100 m s.m. Garigue. H. RUNEMARK & B. NORDENSTAM no. 13534, 11.5.1960.
13. Astipalaia: The small island of Kounoupia, southern part. Garigue. H. RUNEMARK & B. NORDENSTAM no. 15265, 1.6.1960.

Usually, about ten plants raised from each of the seed collections were studied. In most cases these plants were then self-fertilized for one to several generations to maintain a fresh seed reserve.

The cytological technique (staining with Feulgen, pectinase treatment, squash preparation) was described in a previous paper (STRID 1968). To determine the number of nucleoli, section preparations of root tips stained with crystal violet were employed. Voucher specimens, as well as seeds and slides, are deposited at the Institute of Systematic Botany, Lund.

OBSERVATIONS

The chromosome number 2n=12 was found in root tips of all 13 collections. Five pairs of chromosomes are 8—10 μ long and have median or nearly median centromeres. One pair, which is about 5 μ, has a nearly terminal centromere.

Three pairs of satellite chromosomes are generally found in the metaphase plates. They are indicated by *a*, *b*, and *d*, respectively, in Figs. 2—4.

Satellite chromosome *a*: The arm index is about 1.10. The short arm is divided in the approximate proportion 1:4 by a secondary constriction. The diameter of the satellite equals that of the chromosome arms. Thread-like connections between the short arm and the satellite are

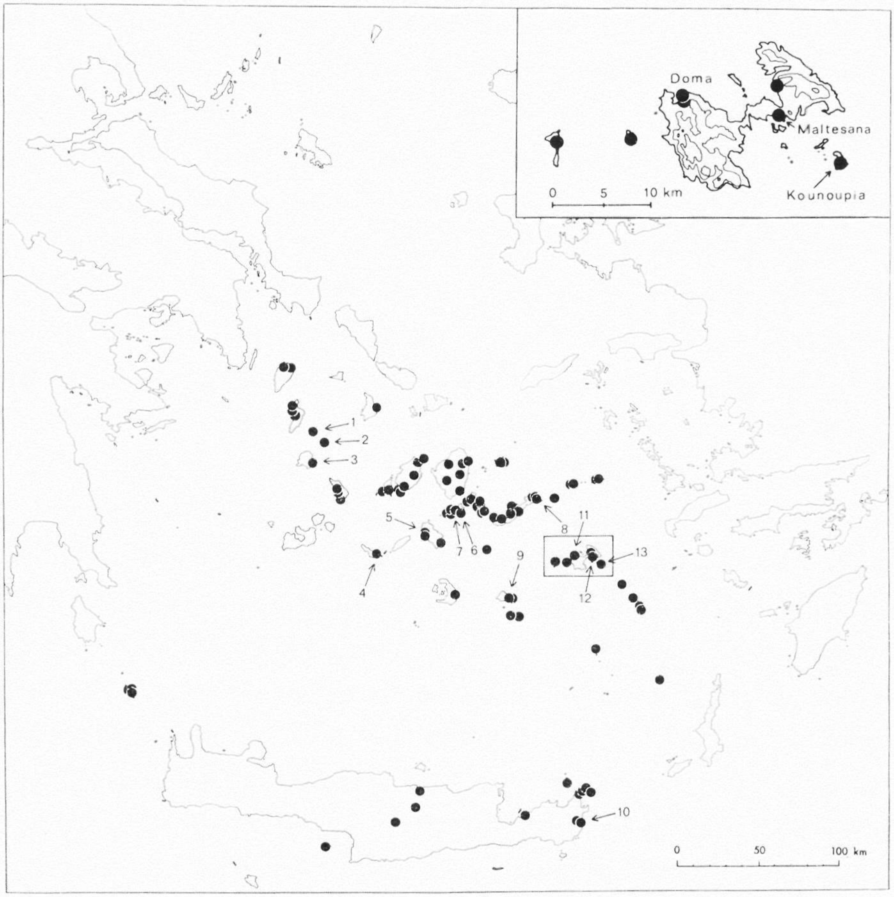

Fig. 1. Total distribution of *Nigella doerfleri* VIERH. — The numbers indicate populations that have been studied in detail cytologically. — Enlarged area: The island of Astipalaia and adjacent small islands (altitude lines indicate elevations of 500 and 1000 feet). The cytologically deviating populations — Doma, Maltesana, and Kounoupia — are indicated.

observed occasionally. In collections nos. 1, 2, 3, 9, and 13, the secondary constriction is usually less conspicuous, and may be invisible in much contracted metaphase chromosomes (*a′* in Fig. 2 C). Faint secondary constrictions are sometimes observed in the short arm, especially in prometaphase stages.

Satellite chromosome *b*: The arm index is about 1.10. The secondary constriction pinches off a short satellite with a slightly smaller diameter than the chromosome arms. Thread-like connections are usually absent. In collection no. 6 the secondary constriction is faint, and the satellite may be difficult to observe.

Satellite chromosome *d*: This is the small chromosome with a nearly terminal centromere. It is difficult to determine whether the faint knobs at the centromeric end of this chromosome represent a very short arm or are parts of the functional centromere. Although truly telocentric chromosomes (formed by misdivision) are known to occur in an exceptional population of *Nigella doerfleri* (STRID 1968), it seems probable in this case that a short arm is present. A small, but distinct, satellite is attached to the long arm. The secondary constriction is usually very conspicuous, and may vary in length, probably as a consequence of the squash technique. The satellite has a smaller diameter that the chromosome arm and is usually not as deeply stained.

Thus, with respect to the satellite chromosomes, the karyotypes of most *Nigella doerfleri* populations can be written *aa bb dd* (occasionally, *a′a′ bb dd* or *aa b′b′ dd* to indicate that certain secondary constrictions are less conspicuous).

A maximum number of six nucleoli were found in interphase nuclei, which agrees with the observations of PEREIRA (1942) in a number of other species of *Nigella*. Variation in size and number indicates occasional fusion of nucleoli, a phenomenon reported already by SOROKIN (1929). Presumably, the nucleoli are organized by the constricted regions of the six satellite chromosomes.

Populations from the Astipalaia area (see Fig. 1), especially coll. no. 11 (Doma), present interesting deviations from the usual pattern of satellite chromosomes. The karyotypes of three collections. — no. 11 (Doma), no. 12 (Maltesana), and no. 13 (Kounoupia) — are shown in Fig. 2 A—C.

Collection no. 11, from he Doma peninsula, is characterized by the absence of satellites on the nearly telocentric chromosomes. Instead, another pair of satellite chromosomes is present (indicated by *c* in Fig. 2 A). This chromosome has a nearly median centromere and a rather small satellite, which in good preparations appears to have a tandem-like structure. With respect to the satellite chromosomes, the karyotype can be written *aa bb cc*. A maximum number of six nucleoli were observed in interphase nuclei. It seems probable that the nucleolar-organizing function of chromosome *d* has been taken over by the new satellite chromosome.

Collection no. 12, from the vicinity of Maltesana, has only two pairs

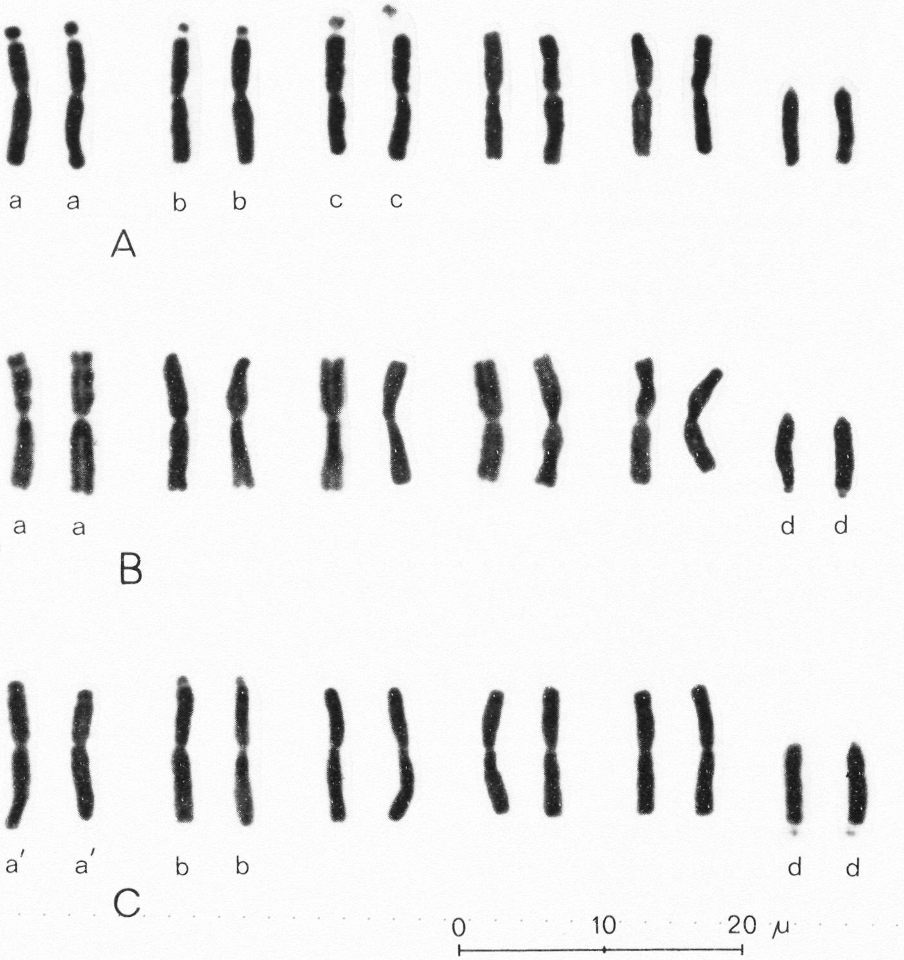

Fig. 2. Karyotypes (photomicrographs) of the three populations from the Astipalaia area. — A. Doma. — B. Maltesana. — C. Kounoupia. The different types of satellite chromosomes are designated by *a*, *b*, *c*, and *d*, respectively; *a′* signifies that the secondary constriction is faint, sometimes invisible in metaphase chromosomes.

of satellite chromosomes (*a* and *d*). The satellite of chromosome *b* has apparently fused with the short arm (Fig. 2 B). The nucleolar organizing function has probably remained intact, however, as no decrease in the maximum number of nucleoli could be observed.

Collection no. 13, from the small island of Kounoupia, agrees with collections nos. 1, 2, 3, and 9 in having one pair of indistinct satellites

Table 1. Mean percentages of stainable pollen in hybrids between *Nigella doerfleri* populations from the Astipalaia area.

♂ ♀	Doma (no. 11)	Maltesana (no. 12)	Kounoupia (no. 13)
Doma (no. 11)	—	95.5	97.9
Maltesana (no. 12)	98.3	—	98.0
Kounoupia (no. 13)	97.3	98.2	—

(*a′*) and two pairs of conspicuous ones (*b* and *d*). With respect to the number of nucleoli, it does not differ from the other collections.

In most cases the differences between populations are small, and might be attributed to minor variations in the coiling and staining properties of particular chromosome segments. Variation within populations was only occasionally observed, a fact that parallels the morphological homogeneity of the predominantly self-fertilized populations of this species.

Collections no. 11, from the peninsula of Doma, is distinctly different from all other collections studied. It would be tempting to postulate that the new, metacentric satellite chromosome (*c*) was formed by translocation of the satellite region of the nearly telocentric chromosome (*d*). When homozygous, the new chromosome arrangements would, of course, impart normal vitality and fertility to the plants.

In order to test the constancy of secondary constrictions in different gene environments, a number of crossings were performed. A full account of the crossing experiments in *Nigella doerfleri* and related species will be presented later. Table 1 gives the mean percentages of pollen stainable with cotton blue in crossings between the three populations from the Astipalaia area. Meiosis was studied in a few hybrid plants. Regular formation of six bivalents was found, as well as clean separation of anaphase groups. The fertility of the hybrids was confirmed by observations on their seed setting.

It is remarkable that all combinations have given perfectly fertile hybrids in spite of the morphological chromosomal differences described above.

Examination of root-tip mitosis indicated that the secondary constrictions of the parental chromosomes remained unchanged. Semi-diagrammatic drawings of metaphase plates from the three Astipalaia populations and their respective hybrids are shown in Fig. 3 A—F. Idiograms of the satellite chromosomes are depicted in Fig. 4 A—F.

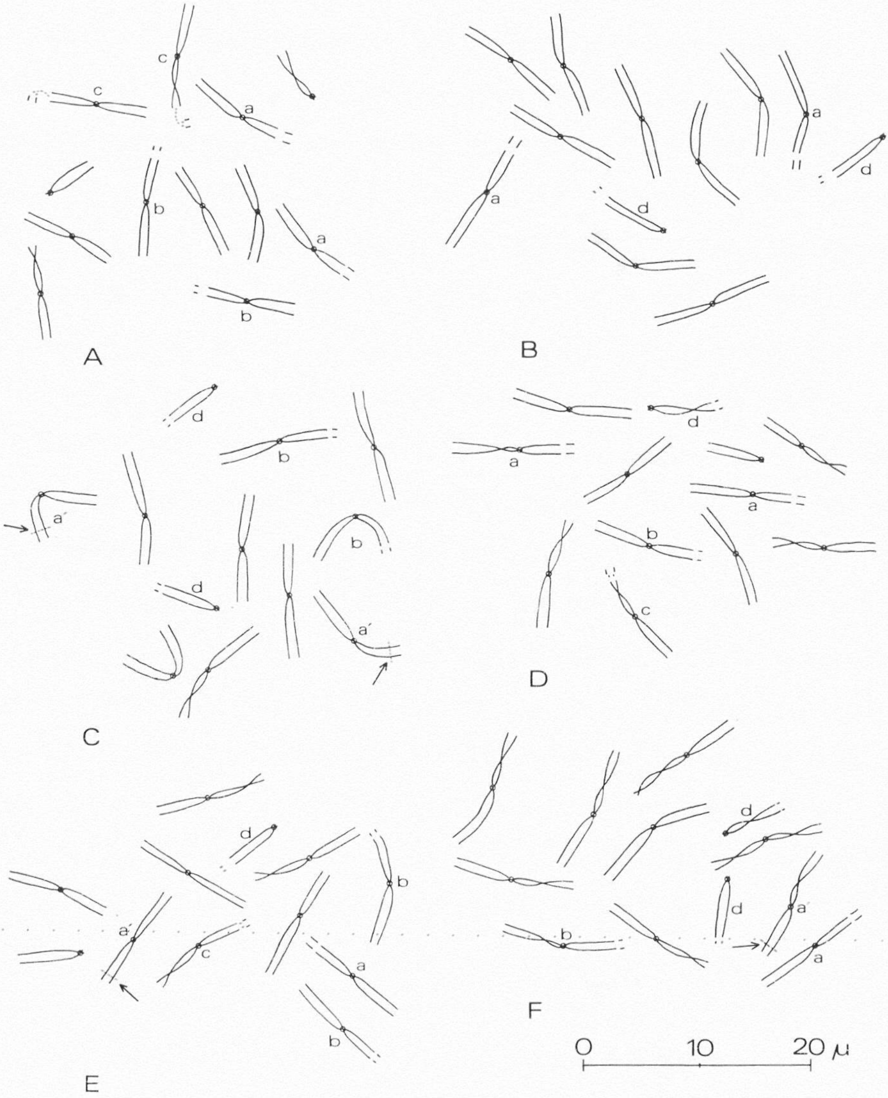

Fig. 3. Semi-diagrammatic drawings of metaphase plates of the three populations from the Astipalaia area and their respective hybrids (cf. Fig. 2). — A. Doma. B. Maltesana. — C. Kounoupia. — D. Doma×Maltesana. — E. Doma×Kounoupia. — noupia. — F. Maltesana×Kounoupia. — The arrows indicate faint secondary constrictions.

Fig. 4. Idiograms of the satellite chromosomes in the three populations from the Astipalaia area and their respective hybrids (cf. Figs. 2 and 3). — A. Doma. — B. Maltesana. — C. Kounoupia. — D. Doma×Maltesana. — E. Doma×Kounoupia. — F. Maltesana×Kounoupia.

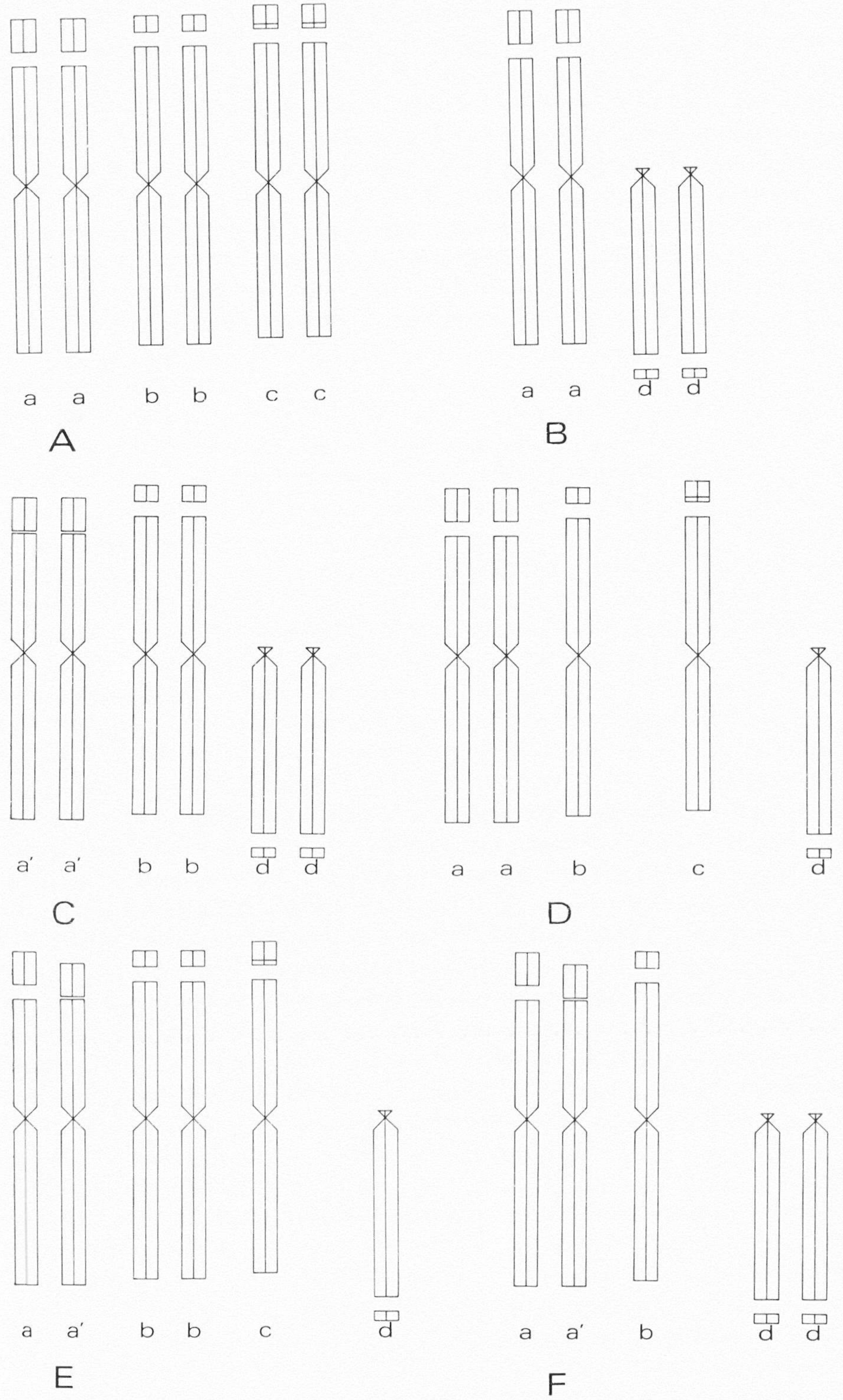

Fig. 4.

DISCUSSION

The six satellites normally present in the mitotic complement of *Nigella doerfleri* are presumably all related to the formation of nucleoli. A maximum number of six nucleoli is surprisingly high in a diploid. Usually, the number of secondary constrictions and nucleoli is more or less correlated with the degree of polyploidy (DE MOL 1928, HENEEN 1962 b).

The internal structure of nucleoli was studied by LA COUR (1966), who found that the nucleolar area is filled with nucleonemata, that is, filamentous, Feulgen-negative bodies originating as loops from the nucleolar chromosome. He suggested that nucleolus formation is a manifestation of specialized gene activity comparable to the formation of puffs in polytene chromosomes or loops in lampbrush chromosomes.

Different nucleolar organizers are probably functionally equivalent, but may differ in strength. It also appears that some organizers may suppress the function of others (NAVASHIN 1934). MCCLINTOCK (1934) found that the function of the nucleolar-organizing region remained intact after it had been broken into two unequal halves by X-rays. After breakage, two nucleoli of different size were produced.

RESENDE (1940) found that the nucleolar-organizing region is not always morphologically distinguishable from the rest of the chromosome. When no visibly contracted region is present, a distal segment of an ordinary chromosome acts as a nucleolar organizer. This agrees with the common observation that many species have no visible secondary constrictions but nevertheless possess nucleoli. In the present study a maximum number of six nucleoli were found regardless of the position and conspicuousness of the secondary constrictions.

Several investigators have shown that the morphology of chromosomes might be altered in interspecific hybrids under influence of the new genotype (see above). The fact that no changes in chromosome morphology were recorded in hybrids between different populations of *Nigella doerfleri* is not surprising, however, as the physiological conditions in cells of closely related populations must be very similar. The cytologically most deviating population (no. 11, Doma) is morphologically very similar to the rest of the cultivated material. In this case morphological differentiation of certain chromosomes is apparently not related to external morphological diversity and the formation of sterility barriers.

In the cytologically deviating population from the Doma peninsula (no. 11) it would be tempting to assume that the satellite region of the nearly telocentric chromosome (*d*) had been translocated to one of the metacentric chromosomes (*c*). However, hybrids between this population and others appeared to be fully fertile. Thus, if the above hypothesis is correct, the translocated segments must be very small with a negligible synaptic activity. Any other explanation would seem less tenable.

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Studies in the Genus Allium I

A New Species of Allium (Liliaceae) from Turkey

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ABSTRACT

A new species of *Allium*, sect. *Scorodon* C. Koch is described: *A. microspathum* Ekberg.

INTRODUCTION

In the collection of living *Allium* species being built up at the Gothenburg Botanical Garden, a plant of an unknown and undescribed species flowered in July 1968. The bulb had been obtained from Mr. J. M. Watson, England, who collected living bulbs in Turkey in 1967.

Allium microspathum Ekberg sp. nov. (Figs. 1, 2).

Sect. *Scorodon* C. Koch

Bulbus ovoideus, c. 12 mm diametro; tunicae exteriores ignotae. *Scapus* solitarius, 15 cm altus, 0.5 mm diametro, teres, usque ad 3/4 vel ultra foliorum vaginis laevibus tectus. *Folia* 4—5, 1.5 mm lata, semicylindrica, valde costata, scabrida; folia inferiora c. 6 cm longa, ante anthesin marcescentia, valde contorta; folium superius c. 3 mm longum. *Spatha* 2.5 mm longa, brunnescens, univalva, persistens. *Umbella* c. 25-flora, hemisphaerica; pedicelli aequales, c. 5 mm longi, bracteolati. *Perigonium* subglobosum; tepala extus fascia centrali brunnescenti-striata provisa, intus nitidula pallide viridia, 2.5—2.7 mm longa, c. 1 mm lata; exteriora elliptica nervo diffuso; interiora elliptico-oblonga, apice emarginato-truncata. *Filamenta* 4.5 mm longa, flava, per 1/5 longitudinis connata et perigonio adnata; filamenta exteriora integra, interiora utrinque prope medium circiter denticulo obtuso provisa; antherae 0.7 mm longae, flavae. *Ovarium* 3-sulcatum, foveolis nectariferis distinctis provisum. *Stylus* 2 mm longus, stigma integrum. *Capsula* ignota.

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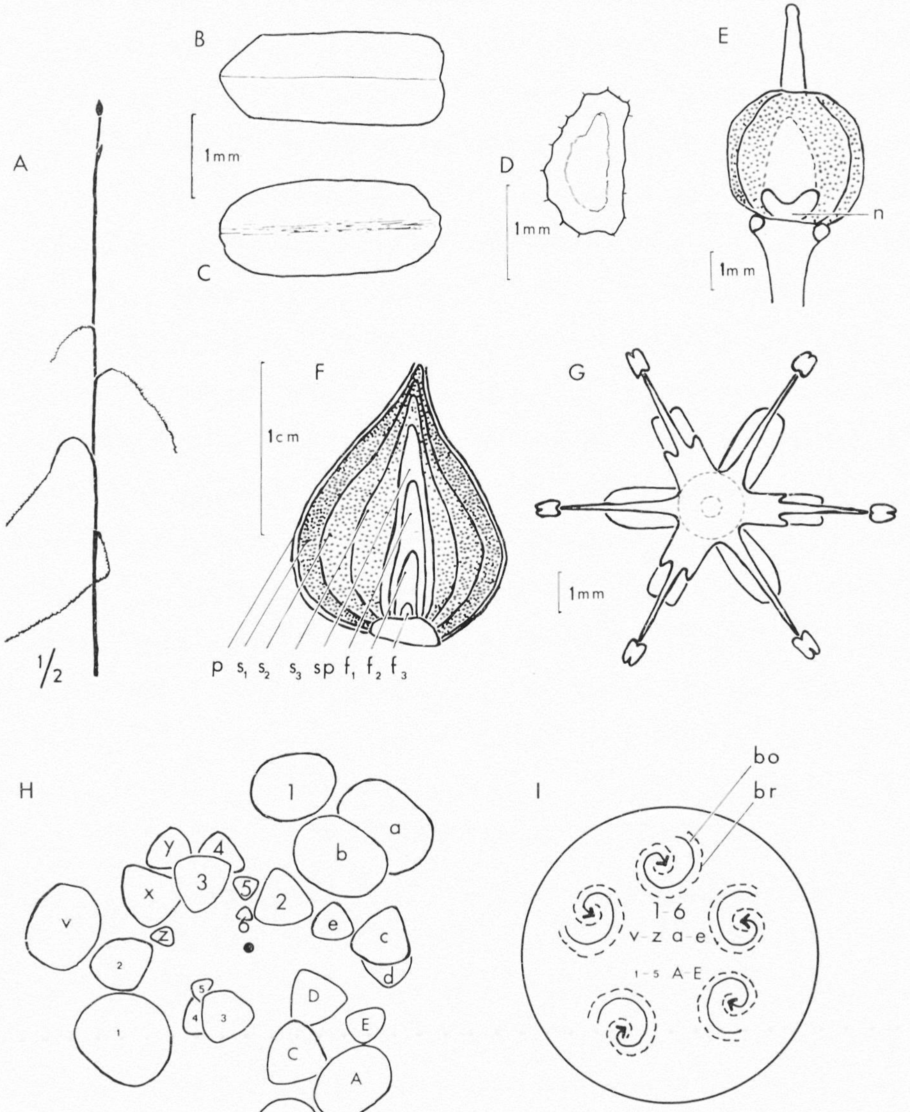

Fig. 1. *Allium microspathum* sp. nov. (C., M. & W. 3659). — A. Habit with spathe. ×0.5. — B. Inner tepal. — C. Outer tepal. — D. Cross section of foliage leaf. — E. Ovary with style and part of pedicel; *n*, nectary pit. — F. Longitudinal section of renewal bulb; *p*, protective leaf; s_1—s_3, storage leaves; *sp*, sprout leaf; f_1—f_3, foliage leaves. — G. Perigon and stamens flattened. — H—I. Organisation of inflorescence, seen from above; five bostryxes (1—6, *a*—*e*, A—E, 1—5 and *v*—*z*); *bo*, bostryx; *br*, bracteole.

Fig. 2. *Allium microspathum* sp. nov. (C., M. & W. 3659, holotype GB). — A. Habit. ×1. — B. Inflorescence and upper leaf. ×3.5. Photo: H. RASPER.

Turkey: Prov. Van, 20 km NNW of Başkale, Güzeldere Tepe and associated ridges and valleys between Halanduran Dağ and Kepir Dağ (general area of İspiriz Dağ), 2800 m. 18. August 1967, J. M. WATSON, C., M. & W. 3659; cult. Hort. Bot. Gothob., July 1968, L. EKBERG, holotypus GB.

The new species is apparently most closely related to *Allium anacoleum* HAND.-MAZZ., *A. arlgirdense* BLAKELOCK and *A. capitellatum* BOISS., but differs markedly from all three species by the very small spathe, the brownish coloured perigon, the emarginate-truncate inner tepals and the denticulate yellow inner filaments. *A. microspathum* has in common with *A. anacoleum* and *A. arlgirdense* the very long upper leaf-sheath covering the scape for 3/4 or more of its length.

That there is a relationship between *A. anacoleum, A. arlgirdense, A. capitellatum* and the new species is supported by the fact that they occur in the same geographical area, viz. NE. Iraq, W. and N. Iran and SE. Turkey.

The organization of the renewal bulb in *A. microspathum* with its different types of leaves, as well as the organisation of the inflorescence are shown in Fig. 1 F, H, I. Terminology and mode of illustration follow MANN (1959, 1960).

The new species, *A. microspathum* belongs to the section *Scorodon* C. KOCH which has *A. rubellum* M.B. as type species.

The sections used in the genus *Allium* in recent papers (W. T. STEARN, A. I. VVEDENSKY, P. WENDELBO) are, however, in most cases large and heterogenous groups. Most probably sections like *Rhizirideum, Scorodon* and *Melanocrommyum* will have to be split into smaller and more natural sections. Work on these problems are in progress.

According to WENDELBO (personal communication) the synonomy of the section *Scorodon* and *Codonoprasum* is as below:

Sect. *Scorodon* C. KOCH in Linnaea 22: 237 (1849).

Syn.: Sect. *Crommyum* subsect. *Haplostemon* § *Brachyspatha* BOISS. Fl. Or. 5: 230 (1882). Sect. *Haplostemon* (BOISS.) HALÁCZY, Consp. Fl. Graec. 3: 240, 250 (1904) p.p.; VVEDENSKY in Fl. SSSR 4: 199 (1935) p.p. Sect. *Haemoprason* STEARN in Herbertia 11: 21 (1944) non HERMANN (1939); WENDELBO in Acta Horti Gotob. 28: 22 (1966).

Sect. *Codonoprasum* (RCHB.) ENDL. Gen. Pl. 146 (1836).

Syn.: Sect. *Crommyum* subsect. *Haplostemon* § *Codonoprasa* (RCHB.) BOISS. Fl. Or. 5: 230 (1882). Sect. *Haplostemon* (BOISS.) HALÁCZY, Consp. Fl. Graec. 3: 240, 250 (1904) p.p.; VVEDENSKY in Fl. SSSR 4: 199 (1935) p.p. Sect. *Rhynchoprason* HERMANN in Feddes Rep. 46: 58 (1939). Sect. *Haemoprason* HERMANN l.c.

ACKNOWLEDGEMENTS

I am much indebted to Professor K. H. RECHINGER of Vienna for translating my description into Latin. I also thank Professor P. WENDELBO of Gothenburg for valuable suggestions.

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New Subgenera, Sections and Species of Allium

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ABSTRACT

The *Allium* species of the 'Flora iranica' area are assigned to 4 subgenera each of which are divided into sections. The following new taxa are described: subg. *Rhizirideum* (KOCH) WENDELBO, subg. *Allium,* subg. *Molium* (KOCH) WENDELBO, and subg. *Melanocrommyum* (WEBB & BERTH.) WENDELBO, the latter with sect. *Acanthoprason* WENDELBO, sect. *Megaloprason* WENDELBO and sect. *Thaumasioprason* WENDELBO; *A. caesioides* WENDELBO from N.W. Himalayas and N.E. Hindukush, *A. choriotepalum* WENDELBO from S.E. Afghanistan, *A. pamiricum* WENDELBO from the Pamirs, *A. panjaoënse* WENDELBO from C. Afghanistan, and *A. registanicum* WENDELBO from S. Afghanistan (all of sect. *Scorodon* C. KOCH); *A. subnotabile* WENDELBO from S.W. Iran and *A. trachycoleum* WENDELBO from N.E. Iraq (both of sect. *Allium*); *A. elburzense* WENDELBO from N. Iran and *A. nevskianum* VVED., nom. et stat. nov. (*A. alexejanum* REGEL var. *hissaricum* LIPSKY) (both of sect. *Acanthoprason* WENDELBO).

INTRODUCTION

In a treatment of the genus *Allium* for K. H. RECHINGER's 'Flora iranica' which is in preparation, more than 130 species are recognized. During work with this treatment many new species have been described (WENDELBO 1958, 1963, 1966, 1967, 1968). It has also become more and more evident that the currently used subdivision of this large genus (500—600 spp.) into relatively few sections (cf. STEARN 1944 pp. 20—21), is outdated. New subgenera and sections, which together with the old ones will accomodate the Iranian and Afghanian species of *Allium,* are described below. In addition a last series of new species are described before the treatment for 'Flora iranica' is completed.

NEW SUBGENERA AND SECTIONS

Subgenus **Rhizirideum** (KOCH) WENDELBO, subgen. nov.

Syn.: Sect. *Rhizirideum* G. DON ex KOCH, Syn. Fl. Germ. 714 (1837).
Typus subgeneris: *A. senescens* L.

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Bulbi rhizomati adnati, plerumque anguste cylindrici-conici usque oblongi-ellipsoidei vel ovoideo-conici, plerumque conferti. Scapus in parte supraterranea foliorum vaginis ± alte obtectus. Ovarium foveola nectarifera provisum.

The species of subgenus *Rhizirideum* are first of all characterized by having the bulbs attached to a rhizome. Sometimes this rhizome is indistinct and possibly absent, but in such cases the affinity of the species in question is revealed by the narrow, elongated form of the usually aggregated bulbs.

Sections belonging to this subgenus are: *Rhizirideum, Schoenoprasum* (KUNTH) DUMORT., *Cepa* (MOENCH) PROKHANOV.

Most probably the section *Rhizirideum* will have to be split into several sections in the future, but as the section is relatively poorly represented in S.W. Asia I have not looked further into this problem.

Phylogenetically subgenus *Rhizirideum* may be looked upon as the more primitive of all the subgenera. It seems possible to derive all the other groups from rhizomatous species without a distinct bulb.

Subgenus **Allium**

Typus subgeneris (typus generis): *A. sativum* L.

Bulbus solitarius, rhizomati non adnatus. Scapus in parte supraterranea foliorum vaginis ± alte obtectus. Folia aut cylindrica aut semicylindrica aut ± plana vel canaliculata. Perigonium campanulatum vel ovoideum.

The three sections *Scorodon* C. KOCH, *Allium* and *Codonoprasum* (REICHENB.) ENDL. are rather closely related to each other, and I have found it convenient to express this relationship by placing them in a common subgenus.

Subgenus **Molium** (KOCH) WENDELBO, subgen. nov.

Syn.: Sect. *Molium* G. DON ex KOCH, Syn. Fl. Germ. 714 (1837) p.p.
Typus subgeneris: *A. neapolitanum* CYR.

Bulbus solitarius, saepe bulbillifer; tunicae exteriores saepe crassae, sculptae. Folia vaginis subterraneis vel supraterraneis ± bene evolutis; lamina plana. Perigonium stellatum usque campanulatum, proportione magnum. Ovarium foveolis nectariferis provisum vel destitutum. Stigma integrum vel trilobum.

MANN 1960 could by his fine morphological study show that the *Molium* alliums formed a distinct and very characteristic Mediterranean group. The section *Briseis* (SALISB.) STEARN shows definite affinities to sect. *Molium* and together the two should form a subgenus. With some doubt the new sect. *Porphyroprason* EKBERG (1969 p. 65) is referred to this subgenus.

Subgenus **Melanocrommyum** (WEBB & BERTH.) WENDELBO, subgen. nov.

Syn.: Sect. *Melanocrommyum* WEBB & BERTH., Hist. Nat. Iles Canaries 3(2): 347 (1848).
Typus subgeneris: *A. nigrum* L.

Bulbus solitarius, raro bulbillifer. Folia omnia basalia, vaginis partem supraterraneam scapi involucrantibus nullis, plana vel canaliculata. Pedicelli ebracteolati.

Melanocrommyum as a section comprises a varied selection of species. I have come to the conclusion that *Melanocrommyum* is better treated as a subgenus comprising several sections. From a phylogenetical point of view it is the most advanced of the subgenera. Below I have listed all the sections belonging to this subgenus.

Sect. **Acanthoprason** WENDELBO, sect. nov.

Typus sectionis: *A. akaka* GMEL.

Scapus sat brevis et crassus quam folia brevior. Umbella plerumque densa pedicellis ± aequilongis. Perigonium stellatum usque ± late campanulatum; tepala supra basin aliquantum connata, nervo mediano demum incrassato ± rigido, marginibus ± involutis.

The species of *Acanthoprason* are characterized by having the scape shorter than the leaves, and first of all by the tepals which become rigid and in some cases almost spinose due to the thickened nerve and the involute margins. Members of this section within the 'Flora iranica'-area are: *A. akaka* GMEL., *A. bodeanum* REGEL, *A. cristophii* TRAUTV., *A. derderianum* REGEL, *A. elburzense* WENDELBO, *A. ellisii* HOOK. F., *A. haemanthoides* BOISS. & REUT., *A. materculae* BORDZ., *A. minutiflorum* REGEL, *A. monophyllum* VVED., *A. nevskianum* VVED., and *A. shelkovnikovii* GROSSH.

The geographical area of this section stretches from E. Iraq, E. Turkey and Trans-Caucasus through Iran, Afghanistan and Tadjikistan. The centre of variation is in N.W. Iran and Trans-Caucasus.

Sect. **Melanocrommyum**

Scapus ± elongatus, folia plerumque excedens. Umbella late fasciculata usque subsphaerica. Perigonium stellatum usque late campanulatum; tepala mox reflexa ± contorta. Ovarium sessile, leave (in vivo quidem).

The species of this section are mainly Mediterranean in their distribution. The centre of variation is in the East Mediterranean, probably in Turkey. Only few species reach Iran and these are mainly confined to the western part of the country, viz. *A. calocephalum* WENDELBO, *A. cardiostemon* FISCH. & MEY., *A. chrysantherum* BOISS. & REUT., *A. colchicifolium* BOISS., *A. kharputense* FREYN & SINT., and *A. olivieri* BOISS. Other characteristic species of this section from outside the area are: *A. atropurpureum* WALD. & KIT., *A. aschersonianum* BARB., *A. asclepiadeum* BORNM., *A. lycaonicum* SIEHE, *A. orientale* BOISS., and *A. stenopetalum* BOISS. & KOTSCHY.

Sect. **Megaloprason** WENDELBO, sect. nov.

Typus sectionis: *A. rosenbachianum* REGEL

Scapus valde elongatus proportione tenuis, strictus, raro brevis flexuosus, folia plerumque excedens. Umbella plerumque sphaerica, densa. Perigonium stellatum; tepala libera, saepe mox reflexa et ± contorta. Ovarium plerumque manifeste stipitatum, verruculosum.

There is a series of species related to *A. rosenbachianum* that clearly belongs to this section, e.g. *A. aflatuenense* B. FEDTSCH., *A. altissimum* REGEL, *A. chitralicum* WANG & TANG, *A. fibriferum* WENDELBO, *A. hirtifolium* BOISS., *A. jesdianum* BOISS. & BUHSE, *A. sarawschanicum* REGEL, *A. stipitatum* REGEL, and *A. suworowii* REGEL. They are in most cases rather tall plants with a large spherical umbel, and have all narrow tepals that soon become reflexed and contorted, as well as an ovary that is more or less distinctly stipitate and verruculose. Much the same habit and the same type of ovary are found in *A. giganteum* REGEL and *A. macleanii* BAKER, but both of these have broader immutate tepals. Species like *A. badakhshanicum* WENDELBO, *A. brachysca-*

pum VVED., and *A. scotostemon* WENDELBO are plants of smaller stature which look rather abberant but still they have to be referred to the section *Megaloprason*.

Sect. **Kaloprason** C. KOCH, Linnaea 22: 235 (1849).

Typus sectionis: *A. caspium* (PALL.) M.B.

The section *Kaloprason* does not seem to have been recognized by any authors on *Allium* since it was described by KOCH. Species like *A. bucharicum* REGEL, *A. caspium* (PALL.) M.B., *A. helicophyllum* VVED., *A. protensum* WENDELBO, and *A. schubertii* ZUCC., share, however, several characteristic features and form a section. The scape becomes much thickened and tapers much towards base, the umbel is usually lax and the pedicels are often markedly unequal.

Sect. **Thaumasioprason** WENDELBO, sect. nov.

Typus sectionis: *A. mirum* WENDELBO

Scapus proportione brevis, crassus. Folia 1—2, scapum excedentia, lata. Umbella sphaerica, densa, fragillima. Perigonium late campanulatum; tepala magna, lata, immutata.

This new section consist of 3 species only, *A. caroli-henrici* WENDELBO, *A. cucullatum* WENDELBO and *A. mirum* WENDELBO, all found in East and Central Afghanistan. These 3 species seem to form an isolated and very distinct group. Especially characteristic are the large tepals that are erect and keep their form in the fruiting stage, as well as the very fragile umbel.

Sect. **Regeloprason** WENDELBO, Acta Horti Gotob. 28: 36 (1966).

Typus sectionis: *A. regelii* TRAUTV.

There is nothing to be added to the comments on this section given in the original paper.

NEW SPECIES

SECT. SCORODON C. KOCH

A. caesioides WENDELBO, sp. nov. (Fig. 1 A)

Bulbus 1—1.5 cm diametro, ovoideus; tunicae exteriores papyraceae, cinereae, nervis parallelis distantibus. *Scapus* unicus rarius bini, 11—22

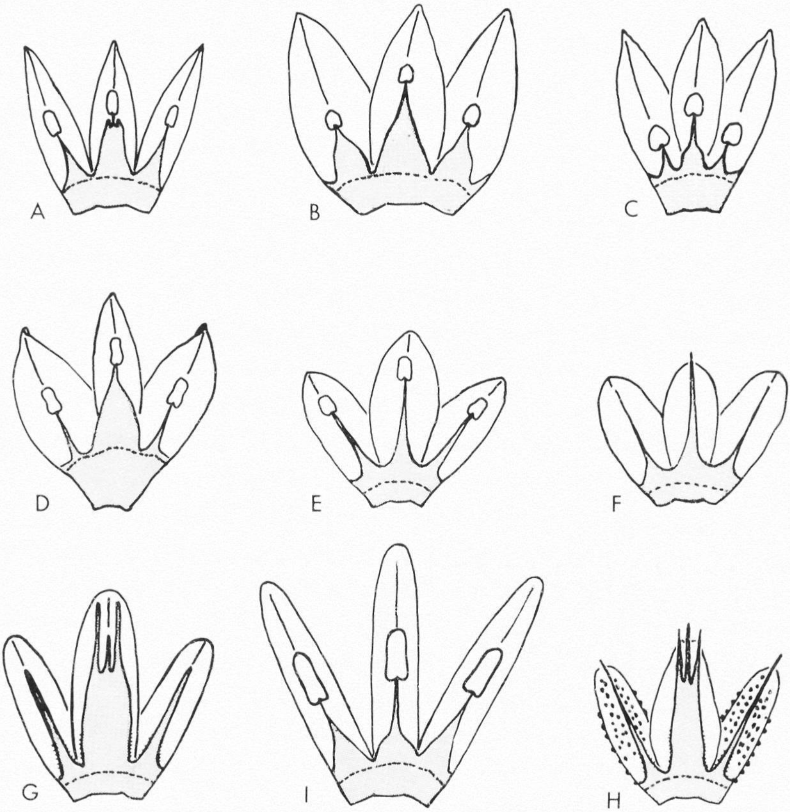

Fig. 1. Outer and inner tepals of new species of *Allium*. — A: *A. caesioides* (Giles 210). — B: *A. choriotepalum* (Rechinger 35864). — C: *A. pamiricum* (Rajkova s.n.). — D: *A. panjaoënse* (Rechinger 36341). — E: *A. registanicum* (Furse 5576). — F: *A. registanicum* (Rechinger 34606). — G: *A. subnotabile* (Archibald 2671). — H: *A. trachycoleum* (Rechinger 11901). — I: *A. elburzense* (Žumer 808). — All ×4. Ekberg del.

(—35) cm longi, per 1/3—1/2 longitudinis foliorum vaginis distantibus scabrido-papillosis vel sublaevibus, paulo infra foliorum laminam inflatis, obtectae. *Folia* 2 (—3), 0.75—1.8 mm lata, semicylindrica, fistulosa, secus nervos scabrida. *Spatha* acuminato-rostrata, basi c. 8 mm longa, rostro c. 6 mm longo, ± persistens. *Umbella* hemisphaerica usque subsphaerica, densa; pedicelli subaequales, usque ad 1.5 cm longi, bracteolis usque ad 6 mm longis instructi. *Perigonium* campanulatum, purpurascenti-violaceum, nervis saturatioribus conspicuis; tepala 5—6.5 mm longa, acuta; exteriora anguste elliptico-oblonga, interiora anguste ovata, quam exteriora c. 1.5-plo latiora. *Filamenta* c. 2/3 tepalorum longitudinis aequantia, per 1/6 longitudinis filamentorum connata et tepalis adnata; exteriora anguste triangularia; interiora basi late triangulari, ad c. 2/3 partis liberae utrinque denticulo provisa; antherae 1 mm longae, mucronatae.

Afghanistan. Badakhshan: Locality not readable, 2700 m, GILES 210, holotypus K. — India. Lahul: Bhaga Thil, an Abhängen im Schatten grösserer Gewächse, häufig. Blüten blau, JÄSCHKE 122 WU; Kyelang, 3060 m, 5.VI.1941, flowers blue, BOR 14653 K; Kyelang, 3000 m, 3—4.VII.1933, KOELZ 5191 K.; N.W. Himalaya: Pindi, 2700 m, 14.VI.1881, ELLIS 1259 K.

A. caesioides belongs to a group of species including among other *A. caesium* SCHRENK, *A. oreophiloides* REGEL and *A. schoenoprasoides* REGEL. It has the slight inflation of the upper part of the leaf-sheath also found in *A. schoenoprasoides* but differs from this species in the semicylindric and fistular leaves, in the less dense umbel as well as in the different colour of the tepals which also have a strong nerve. From *A. oreophiloides* the new species is distinguished by the stouter and taller scape, by the denser inflorescence and apparently also by the colour of the tepals in addition to the inflation of the leaf sheath. *A. caesium* has a somewhat campanulate-urceolate perigone of a more bluish colour (in pressed specimens); the tepals are apparently of a thicker consistency and the filaments are comparatively longer and has a longer antheriferous cusp and better developed lateral teeth to the inner filaments. *A. caesioides* is also distinguished by the less rigid leaves with rather indistinct longitudinal ribs as well as by the mucronate anthers.

Apparently *A. caesioides* comes closest to *A. caesium*, but differs from that species also in its ecological requirements. VVEDENSKY (1944 p. 170) gave the following information on *A. caesium*: 'In the steppe zone in salt-marshes, in semi-desert; in the southern part in the foothills and mountains up to 2000 m'. *A. caesioides* grows at higher altitudes, and according to JÄSCHKE also in shade of higher plants.

A. caesioides is a N.W. Himalayan plant reaching as far as the northeasternmost parts of the Hindukush.

A. choriotepalum WENDELBO, sp. nov. (Fig. 1 B)

Bulbus 1—1.5 cm diametro, ovoideus; tunicae exteriores coriaceae, purpurascenti-brunneae, grosse reticulato-nervosae; bulbilli usque ad

1.5 cm longi, tunicis nitentibus pallide flavis, reticulato-nervosis. *Scapus* 24—38 cm altus, ± curvatus, in sicco ± violaceus, per 1/5—1/4 longitudinis foliorum vaginis laevibus tectus. *Folia* 2, florendi tempore emarcida, c. 2 mm lata, semicylindrica, fistulosa, laevia. *Spatha* caduca, basis tantum persistens. *Umbella* hemisphaerica, densa; pedicelli subaequales, usque ad 10 mm longi, ebracteolati. *Perigonium* ovoideum; tepala c. 6.5 mm longa, elliptica, acuta, subcoriacea, exteriora quam interiora sublatiora, exteriora dorso atrolilacino-nervosa marginem versus expallescentia, margine fere albo, interiora fere alba, nervo ± viridi-violaceo. *Filamenta* inaequalia, per c. 1 mm connata, exteriora 3 mm longa, triangulari-ovata, tepalis per c. 1 mm adnata; interiora c. 4 mm longa, ovato-caudata, quam exteriora latiora, tepalis per 1.5 mm adnata; antherae vix 2 mm longae, flavescenti-albae. *Stylus* inclusus, brevis, crassus.

Afghanistan. Urgun: Urgun, ad versuras, 2200—2300 m, 9.VI.1967, RECHINGER 35864, holotypus W, isotypus BG.

This new species belongs to the *A. rubellum* group which seems to have a centre in Afghanistan. It is distinguished from the other species by the thickish, lilac tepals and the large, ca. 2 mm long, whitish anthers.

A. pamiricum WENDELBO, sp. nov. (Fig. 1 C)

Syn.: *A. jacquemontii* VVED., Fl. SSSR. 4: 215 (1935); Fl. Tadjik. SSR. 2: 322. t. *58*. f. *1*. (1963) non KUNTH (1843).

Bulbus ovoideus, 0.5—1 cm diametro; tunicae exteriores cinereae, subpapyraceae, nervis fere parallellis; bulbilli pauci, albi, non alati, tenuiter nervosae. *Scapus* (10—) 15—35 cm altus, ad 1/4—1/3 foliorum vaginis laevibus distantibus obsitus. *Folia* 2 (—3), quam scapus breviora, (0.5—) 1—2 mm lata, semicylindrica, canaliculata, fistulosa, laevia, rarius scabrida. *Spatha* ± caduca. *Umbella* hemisphaerica, densa ± multiflora; pedicelli subaequales, tepalis aequilongi vel eis 1.5 (—2)-plo longiores, ebracteolati. *Perigonium* campanulatum, roseum nervis saturatioribus; tepala 4.5—5 (—6) mm longa, subaequalia, subacuta, exteriora anguste oblongo-ovata, paulo attenuata, interiora elliptica, quam exteriora paulo breviora. *Filamenta* 1/2—2/3 longitudinis tepalorum attingentia, per 1/2—1/3 longitudinis filamentorum connata et perigonio adnata, integra; exteriora anguste triangularia; interiora late triangularia, quam exteriora duplo latiora et aliquantum longiora, quam basis tepalorum paulo latiora; antherae c. 3/4 mm longae, flavae. *Stylus* inclusus, filiformis; stigma capitatum.

U. S. S. R. Tadjikistan: Schugnan; in valle fl. Gunt prope aestia fl. Schachdara, 2.IV.1934, RAJKOVA s.n., holotypus BG, isotypus TAK. — Afghanistan. Wakhan: bei Quazi-Deh, 2950 m, ROEMER 119 M.

This new species has been mistaken for *A. jacquemontii* KUNTH which occurs in E. Afghanistan, N.W. Pakistan, and N.W. India. *A. pamiricum* differs from that species in the papyraceous bulb-tunics with nearly parallel nerves, in having filaments adnate to tepals for a somewhat longer distance, somewhat differently shaped tepals and yellow, not violet, anthers.

A. panjaoënse WENDELBO, sp. nov. (Fig. 1 D)

Bulbus 1—1.5 cm diametro, ovoideus; tunicae exteriores pallide cinerascenti-brunneae, potias tenues, diffractae, nervis conferte reticulatis. *Scapus* 6—22 cm longus, curvatus, per 1/3—1/2 longitudinis foliorum vaginis laevibus vel minute scabrido-papillosis obtectus. *Folia* 2, scapum circiter aequantia, 0.3—1.5 mm lata, semicylindrica, superne canaliculata, fistulosa, secus nervos ± minute scabrido-papillosa. *Spatha* 6—10 mm longa, acuminata, bivalvis. *Umbella* hemisphaerica vel hemisphaerico-fasciculata, densa; pedicelli perigonio breviores, raro aliquantum longiores, ebracteolati. *Perigonium* campanulatum; tepala alba brunnescenti-purpureo- usque purpureo-nervosa, imprimis exteriora fascia colorata secus nervum provisa et in parte apicali colorata, obtusa, apice aliquantum reflexa, margine ± minute papillosa; tepala exteriora quam interiora aliquantum breviora, rarius aequilonga, 6—7.5 mm longa, elliptico-obovata, interiora 6—8 mm longa, anguste elliptico-oblonga, basi saccata. *Filamenta* inaequalia, per 2 mm connata; exteriora lineari-subulata, quam interiora manifeste breviora, tepalis per c. 2 mm adnata; interiora 4—5 mm longa, basi late triangulari-ovata, per 3—4 mm tepalis adnata; antherae c. 1 mm longae, flavae. *Capsula* valvis late ellipticis, 4—5 mm longa, 2.5—3 mm lata, apice emarginata.

Afghanistan. Panjao: Kotal-e Narges, 3100 m, 2.VII.1962, HEDGE and WENDELBO 4962, holotypus BG, isotypus E; 12 km W Panjao, 2650—2800 m, 21—22.VI.1967, RECHINGER 36164 W. — Bamian: In declivibus borealibus jugi Shahtu, 2800—3000 m, 23—28.VI.1967, RECHINGER 36341 W. — Ghazni: Jaghuri, in jugo Kotal-e Ketschru NW Sang-i Masha, 2880 m, 2.VII.1962, RECHINGER 17523 W; in faucibus Say Khoshkak (Nawar Kotal) inter Okak et Behzud (Diwal Kotal), 3150 m, 6.VII.1962, RECHINGER 17831 W.

The habit of *A. panjaoënse* is much the same as that of a rather small-grown *A. griffithianum* BOISS. or *A. bracteolatum* WENDELBO. From the latter it is easily distinguished by the lack of bracteoles. From the former it differs in having the outer tepals somewhat shorter — not distinctely longer — than the inner ones, and in having the margins of the tepals minutely papillose-ciliate. There is also some difference in the colours of the perigone, in *A. panjaoënse* there is a lot of brown in the coloured band along the nerve of the tepals.

A. registanicum WENDELBO, sp. nov. (Fig. 1 E, F)

Bulbus c. 1 cm diametro, ovoideus; tunicae exteriores atro-brunneae, in fibras grosse reticulatas ± distincte dissolutae. *Scapi* 1 (—2), 15—45 cm alti, curvati, in parte subterranea foliorum vaginis leavibus tecti. *Folia* 2—3, subopposita vel subverticillata, scapum subaequantia, (0.3—) 0.7—2 mm lata, in parte inferiore semi-cylindrica subcanaliculata, in parte superiore plana, non fistulosa. *Spatha* c. 10 mm longa, in valvas plures fissa, mox caduca. *Umbella* fasciculata, densa; pedicelli fructiferi inaequales, usque ad 20 mm longi, bracteolati. *Perigonium* campanulatum, albido-lavandulaceum (e collectore), in sicco lilacinum nervis purpureo-violaceis; tepala 4.5—5.5 mm longa, elliptica vel elliptico-oblonga, obtusa, inaequalia, exteriora breviora, quam interiore latiora et magis elliptica, interiora basi subsaccata. *Filamenta* (in typo) quam tepala subbreviora vel ea aequantia vel subsuperantia, e basi anguste triangulari subulata, prope basin connata et tepalis adnata; interiora quam exteriora sublatiora; antherae 1.2 mm longae, violaceae. *Stylus* exsertus, filiformis; stigma capitatum. *Capsula* valvis 4 mm longis, 5 mm latis, late obcordatis, tepalis persistentibus inclusa.

Afghanistan. Kandahar: Girishk to Kandahar, sandy desert with low dunes and surface caked hard, 800 m, 25.IV.1964, FURSE 5576, holotypus K; in marginibus deserti Registan, 4—5 km SE Safer, 19.V.1967, RECHINGER 34606 W.

A. registanicum is habitually rather like members of the *A. rubellum* group but is clearly distinguished by its coarsely reticulate-fibred outer bulb-tunics, by the bracteolate umbel as well as by the filaments which are about as long as the tepals.

SECT. ALLIUM

A. subnotabile WENDELBO, sp. nov. (Fig. 1 G)

Bulbus vix 1 cm diametro, ellipsoideus; tunicae exteriores ut videtur integrae, subcoriaceae, interiores brunneae, reticulato-nervosae, partim in reticulum fibrosum fissae; tunica bulbi juvenilis purpurascenti-violacea. *Scapus* 37 cm longus, per 2/5 longitudinis vaginis foliorum obtectus; vaginae nervo mediano foliorum papilloso decurrente excepto laeves. *Folia* 4, quam scapus breviora, c. 3 mm lata, canaliculata, costata, non fistulosa, margine et secus carinam, papilloso-scabrida. *Spatha* caduca. *Umbella* densa, sat pauciflora, subsphaerica; pedicelli inaequales usque ad 8 mm longi, infra florem aliquantum indistincte verruculosi; bracteolae breves, latae, lobatae. *Perigonium* campanulato-urceolatum, album, nervis indistinctis apicem versus aliquantum rubescentibus; tepala inaequalia, obtusa, apiculo cucullato reflexo; exteriora quam interiora cymbiformia manifeste breviora, in dorso imprimis secus carinam grosse verruculosa; interiora c. 6 mm longa, anguste ovato-oblonga, dorso minute dense verruculosa. *Filamenta* inaequalia, in parte inferiore marginis papillosa; exteriora c. 4.5 mm longa, anguste triangulari-subulata; interiora c. 5 mm longa, tricuspidata, cuspis antherifera vix plus quam 1/3 longitudinis baseos ovatae et c. 2/3 longitudinis cuspidum lateralium attingens. *Capsula* c. 3.5 mm longa.

Iran. Luristan: 30 km W of Khorramabad, NW facing hillside among *Quercus brantii*, heavy clay over limestone, 1280 m, 11.VII.1966, ARCHIBALD 2671, holotypus GB.

The new species shows considerable similarities to *A. notabile* FEINBR. from Iraq, but is distinguished by the much larger flowers, about twice as long, and the only indistinctely verruculose pedicels as well as by the included, minutely ciliate filaments.

A. **trachycoleum** WENDELBO, sp. nov. (Fig. 1 H)

Bulbus c. 1.5 cm diametro; tunicae exteriores ignotae; bulbilli 0.7—1 cm longi, cymbiformes extremis ambabus apiculatibus, brunnei, nitidi. *Scapus* c. 80 cm longus, per c. 1/3 vaginis foliorum scabridis obtectus. *Folia* 5, quam scapus breviora, c. 4 mm lata, canaliculata, nervis scabridis. *Spatha* caduca. *Umbella* 5 cm diam., sphaerica, multiflora, densa; pedicelli inaequales, exteriores c. 1.5 cm longi, basi bracteolis c. 1 cm longis laciniatis provisi, interiores c. 3 cm longi. *Perigonium* campanulatum, album; tepala 5—6 cm longa, exteriora anguste elliptico-ovata, dorso et margine pustulosa, obtusa, interiora ovata, laevia, apice truncata. *Filamenta* quam tepala aliquantum longiora, prope basin connata et tepalis adnata, ciliata; exteriora lineari-subulata, interiora ad c. 2/3 longitudinis tricuspidata, cuspide antherifera c.

dimidium longitudinis baseos anguste rectangularis et cuspidum lateralium aequantia. *Stylus* exsertus.

Iraq. Mosul: Ad confines Turciae prov. Hakari, inter Dohuk et Amadiya, in quercetis saxosis supra Sirsauk, 1200 m, 10—12.VII.1957, RECHINGER 11901, holotypus W.

A. trachycoleum is closely related to *A. qaradaghense* which also occurs in N.E. Iraq. It is easily distinguished from the latter by the much larger perigone, by the scabrid leaf-sheaths and the scabrid-nerved leaves. An important difference is found in the inner filaments, which in *A. trachycoleum* have the lateral cusps of the same length as the antheriferous cusp whereas they are twice as long in *A. qaradaghense*.

SECT. ACANTHOPRASON WENDELBO

A. elburzense WENDELBO, sp. nov. (Fig. 1 I)

Bulbus subglobosus, 1.5—3 cm diametro; tunicae exteriores coriaceae, cinerascenti-brunneae, aliquantum fracteae. *Scapus* 5—16 cm longus, usque ad 8 mm diametro, validus, curvatus, in sicco subcostatus. *Folia* 1—2, basalia, (1—) 2—6.5 cm lata, elliptica usque anguste elliptico-oblonga, crassa, margine laevia, apice cucullata, glaucescenti-viridia. *Spatha* usque ad 2.5 cm longa, apiculata, 4-loba, persistens, basi basin pedicellorum includente. *Umbella* hemisphaerica usque late fasciculata, multiflora, densa; pedicelli usque ad 3.5 cm longi, subaequales. *Perigonium* stellatum, purpurascens; tepala 10—12 mm longa, 1.5—2 mm lata, linearia, subinaequalia, apicem et basin versus subattenuata, obtusa, ± immutata nec autem rigida, margine demum leviter involuta. *Filamenta* c. 2/3 longitudinis tepalorum attingentia, e basi leviter dilatata lineari-subulata, usque ad paulo supra basin connata et tepalis adnata, purpurascentia; antherae 2 mm longae, purpurascenti-violaceae. *Ovarium* subglobosum, breviter crasse stipitatum; loculis 3—4-ovulatis. *Stylus* filamenta non excedens. *Capsula* 5—8 mm diametro, depressa.

Iran. Elburz Mts.: Ab-e Ali, south of Demavend, 1900 m, 15.V.1959, WENDELBO 752, holotypus BG, isotypus TAK; Haraz valley, above Siah Bisheh, 900 m, 27.IV. 1959, WENDELBO 380 BG, TAK; Tovchal, Abshar, 2000—2500 m, 16.V.1966, ŽUMER 808 BG.

A. elburzense is distinguished from the other species of its section by the combination of broad leaves, rather long tepals with a hardly thickened nerve and more or less angular-based filaments.

A. nevskianum VVED. nom. et stat. nov.

Syn.: *A. alexejanum* REGEL var. *hissaricum* LIPSKY, Acta Horti Petrop. 18 (1): 136 (1901).

Material of HEDGE and WENDELBO 4732 quoted below was sent Dr. VVEDENSKY under the name *A. derderianum* REGEL. VVEDENSKY, in litt., informed me that the material belonged to *A. alexejanum* var. *hissaricum*, a variety which he wanted to raise to specific rank.

Afghanistan. Bamian: Kargana-tu on road to Band-i Amir, 3100 m, HEDGE and WENDELBO 4732 BG, E, TAK; Band-i Amir, ad lacum Zolfikar, 2900 m, RECHINGER 18426 W; — Ghazni: in monte Saperlebuli ad marginem austroorientalem altoplanitiei Dasht-i Nawar, 3200—4200 m, RECHINGER 37317 W.

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I am indebted to Professor K. H. RECHINGER for sending all his material of *Allium* on loan and for help with translation of the Latin descriptions; to the Directors and Keepers of the herbaria of Royal Botanic Gardens, Kew; the Komarov Botanical Institute of the Academy of Sciences, Leningrad and the Botanical Institute of the University, Vienna, for loan of material. To Dr. A. I. VVEDENSKY of Tashkent I am grateful for valuable suggestions, and to Fil. mag. L. EKBERG for preparation of drawings of flower details.

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Studies in the Aegean Flora XIV

Studies in Scutellaria Section Vulgares Subsection Peregrinae from Greece and Adjacent Turkey

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ABSTRACT

The paper treats two form series of *Scutellaria* sect. *Vulgares* subsect. *Peregrinae* from Greece and adjacent Turkey. They differ in corolla colour, in habit and in the size of the bracts

One of the form series is white-flowered, and within it two main complexes (*S. albida* and *S. velenovskyi* complexes) are recognized differing mainly in stem pubescence. One new species is described, *S. naxensis* Bothm. from Naxos, belonging to the *S. velenovskyi* complex.

The other form series is violet-flowered, and in it one complex (*S. rubicunda* complex) is recognized. In *S. rubicunda* Hornem. two subspecies [ssp. *icarica* (Rech. fil.) Rech. fil. and ssp. *samia* Rech. fil.] are united under the name *S. rubicunda* Hornem. ssp. *icarica* (Rech. fil.) Rech. fil.

INTRODUCTION

The genus *Scutellaria* L., of the family *Labiatae*, is represented in Greece by the sections *Lupulinaria* Ham. and *Vulgares* Benth. In the former, only *S. orientalis* L. is present in Greece. It grows in the mountains of the Greek mainland, Crete and Samos (Boissier 1879, Halácsy 1902, Rechinger 1943). Sect. *Vulgares* is represented by the subsections *Galericulatae* Boiss. and *Peregrinae* Boiss. In northern Greece, *S. galericulata* L. and *S. hastifolia* L., members of subsect. *Galericulatae*, occur, the former with a circumboreal, and the latter with a north and central European distribution.

Subsect. *Peregrinae* has its distribution center in Asia Minor and further southeastwards. Its species are more or less erect with broad, serrated, petiolated leaves, and with flowers disposed in terminal racemes. The bracts, which differ in shape from the stem leaves, are small with entire margins.

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The present study is restricted to different groups of subsect. *Peregrinae* in Greece and adjacent Turkey.

MATERIAL AND METHODS

For a morphologic analysis, material from the following herbaria have been examined: Edinburgh (E), Lund (LD) and Vienna (W and WU). For abbreviations, see Index Herbariorum, Ed. 5. 1964. In addition also collections made in 1958—1968 by the author and his associates have been studied. A total of 310 sheets were examined.

A limited material has also been cultivated in the Lund Botanical Garden for cytological investigations. The plants were prepared in the following way: after cooling for about 12 hours at 2—4°C, root tips were fixed in the Svalöf modification of Navashin-Karpechenko, cut with a microtome in 14 μ sections and stained in 1 % crystal violet.

CYTOLOGY

In subsection *Peregrinae* the chromosome numbers for *Scutellaria albida* L. and *S. altissima* L. were previously known. SCHEEL (in DARLINGTON & WYLIE 1955) reported 2n=32 for *S. albida*, while REESE (1953) reported 2n=34 for *S. altissima*.

RESULTS. In the taxa counted, the chromosome number is 2n=34. The chromosomes are rounded or somewhat rod-shaped with a length of 0.75—1 μ (Fig. 1 B). A closer cytological study of the chromosome morphology has not been possible owing to the small size of the chromosomes.

S. naxensis BOTHM. — 2n=34.

Naxos. S Ammomaxis Oros, valley, 280 m. 1958, RUNEMARK and SNOGERUP s. n. (LD). — 2 km S Ammomaxis Oros, 260—300 m. 1958, RUNEMARK and SNOGERUP 10584 (LD). — Fanaris, W exposed limestone rock, 700 m. 1958, RUNEMARK and SNOGERUP 11955 (LD). — Koronos Oros, S-exposed rocks, ca. 900 m. 1958, RUNEMARK and SNOGERUP 12396 (LD).

S. velenovskyi RECH. FIL. ssp. **perhispida** (BORNM.) RECH. FIL. — 2n=34.

Rhodes. Cliffs SE Salakos, ca. 300 m. 1967, RUNEMARK and BENTZER 29360 (LD).

S. rubicunda HORNEM. ssp. **hellenica** RECH. FIL. — 2n=34.

Peleponnisos. Argolis, large ± vertical rocks facing N, ca. 0.5 km S of Ag. Vasilios (N Argos), ca. 250 m. 1966, STRID 23302 (LD).

S. rubicunda HORNEM. ssp. **icarica** (RECH. FIL.) RECH. FIL. — 2n=34.

Ikaria. N Ag. Nikolaos, 100—200 m. 1958, RUNEMARK and SNOGERUP 11242 (LD). — Kaka Raphija, 250—300 m. 1958, RUNEMARK and SNOGERUP 12619 (LD).

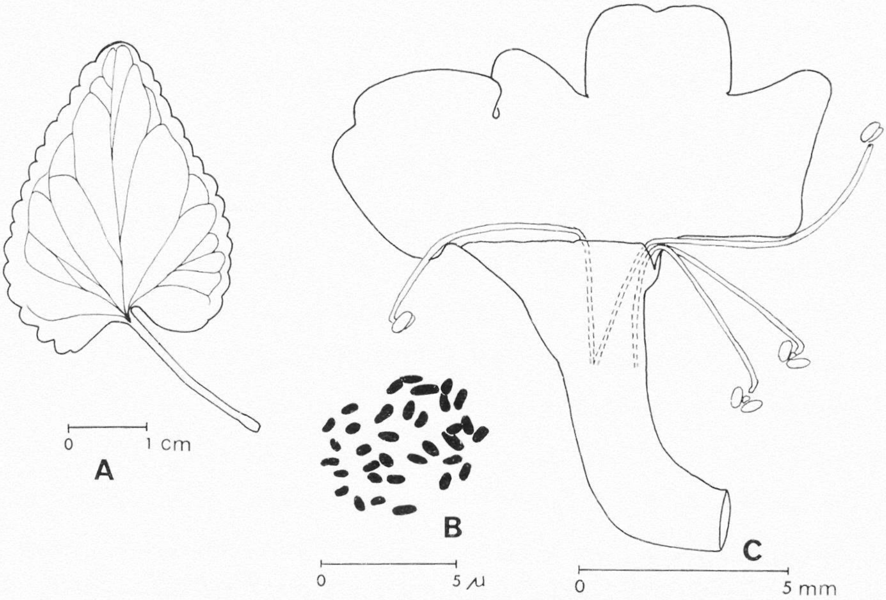

Fig. 1. — A, C. Leaf and corolla, respectively, of *Scutellaria naxensis* Bothm., Naxos [Runemark 3957 (LD)]. — B. Chromosomes of *S. rubicunda* Hornem. ssp. *icarica* (Rech. fil.) Rech. fil., Ikaria [Runemark and Snogerup 12619 (LD)]. 2n=34.

TAXONOMIC TREATMENT IN SCUTELLARIA

The morphological homogeneity of the entire genus together with minute differences in reproductive parts among taxa makes the systematical treatment in *Scutellaria* difficult. In other genera of the *Labiatae*, the taxonomy is based on differences in the floral parts, but in *Scutellaria* classification is built mainly on vegetative characters (Epling 1942). The taxonomy in this genus is rather confused because previous authors have disagreed as to the importance of certain vegetative characters.

Habit, pubescence, size and shape of the bracts and leaves are regarded as important taxonomic characters in *Scutellaria*. Of the floral parts, the size and shape of the corolla and calyx are of some importance.

In his revision of subsect. *Peregrinae* Rechinger (1941) testifies as to these difficulties, which also have been confirmed by the present author.

TAXONOMY

S. altissima L. (RECHINGER 1941) and *S. columnae* ALL. (HALÁCSY 1902 and RECHINGER 1941) are known from northern Greece. They both have large flowers and leaves, and are probably not closely related to the other taxa of subsect. *Peregrinae* native to Greece. These two taxa are not treated in the present investigation.

In the rest of subsect. *Peregrinae* from Greece and adjacent Turkey, two main form series are recognized that differ in habit, size and shape of the bracts and corolla colour. The last character is somewhat uncertain as notes about the corolla colour on herbarium sheets are rather rare and often impossible to state in sicco.

The form series perhaps do not represent natural entities, as the evolutionary pattern may be rather complex in subsect. *Peregrinae*. At present, the knowledge about sterility barriers and possibilities for crossings within subsect. *Peregrinae* is small. Many of the problems within and between the form series can only be solved by an investigation based on crossing experiments.

The position of *S. vacillans* RECH. FIL. is uncertain. Therefore, it is not referred to any of the form series.

Form series I. Usually white-flowered with large bracts, 1.25—2 times longer than the calyces (scutellum included) in the middle of the inflorescence. Bracts rarely equalling the calyx or slightly longer. Bracts ovate or oblong and acute (not acuminate). Plants usually erect, stout and pyramidally branched.

Within form series I, two main complexes are recognized. The *S. albida* complex (I A, pp. 41—46) has a main stem indumentum of short more or less hooked non-glandular hairs, while the *S. velenovskyi* complex (I B, pp. 46—50) has a stem pubescence of long and short more or less non-glandular hairs mixed with numerous glandular hairs of intermediate length.

Form series II. Flowers usually violet or purple. Bracts acuminate and shorter than the calyces. Specimens often small and basally branched. Only the *S. rubicunda* complex (pp. 50—52) belongs to this series.

I A. SCUTELLARIA ALBIDA COMPLEX

Bracts rounded, about 1.25—1.5 times longer than the calyx (scutellum included), with somewhat acute apices. Indumentum of stem of small non-glandular hairs, ± hooked and adpressed (Fig. 3). Glandular hairs absent or extremely rare.

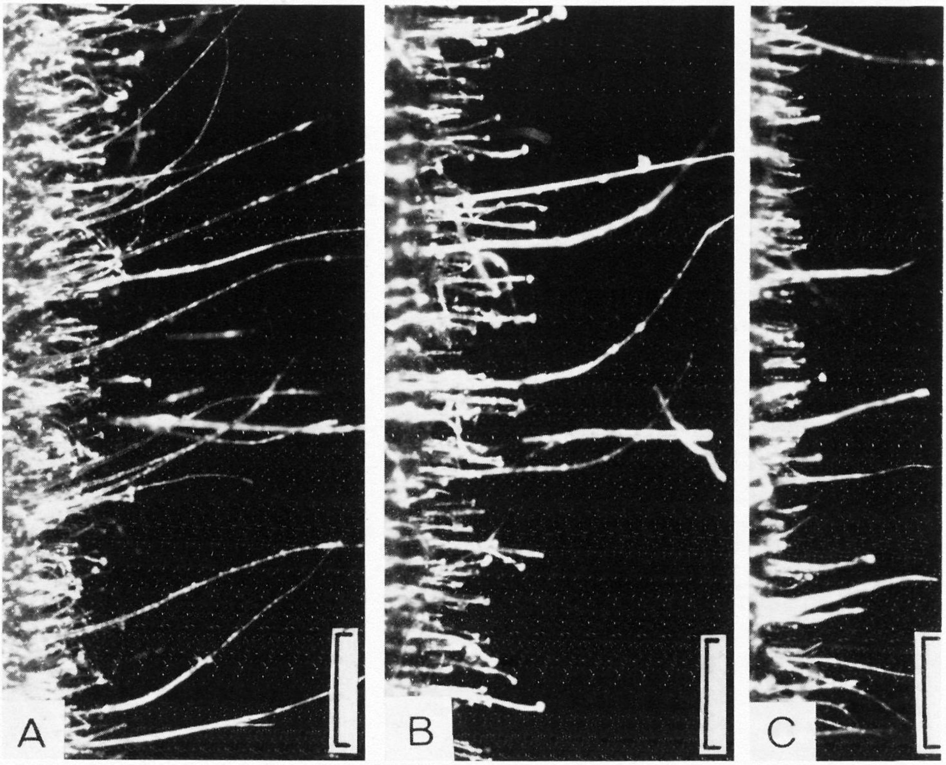

Fig. 2. Stem pubescence in *Scutellaria*. — A. *S. naxensis* BOTHM., Naxos [RUNEMARK and SNOGERUP 9941 (LD)]. — B. *S. velenovskyi* RECH. FIL. ssp. *velenovskyi*, "Monastir" (Bulgaria) [KECK and PICHLER, typus, (WU)]. — C. *S. vacillans* RECH. FIL., Kareikos [SINTENIS 668 (E)]. — The given scale units are all equal to 0.5 mm.

To this complex belong *S. albida* L., *S. pallida* BIEB., *S. woronowii* JUZ., *S. sieberi* BENTH., and *S. condensata* RECH. FIL.

RECHINGER (1941) described the species *S. pycnotricha*, but later on (RECHINGER 1962 b) he reduced it to a subspecies under *S. condensata*. Both *S. condensata* s. str. and *S. condensata* ssp. *pycnotricha* are Kurdistanian taxa with imbricate bracts and tight inflorescences; they

Fig. 3. Stem pubescence in *Scutellaria*. — A. *Scutellaria albida* L., Bologna [FIORI, BÉGUINOT, and PAMPANINI 481 (WU)]. — B. *S. albida* L., Andros [SNOGERUP and BOTHMER 31646 (LD)]. — C. *S. sieberi* BENTH., Crete [RUNEMARK, SNOGERUP et al. 17338 (LD)]. — D. *S. condensata* RECH. FIL. ssp. *condensata*, Kyl-Maghara-Dagh [SINTENIS 2903 (LD)]. — E. *S. woronowii* JUZ., Artwin [WORONOW 274, typus, (WU)]. — The given scale units are all equal to 0.5 mm.

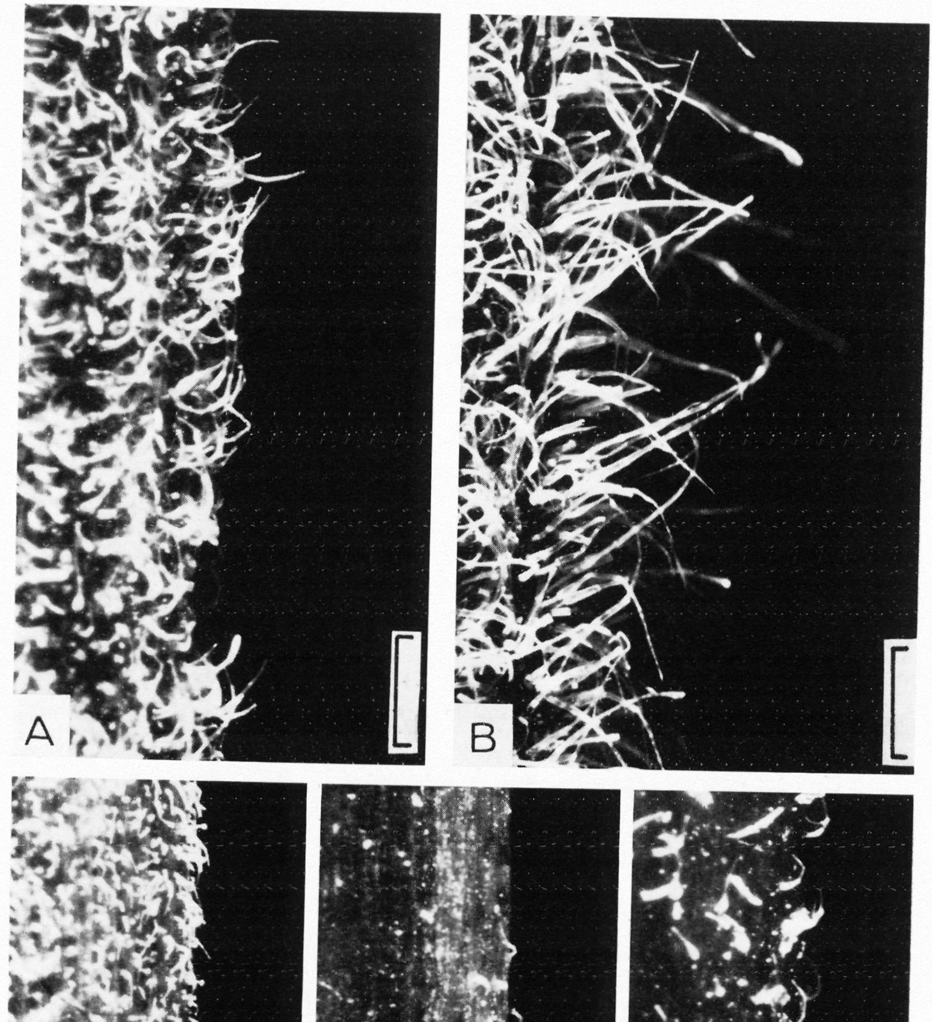

Fig. 3.

differ only in pubescence. Ssp. *condensata* has an extremely sparse indumentum (Fig. 3 D), but ssp. *pycnotricha* — of which I have seen no material — has long, dense, non-glandular hairs mixed with glandular ones, which indicates a possible relationship with *S. velenovskyi.*

S. sieberi, endemic to Crete, has a tight and imbricate inflorescence, too, but differs from the Kurdistanian species especially by its very dense, woolly indumentum of non-glandular hairs on the main stem (Fig. 3 C).

S. albida L. covers a large area from Italy (only a few localities) to western Turkey (Fig. 4). It is most common in Bulgaria and NW Turkey (around Istanbul). Material of *S. albida* from the Athos Peninsula and Thessaly differs from Bulgarian and Anatolian material by its smaller and more acute bracts.

S. woronowii JUZ., closely related to *S. albida,* is distributed in N Anatolia. *S. woronowii* is of small size (30—40 cm tall), lignified and branched at the base (cf. *S. rubicunda* and *S. vacillans*). The flowers are 11—12.5 mm long. The calyces are in the fruiting stage 6—7 mm long with a sparse indumentum. The bracts are somewhat smaller and more acute than in *S. albida.* JUZEPCZUK (1951, 1954) reports a violet or purple corolla colour in *S. woronowii.* Only one collection studied had violet flowers (Artwin, coll. WORONOW, typus). From the Artwin district, however, some other collections [BALL 1622 (E); STAINTON and HENDERSON 6082 (E)] are noted as creamy with a violet (or purple) spot on the lower petal. Completely white-creamy-flowered specimens are also represented. As there are no other distinguishing characters, the variation in corolla colour seems to be of restricted taxonomic importance and may be a result of introgression.

One collection from the Amasra Peninsula in Turkey [KHAN, PRANCE and RATCLIFFE 780 (E)] is extremely low (< 10 cm) with small leaves (1—1.5 cm). It deviates much from other collections in the area, but must be referred to *S. woronowii,* as it corresponds to this species in pubescence, flowers and bracts.

RECHINGER (1941) reported *S. albida* ssp. *pallida* and *S. vacillans* ssp. *colchica* from Kurdistan. The former taxon was a new combination based on *S. pallida* BIEB. from Crimea, which, according to JUZEPCZUK (1954), is an endemic species on this peninsula (see below). RECHINGER

Fig. 4. Distribution ranges for ● *Scutellaria albida* L.; ■ *S. woronowii* JUZ.; ◐ intermediates between *S. albida* and *S. woronowii.* (*S. albida* is also known from a few localities in central Italy).

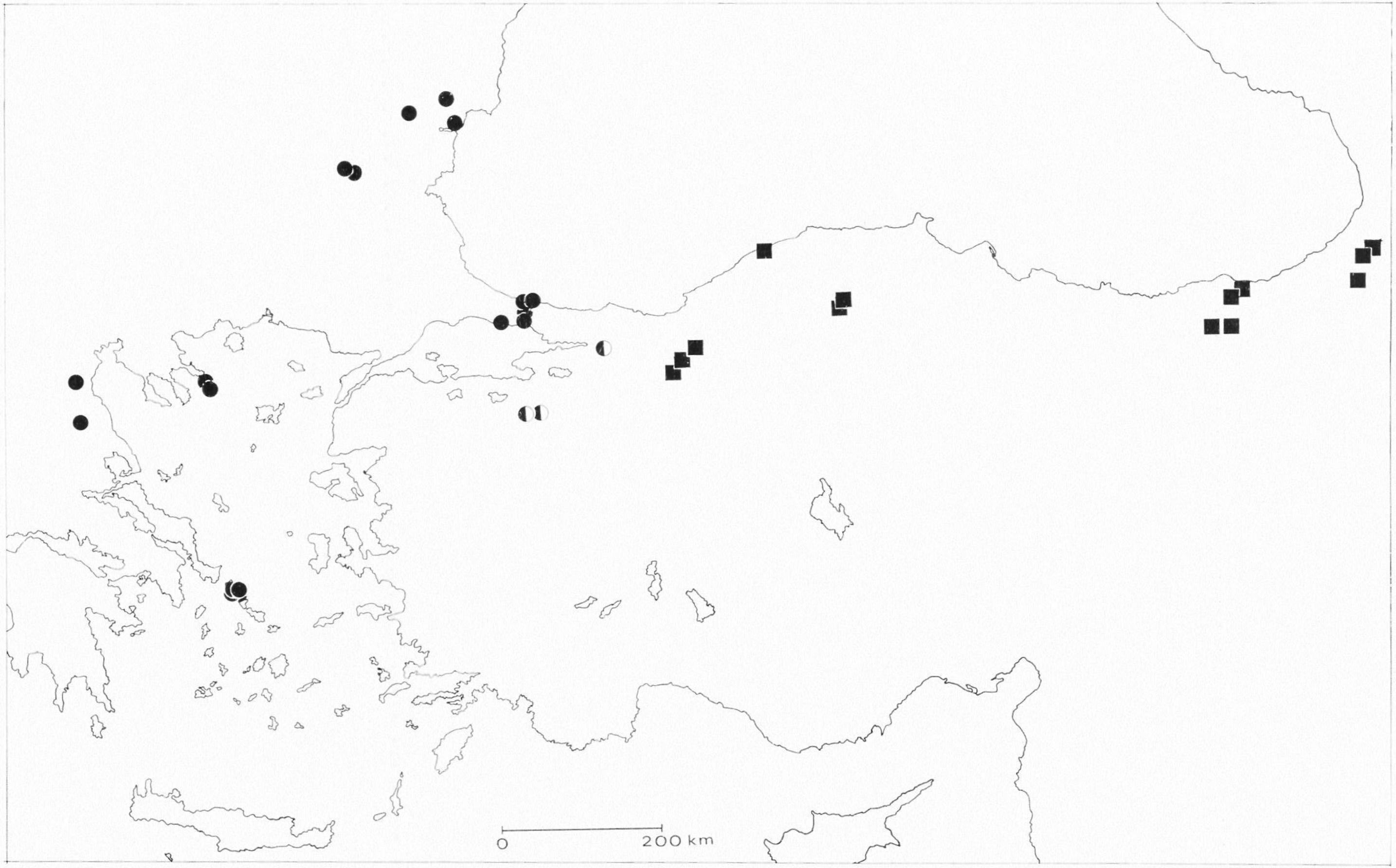

Fig. 4.

was uncertain about the systematical position of the taxa, but from later collections by DAVIS et al., it is evident that *S. vacillans* ssp. *colchica* and *S. albida* ssp. *pallida* sensu RECHINGER from Kurdistan have to be referred to *S. woronowii* JUZ. The habit of this species is remindfull of *S. vacillans*, but the stem pubescence is quite different (Figs. 2 C, 3 E). As discussed below, *S. vacillans* may be of hybrid origin. For this reason a connection with this Anatolian taxon is doubtful.

From Crimea (Tauria), *S. pallida* is described by MARSCHALL VON BIEBERSTEIN (1808). The collections from "Tauria" by PARREYS are very fragmentary; thus, a taxonomy built on this material must be very uncertain. RECHINGER (1941) reduced *S. pallida* to a subspecies of *S. albida,* as it resembled this species in many characters (large bracts and the same pubescence on the rachis). JUZEPCZUK (1954) retains *S. pallida* BIEB. as a separate species. It differs from *S. albida* in the shape of the bracts, which in *S. pallida* are more acute and narrow. The indumentum of *S. pallida* consists of somewhat longer and straighter hairs; and in the upper part of the stem, just below the inflorescence, glandular hairs are mixed with non-glandular ones.

Both *S. albida* and *S. pallida* occur on the Crimea, but the latter is endemic and known only from a few localities in the southern part of the peninsula. They also hybridize with each other (JUZEPCZUK 1954).

I B. SCUTELLARIA VELENOVSKYI COMPLEX

Indumentum of main stem consisting of long and short non-glandular ± straight hairs, and frequently glandular hairs, intermediate in size (Fig. 2 A, B). Bracts 1.25—2 times as long as the calyces (scutellum included).

To this complex belong *S. velenovskyi* RECH. FIL. and *S. naxensis* BOTHM. sp. nov.

On Naxos, RUNEMARK et al. have made 13 collections of a *Scutellaria* with large bracts. This material belongs undoubtedly to the *S. velenovskyi* complex with characteristic stem pubescence, but it deviates so much from *S. velenovskyi* that I prefer to describe it as a separate species.

Scutellaria naxensis BOTHM. sp. nov.

Herba 20—35 (—45) cm alta, a basi ramosa vel habitu pyramidali. Folia 30—40 (—60) mm longa, 20—35 (—50) mm lata, margine crenata, basi cordata, petiolo lamina paulo breviore. Inflorescentia laxa (5—) 10—15 (—18)

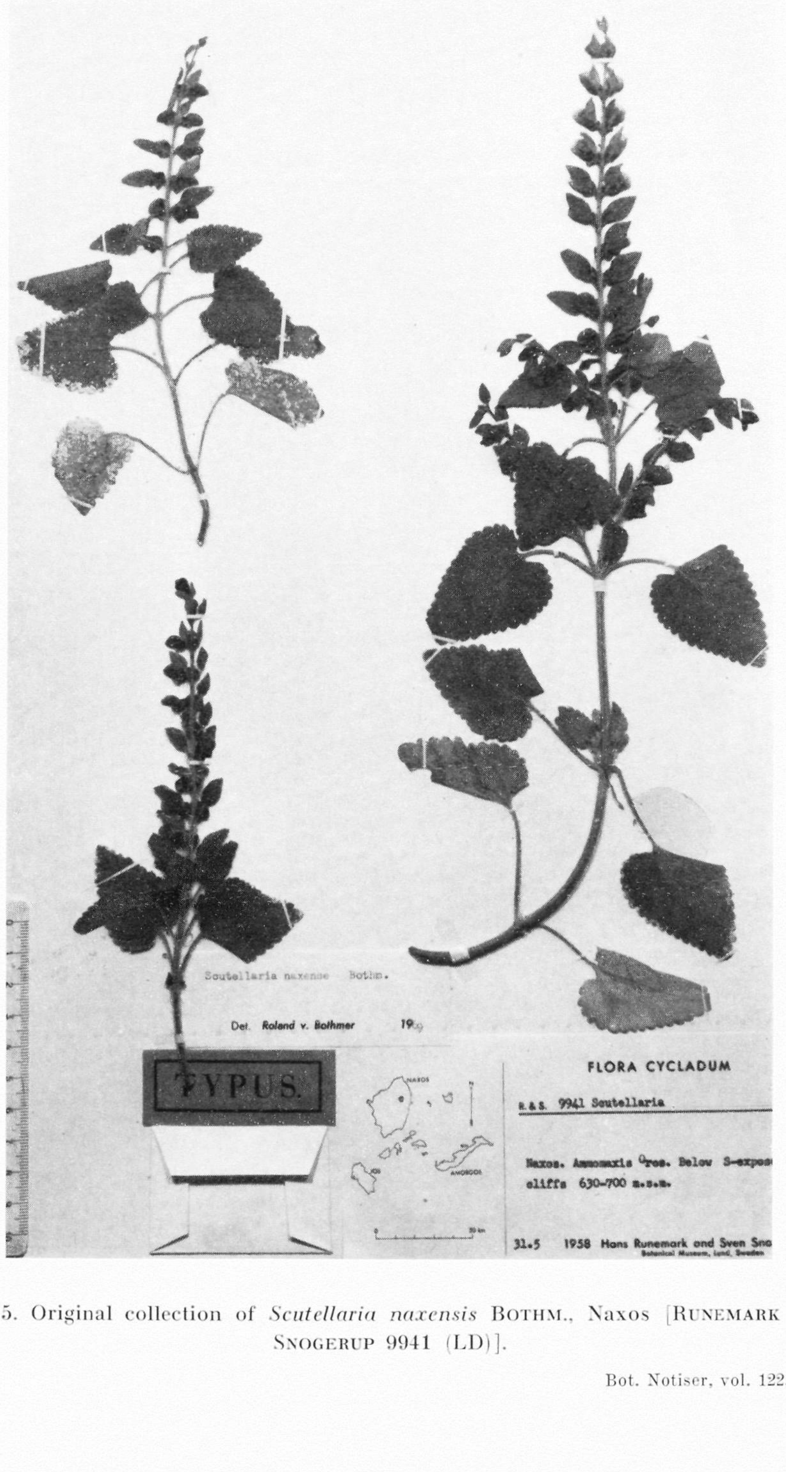

Fig. 5. Original collection of *Scutellaria naxensis* BOTHM., Naxos [RUNEMARK and SNOGERUP 9941 (LD)].

cm longa. Bracteae in media parte inflorenscentiae calyce ad duplo longiores, ovales vel ovatae, subacutae, non acuminatae. Calyx in statu florescenti 4.5—5.5 mm, in fructificatione 7.0—8.5 mm longus. Scutellum rotundatum, membranaceum. Corolla pallide coerulea (?), 11.5—13 mm longa, tubo amplo. Pubescentia in caule et inflorescentia triplex, pilis eglandulosis 1.2—2.3 mm longis, pilis eglandulosis 0.1—0.4 mm longis et pilis glandulosis 0.2—0.7 mm longis composita. Pubescentia scutelli sparsa, plerumque pilis longis eglandulosis (1.9—2.8 mm longis) formata. Calyx omnibus typis pilorum densissime pubescens. Semina 1.5—1.7 mm longa.

Naxos: Ammomaxis Oros, below S-exposed cliffs, 630—700 m. 31.5 1958, Runemark and Snogerup 9941 (LD, holotype).

S. naxensis. 25—30 cm (smaller in cultivation). *Leaves* with crenate margins (Fig. 1 A) and the petioles shorter than lamina. *Inflorescences* 7—17 cm long, the lateral ones usually smallest. Indumentum of the rachis dense, consisting of 0.2—0.7 mm long, glandular hairs, short, 0.1—0.4 mm, non-glandular hairs, and long, 1.2—2.3 mm, non-glandular hairs. Pubescence of the inflorescence denser and more shaggy than on the stem, especially the glandular hairs are longer and more frequent. *Calyces* in the flowering stage 4.5—5.5 (—6) mm, in the fruiting stage 7.0—8.5 (—9) mm. *Scutellum* broad, rounded and semi-membraneous. Pubescence on the scutellum very sparse with long, 1.9—2.8 mm, non-glandular hairs, short, 0.1—0.3 mm, non-glandular hairs and glandular hairs 0.4—0.8 mm. Pubescence on the calyx extremely dense with long non-glandular hairs especially frequent. *Flowers* 11.5—13.0 mm long with a broad corolla tube (Fig. 1 C). Corolla colour uncertain, but probably white or pale blue (collectors information). *Seeds* 1.5—1.7 mm long, tuberculate with stellate hairs.

Comparison between *S. naxensis* and *S. velenovskyi*:

Character Species	Habit	Calyx in fruit stage (mm)	Corolla (mm)	Length of bracts/ length of calyx
S. naxensis	Branching at base or pyramidally	7—8.5 (—9)	11.5—13.0	1.25
S. velenovskyi	Branching pyramidally[1]	(7—) 9—11	(12.5—)15—17	(1.25—) 1.5—2

[1] See below.

Fig. 6. Distribution range for *Scutellaria velenovskyi* Rech. fil. — except ssp. *subsimilis* Rech. fil. that is native to eastern Syria and western Iran —: ▲ ssp. *velenovskyi*; ■ ssp. *goulimyi* Rech. fil.; ● ssp. *perhispida* Rech. fil.

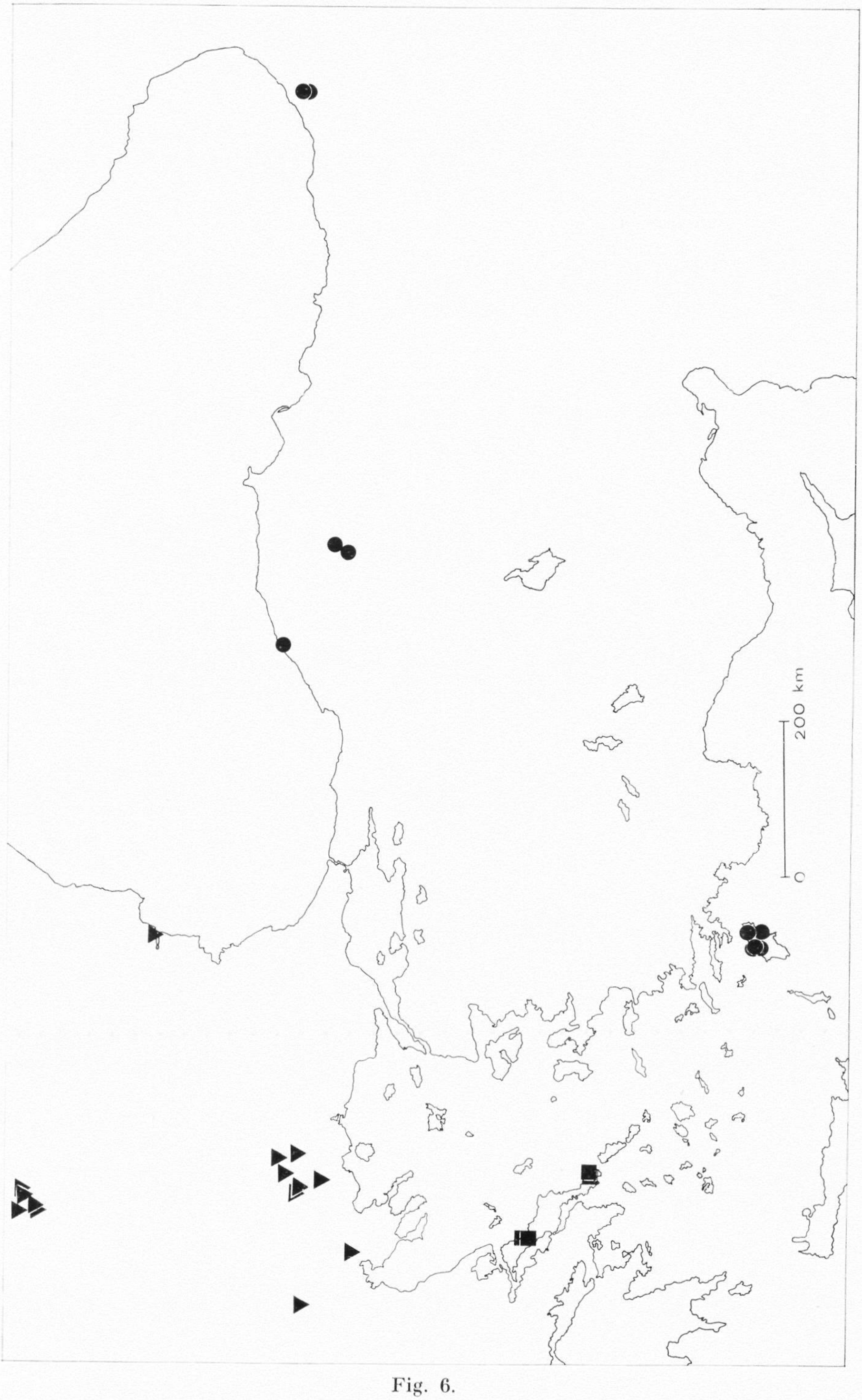

Fig. 6.

S. velenovskyi has a large distribution range from the Balkan Peninsula to Syria (Fig. 6). RECHINGER (1941, 1962 a) subdivided the species into four subspecies. Only two collections of ssp. *goulimyi* RECH. FIL. from Euboea [RECHINGER 18929 (W) and 16701 (W)] have some characters common to *S. naxensis*. They are low-grown with small leaves, and one of them is branched basally. The flowers are 12.5—15 mm, but in other collections [e.g. RUNEMARK and SNOGERUP 11750 (LD)] from Euboea, the flowers are 15—17 mm long.

II. SCUTELLARIA RUBICUNDA COMPLEX

Bracts small, acuminate, much shorter than or rarely equalling the calyx. Corolla colour violet or purple, seldom white (*S. geraniana*). Plants low-grown and basally branched. Pubescence extremely variable.

The *S. rubicunda* complex is represented in Greece by *S. rubicunda* HORNEM., *S. geraniana* (HAL.) RECH. FIL., *S. hirta* S. & S., and *S. rupestris* BOISS. & HELDR.

The group is heterogeneous, and in this paper only some of the taxonomic problems will be discussed. A more detailed study was made by RECHINGER (1941, 1943) and GREUTER and RECHINGER (1967).

In 1934, RECHINGER described a new species from Ikaria, *S. icarica* RECH. FIL., but later on (1941) he reduced it to a subspecies of *S. rubicunda* HORNEM. At the same time, he described *S. rubicunda* ssp. *samia* RECH. FIL. based on some collections from Samos. RECHINGER's collections from the two east Aegean islands are very different and were not considered to be closely related. Unfortunately, RECHINGER's Ikarian material was collected on the upper reaches of Mt. Atheras (ca. 950 m) and at this altitude, a low-grown form occurs. It is probably a mountain modification or possibly a mountain ecotype. I have seen eleven flowering collections from Ikaria, and one of these, also from the top of Mt. Atheras, 1000 m [RUNEMARK and SNOGERUP 12470 (LD)], is similar to RECHINGER's type material of ssp. *icarica*. Material from lower altitudes on Ikaria resembles collections from Samos. Transitional forms between the mountain form and material from lower altitudes exist.

Description of Ikarian and Samian material

HABIT. Full-grown specimens ramose and somewhat lignified at the base, often (at least on Ikaria) with a horizontal, creeping main stem from which the inflorescences arise. Inflorescences on adult plants rather sparse with about 1 cm between the whorls. Especially on Ikaria, there is a great variation in plant length. Young flowering plants and plants from high altitudes (ca. 1000 m) are low-grown, 10—15 cm, while older specimens are about 20—35 cm tall. The collections from Samos that I have seen have been 20—45 cm long.

INDUMENTUM OF THE STEM. A great variation in pubescence exists on the main stem, both in types of hairs, as well as in density and length. The glandular hairs on the stem are quite different from those on the inflorescence axis. They are much shorter, usually more dense and the gland is very small.

There is a small difference between Ikarian and Samian material in this character. The latter has a somewhat sparser and shorter indumentum on the stem. The pubescence of the "mountain type" on Ikaria is also less dense, and the hairs are shorter than in other Ikarian collections.

LEAVES. 1.3—2.8 cm in length, 1.2—2.4 cm in breadth. Leaf margin crenate or serrate. Leaf base truncate or somewhat cordate.

INFLORESCENCE LENGTH. 4.5—6.5 cm in material from Ikaria and 6.0—7.5 cm in Samian material. Apical inflorescences somewhat longer than the lateral ones. The collections from the top of Mt. Atheras, ca. 1000 m [RUNEMARK and SNOGERUP 12470 (LD) and RECHINGER 2212 (W)], and also some specimens at a lower altitude on Ikaria, have only one or two flowers.

INDUMENTUM ON THE RACHIS. Pubescence very dense and woolly. Glandular hairs 0.5—0.75 mm long. There are usually two types of non-glandular hairs, one ca. 0.5 mm and the other 1.5—2.0 mm long, but intermediate hairs occur.

Material from Samos and Ikaria have a similar indumentum on the inflorescence axis, except for the "mountain type" from Ikaria, which has a sparse indumentum of much shorter hairs than the low-altitude specimens. The long non-glandular hairs are 1.0—1.3 mm and the short ones are 0.2—0.3 mm long. The glandular hairs are 0.3—0.4 mm in length.

COROLLA, CALYX AND BRACTS. Length of the corolla 11.0—13.0 mm in both Ikarian and Samian material. Calyces in the flowering stage ca. 4.0 mm long and in the fruiting stage 6.5—7.5 mm.

The "mountain type" from Ikaria deviates with somewhat shorter calyces both in the flowering and in the fruiting stages (ca. 3.5 mm and ca. 6 mm respectively) and length of corolla 11—12 mm.

Rechinger (1941) states that his collections from Samos have blue flowers in contrast to Ikarian material, which has purple flowers. However, on two sheets collected on Samos by Gathorne-Hardy (E), the colour of the corolla is described to be "purple". Living plants of *S. rubicunda* that I saw on Ikaria had purple flowers.

The investigation shows that *S. rubicunda* ssp. *icarica* and ssp. *samia* must be referred to the same taxon, and the former name is chosen for it — *Scutellaria rubicunda* Hornem. ssp. *icarica* (Rech. fil.) Rech. fil.

The close relationship between the Samian and Ikarian specimens of *S. rubicunda* is interesting to note, as Ikaria seems to have a rather isolated flora without any closer affinity with the floras of the Kikladhes and Samos.

In *S. rubicunda,* the "mountain form" of ssp. *icarica* from Ikaria resembles ssp. *cephalonica* (Bornm.) Rech. fil. from Kephallinia in westernmost Greece in habit. The low-grown type of ssp. *icarica* has, however, longer calyces both in the flowering and in the fruiting stages, longer and broader leaves, and denser indumentum of the inflorescence.

S. rubicunda ssp. *icarica* resembles *S. subvelutina* Rech. fil., which is distributed in Turkey, Syria, and Israel. *S. subvelutina* is a heterogeneous species, but there are some characters differing from the Samian and Ikarian taxon. *S. subvelutina* has a longer calyx and corolla, the leaves are usually longer and broader, and the whorls are sparser. The indumentum on rachis and stem is much more sparse and consists of shorter hairs. The long non-glandular hair type in *S. rubicunda* ssp. *icarica* is almost wholly lacking in the Asiatic species.

Rechinger (1941) indicates that one collection of *S. subvelutina* collected by Boissier from Denisleh (not seen by me) is especially close to *S. rubicunda.* Probably *S. subvelutina* must be referred to the *S. rubicunda* complex, and perhaps also *S. megalaspis* Rech. fil. and *S. brevibracteata* Stapf. A more thorough study of the *S. rubicunda* complex, including taxa native to Asia Minor, is planned by the author.

SCUTELLARIA VACILLANS

There is a great deal of variation in *S. vacillans* though it covers only a small area (Fig. 7 A). Most of the specimens are small, branched and

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Fig. 7. Distribution ranges for: A. *Scutellaria vacillans* Rech. fil. — B. *S. naxensis* Bothm.

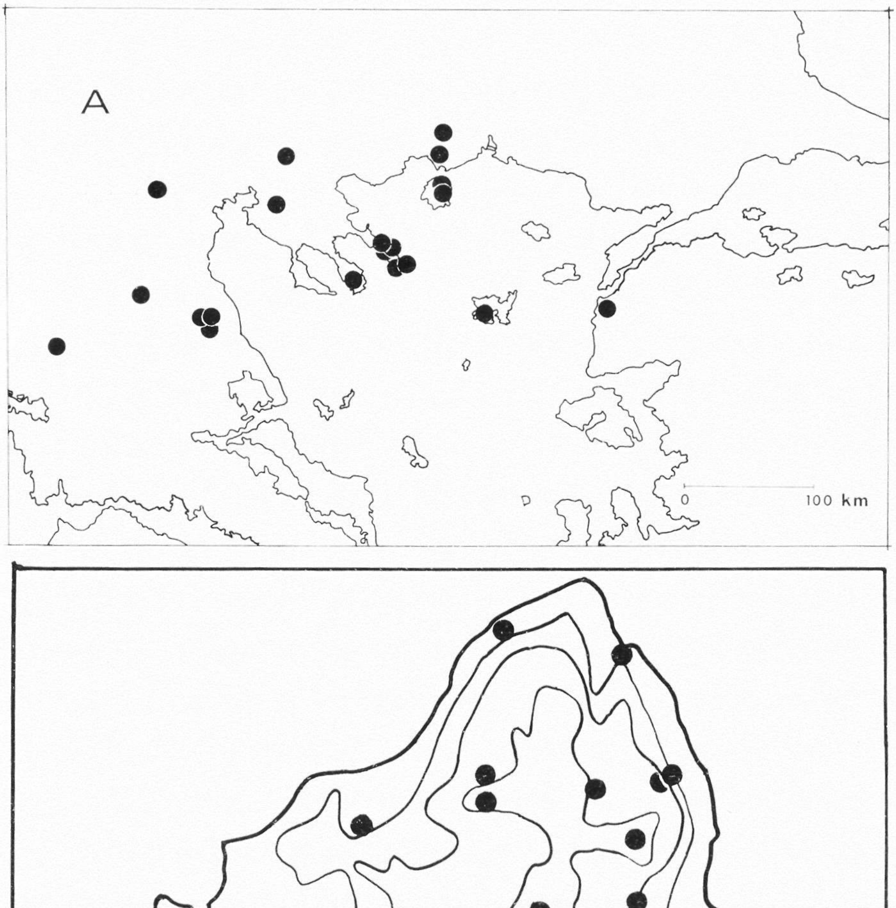

Fig. 7.

lignified at the base; but some are rather stout and pyramidally branched. The corolla colour varies from white to violet. The bracts are slightly larger than the calyces, which is a stable character in this species.

In its ascendant habit, basal branching and indumenta of stem and inflorescence, *S. vacillans* is remindfull of *S. naxensis,* but the latter species has smaller flowers (11.5—13.0 mm and 13.0—15.0 mm respectively) and a much broader corolla tube. The scutellum in the fruiting stage is larger in *S. naxensis* (7.5—8.5 mm) and more rounded than in *S. vacillans* (< 7.0 mm).

In Thessaly and Macedonia, where *S. vacillans* is indigenous, several taxa in subsect. *Peregrinae* meet. There are members of the *S. rubicunda* complex (*S. geraniana, S. rubicunda* ssp. *parnassica,* ssp. *hellenica* and ssp. *adenotricha*), *S. velenovskyi* complex (*S. velenovskyi* ssp. *velenovskyi*) and *S. albida* complex (*S. albida* s. str.). Considering the great heterogeneity, *S. vacillans* could be a hybrid complex between taxa in that area. Transition from white (*S. albida, S. velenovskyi* and *S. geraniana*) to violet corolla colour (*S. rubicunda*), or from small, low-branched plants (*S. rubicunda* and *S. geraniana*) to tall pyramidally branched ones (*S. albida* and *S. velenovskyi*) occur. The intermediate size of bracts is also an indication of a possible hybrid origin of *S. vacillans,* which even RECHINGER (1941) discusses.

The pollen fertility in 15 populations of *vacillans* was investigated. In 13 populations there was 90—100 % good pollen, while in two populations the fertility was lower (85—90 % and 70—75 % good pollen).

EVOLUTIONARY PATTERN

Scutellaria, throughout its distributional range in both hemispheres, is mostly montane, preferring mesophytic areas. In Greece the taxa in subsect. *Peregrinae* usually are found at high altitudes (300—2000 m) beside rills and springs, or at the base of limestone rocks and in maquis with good water supply. The restriction of the species to mesophytic biotopes causes many disjunctions in distribution ranges, as such localities are unevenly distributed in the eastern Mediterranean. In Greece and Asia Minor geographical isolation between *Scutellaria* populations, earlier more or less connected to one another, occur. This has caused a differentiation into several local races and forms (RECHINGER 1941, GREUTER and RECHINGER 1967, and JUZEPCZUK 1954).

In 1968, SNOGERUP and BOTHMER collected five populations of *S. albida* on Oros Kouvara on Andros. No other localities for the species were found despite many suitable biotopes. The populations within this small area compose a distinct, uniform local race, characterized by a dense woolly indumentum that imparts an almost white appearance to the single specimen (Fig. 3 B, cf. also RECHINGER 1943).

The areas in the Kikladhes where species of *Scutellaria* are frequent are probably refuges from an older distribution during pluvial periods (RUNEMARK 1961). On these islands other montane or central European species are growing that are also probable relics, e.g. *Blechnum spicant* (L.) ROTH [Andros, SNOGERUP and BOTHMER 32352 (LD)], *Solidago virgaurea* L. [Naxos, RUNEMARK and SNOGERUP 9767 and 12402 (LD), Tinos, RUNEMARK and ENGSTRAND 36663 (LD)] and *Clinopodium vulgare* L. (Andros, Tinos and Naxos, BOTHMER 1967).

The general distributions of the main form series (the white and the violet flowered) are large; but the taxa (species and subspecies) usually cover narrow geographical areas. The *S. rubicunda* complex has a more narrow distribution range in Europe and is restricted to Greece and Sicily, whereas the white-flowered form series is distributed on the whole Balkan Peninsula and in central Italy.

Local endemic taxa of *Scutellaria* are almost unknown in other parts of the world and members of the genus growing on islands are extremely rare (EPLING 1942). In subsect. *Peregrinae* from the east Mediterranean area, insular populations are, however, not rare.

A special pattern of endemism has evolved on some of the bigger islands. Cyprus, Crete and Sicily have two endemic taxa each. On Crete *S. sieberi* BENTH. and *S. hirta* S. & S. are frequent. The former is a member of the *S. albida* complex and the latter belongs to the *S. rubicunda* complex. On Cyprus *S. sibthorpii* (BENTH.) HAL. and *S. cypria* RECH. FIL. occur, and on Sicily *S. columnae* ALL. ssp. *gussonei* RECH. FIL. and *S. rubicunda* HORNEM. ssp. *linneana* (CAUREL) RECH. FIL. are native. Hybrids between the Sicilian taxa are known from some localities (RECHINGER 1941). On Crete some specimens from the Sphakia area [SNOGERUP 20966 and 21000 (LD), and RUNEMARK, SNOGERUP et al. 17338 (LD)] show intermediate characters (bracts and indumentum) between *S. sieberi* and *S. hirta*, which are also known from that area.

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Studies in the Genus Allium II

A New Subgenus and New Sections from Asia

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ABSTRACT

A new subgenus *Bromatorrhiza* EKBERG and two sections of this subgenus, *Bromatorrhiza* and *Coleoblastus* EKBERG are described together with sect. *Porphyroprason* EKBERG of subgenus *Molium* (KOCH) WENDELBO. The genus *Milula* shows relationship to *Allium* subgen. *Bromatorrhiza* and is a member of the tribe *Allieae*.

INTRODUCTION

TRAUB (1968 p. 159) published a new subgenus *Amerallium* TRAUB, which included the indigenous American and some European-Mediterranean species of *Allium*. He also reviewed those subdivisions of the genus occurring in the old world and provisionally recognized by STEARN (1944 p. 20) preliminary to further investigation. It is now clear, that the latter system is partly outdated and needs much modification. As STEARN stated, too little attention has hitherto been given to the internal structure of the bulb. A knowledge of the organization and development of the bulb is, indeed, of the greatest importance for the understanding of the interrelationship within the genus *Allium* (cf. MANN 1960 p. 770).

In the Botanical Garden of Gothenburg a good collection especially rich in SW. Asiatic *Allium* species has been built up. Thus I have been able to study species from different groups of the genus. Species in the sections listed below and some additional Sino-Himalayan and American species have been studied: *Acanthoprason* WENDELBO, *Allium, Briseus* (SALISB.) STEARN, *Codonoprasum* (RCHB.) ENDL. *Kaloprasum* C. KOCH, *Megaloprason* WENDELBO, *Melanocrommyum* WEBB & BERTH., *Molium* KOCH, *Regeloprason* WENDELBO, *Rhizirideum* KOCH, *Scorodon* C. KOCH, *Thaumasioprason* WENDELBO, and *Xanthoprason* F. HERMANN.

ALLIUM, SUBGENUS BROMATORRHIZA SUBGEN. NOV. AND ITS SECTIONS

Subgenus **Bromatorrhiza** Ekberg, subgen. nov.
Typus subgeneris: *Allium wallichii* Kunth

Radices numerosae, fasciculatae, incrassatae, penariae, apice ± ramosae; radices anni praecedentis exsuccae; rhizoma non evolutum; folia et cataphylla non penaria; vaginae foliorum anni praecedentis in fibras dissolutae.

This new subgenus is characterized by the fasciculate storage roots and lack of cataphylls with storage function. The storage roots are fully developed in the autumn and yield nutriment to the growing plant during the next vegetative season, thus becoming thin and wrinkled; these old roots easily break off, due to an abscission layer. Leaf sheaths of the last year, homologous with some of the outer tunics of a true *Allium* bulb, become fibre-like threads. Although the storage system in the subgenus *Bromatorrhiza* is entirely different from that of the rest of the genus, there is no reason to split off this group as a separate genus. Other characters indicate that the species of subgenus *Bromatorrhiza* are typical members of the genus; they certainly possess the most well-known of all *Allium*-characters, the alliaceous smell.

1. Sect. **Bromatorrhiza** (Fig. 1).

Typus sectionis=typus subgeneris: *Allium wallichii* Kunth

Scapus sectione transversali ± angulatus nonnunquam teres, saepe alatus. Folia plura, saepe manifeste carinata.

This section is characterized by an angular scape (an exception is *A. fasciculatum*) and often sharply carinate leaves. The primordia of the foliage leaves of the next year form together a bulb-like organ, which lacks the swollen storage cataphylls characteristic of a normal bulb. Vegetative reproduction may take place by means of buds at the base of the leaves or shoots arising from peripheral parts of the disc-like bulb-plate. At first the shoots resemble the storage roots shape. In *A. wallichii* nectar is secreted by cells at the middle of the ovary, but no nectary pits can be seen.

The following species belong to the section *Bromatorrhiza*: *A. cyathophorum* Bureau & Franch., *A. fasciculatum* Rendle, *A. macranthum* Baker, and *A. wallichii* Kunth. I also include a group of species closely related to *A. wallichii*: *A. bulleyanum* DIELS, *A. hookeri* THW., *A. lancifolium* STEARN and *A. polyastrum* DIELS. These species are at present not properly understood and with further investigation may prove to be synonymous with other species.

2. Sect. **Coleoblastus** EKBERG, sect. nov. (Fig. 2).

Typus sectionis: *Allium mairei* H. LÉV.

Caulis teres, tenuis, prope basin gemmifer; gemma plantam anni sequentis proferens. Folia tenuia.

This section is characterized first of all by buds — gemmae — attached near the base of the somewhat elongated stem. This character seems to be unique within the genus, in other species such buds are attached to the disclike stem or bulb-plate. The inflorescence has bracteoles at the base of the pedicels; in *A. mairei* H. LÉV. there are two bostryxes (helicoid cymes) each subtended by a bracteole. Such bracteoles have not been found in members of the sect. *Bromatorrhiza*. No nectary pits can be traced. To this section I refer *A. acidoides* STEARN and *A. mairei* H. LÉV.

MILULA AND ITS RELATION TO ALLIUM

The genus *Milula* described by PRAIN 1895 was originally placed in a subtribe of its own *Miluleae*, close to subtribe *Allieae*. K. KRAUSE (1930 p. 329) treated *Miluleae* as a separate tribe, and finally HUTCHINSON (1934 pp. 100, 130) placed this tribe in *Liliaceae* and the tribe *Allieae* in *Amaryllidaceae*.

STEARN (1960 p. 189) pointed out that the genus *Milula* 'would indeed be an *Allium* but for its spiciform inflorescence and gamophyllous perianth'.

In connection with my studies of the species that have been placed in *Allium* subgenus *Bromatorrhiza*, I have also had possibility of examining material of *Milula spicata* PRAIN which occurs in much the same geographical area, Nepal and SE. Tibet.

Milula has the same type of storage roots as in the species of subgenus *Bromatorrhiza*. In addition it must be pointed out the characteristic alliaceous smell.

The spathe of *Milula* has great similarities to the spathe of species of the subgenus *Bromatorrhiza*, and points to a close relationship to *Allium*.

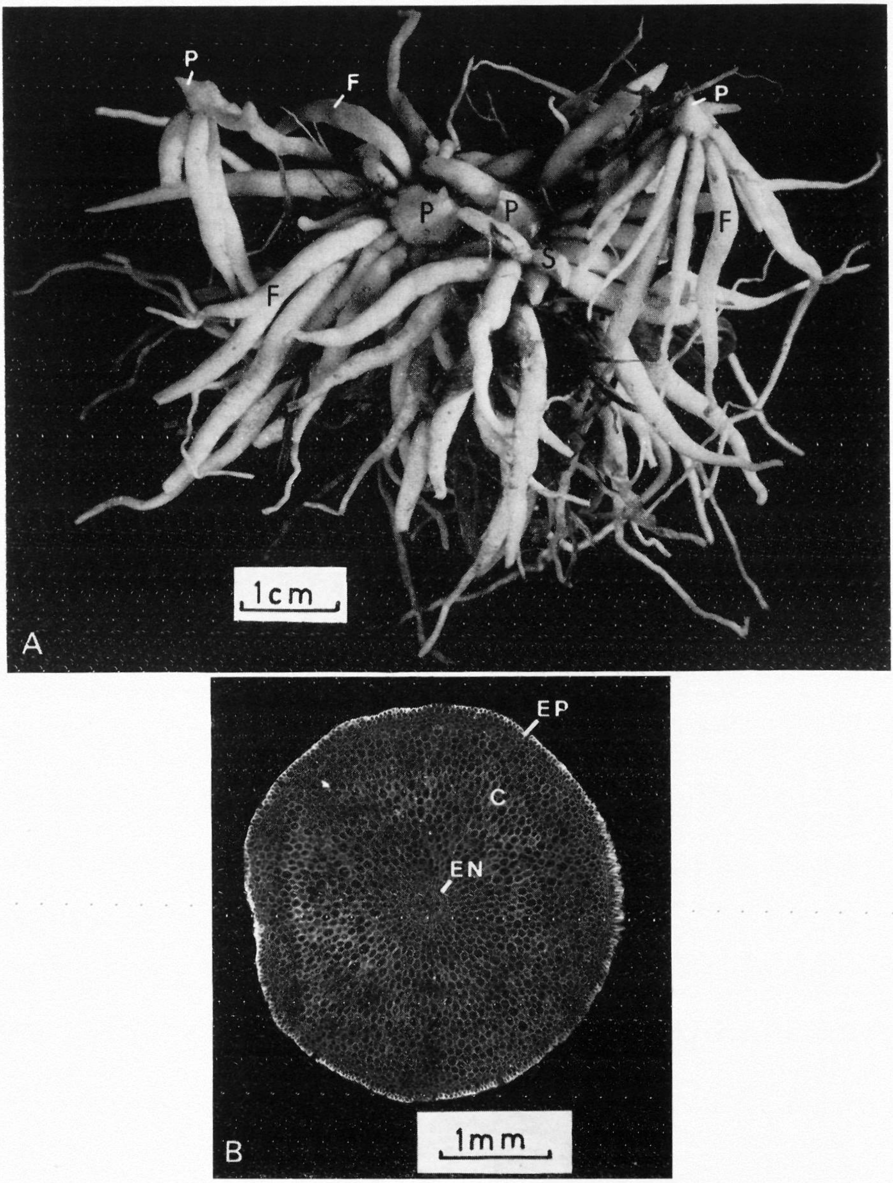

Fig. 1. *Allium macranthum* Baker. — A. Foliage leaves removed. F, storage root; P, leaf primordia gathered into a bulb-like organ; S, shoot. — B. Cross section through a storage root. EP, epidermis; C, cortex with storage tissue; EN, endodermis. Photo H. Rasper.

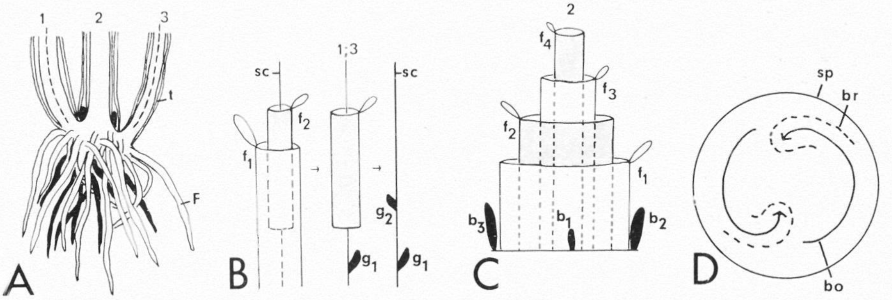

Fig. 2. *Allium mairei* H. Lév. Diagrams of a plant at the time of flowering. — A. Basal part of a plant with three leaf-bundles 1, 2, 3; F, fasciculate root; *t*, thread-like remains of the old leaf-sheaths. — B. Basal part of the leaf-bundles 1 and 3 in A; *f*, foliage leaf-sheath; *g*, gemma; *sc*, scape. — C. Basal part of leaf bundle 2 in A which has no scape; *b*, buds; *f*, foliage leaf-sheath. — D. Inflorescence; *bo*, bostryx; *br*, bracteole; *sp*, spathe.

Thus it seems as the main difference between *Allium* and *Milula* would lay in the inflorescence, viz. an umbel and a spike. There is, however, a great variation in the inflorescence of *Allium*. In many species the inflorescence is compact and head-like; in *A. regelii* Trautv. (sect. *Regeloprason*) there are several superposed verticils of flowers. I think the spiciform inflorescence should not be overemphasized in a discussion of the systematic position of *Milula*. In *Primula*, a genus of about the same number of species as in *Allium*, there are likewise different types of inflorescences. The usual type of inflorescence is an umbel. In sect. *Muscarioides* Balfour and sect. *Soldanelloides* Pax there are capitate and spicate inflorescences; e.g. *Primula vialii* Franchet has a long dense spike. In sect. *Sphondylia* Duby and in sect. *Proliferae* Pax (=*Candelabra* Balfour) the inflorescence consists of several superposed verticils of flowers.

The gamophyllous perianth of *Milula* does not necessitate removing *Milula* far from *Allium*. In sect. *Regeloprason* the tepals are united for about 1/3 of their length and in some species of the section *Acanthoprason*, e.g. *A. akaka* Gmel., the tepals are united at the base for a short distance.

With some hesitation I accept the genus *Milula* as being distinct from *Allium*, but I cannot see any reasons whatsoever for maintaining *Miluleae* as either a tribe or a subtribe. *Milula* is closely related to *Allium* and is clearly a member of the tribe *Allieae*.

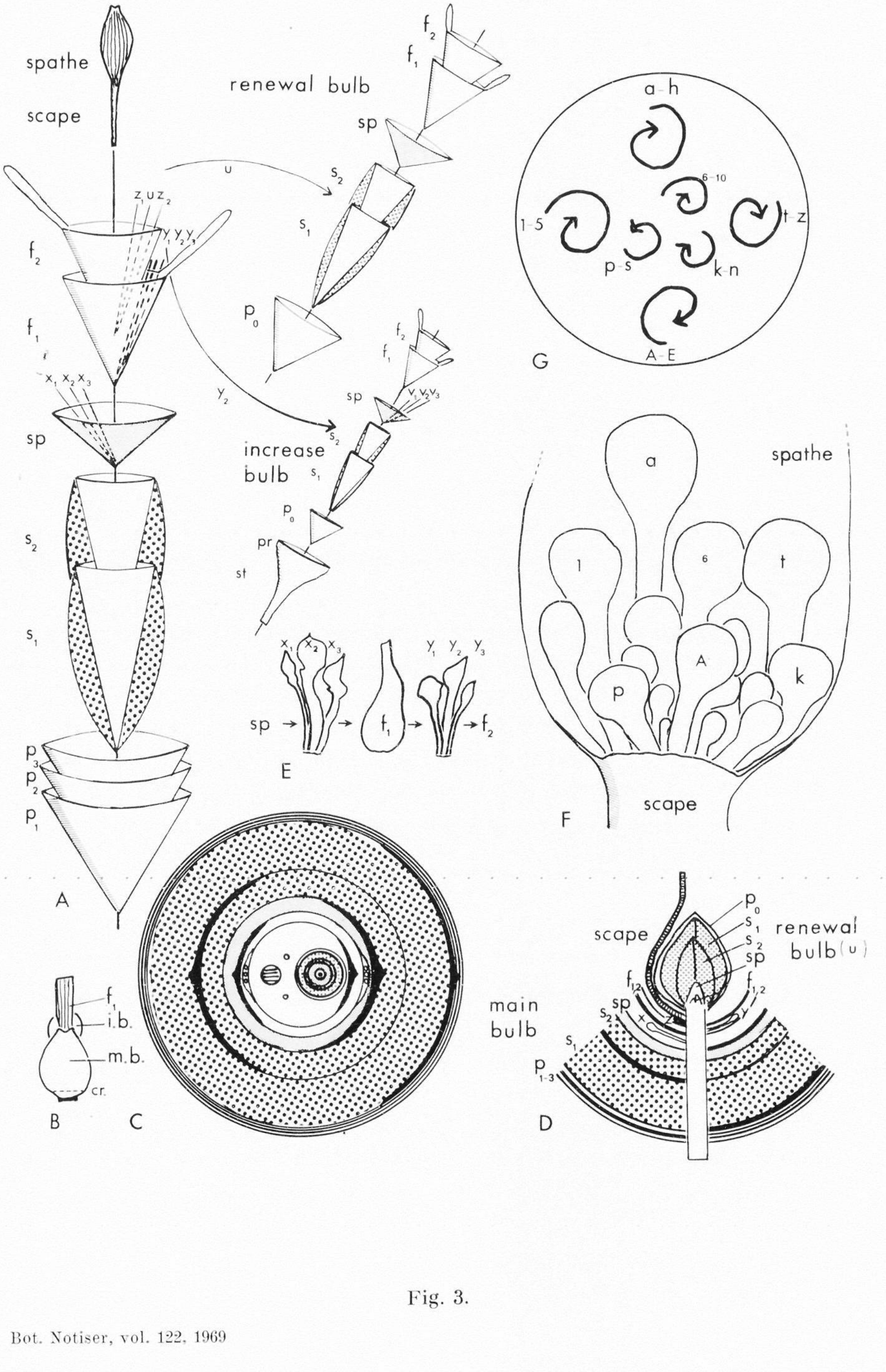
spathe
scape
f_2
f_1
z_1 u z_2
y_1 y_2 y_3
x_1 x_2 x_3
sp
s_2
s_1
p_3
p_2
p_1
A
u
y_2
renewal bulb
f_2
f_1
sp
s_2
s_1
p_0
increase bulb
f_2
f_1
sp
v_1 v_2 v_3
s_2
s_1
p_0
pr
st
x_1 x_2 x_3
y_1 y_2 y_3
sp
f_1
f_2
E
a–h
6–10
1–5
t–z
p–s
k–n
A–E
G
spathe
a
1
6
t
A
p
k
scape
F
f_1
i.b.
m.b.
cr.
B
C
main bulb
scape
p_0
s_1
s_2
sp
renewal bulb (u)
$f_{1,2}$
sp
s_2
s_1
p_{1-3}
$f_{1,2}$
x
z
y
D

Fig. 3.

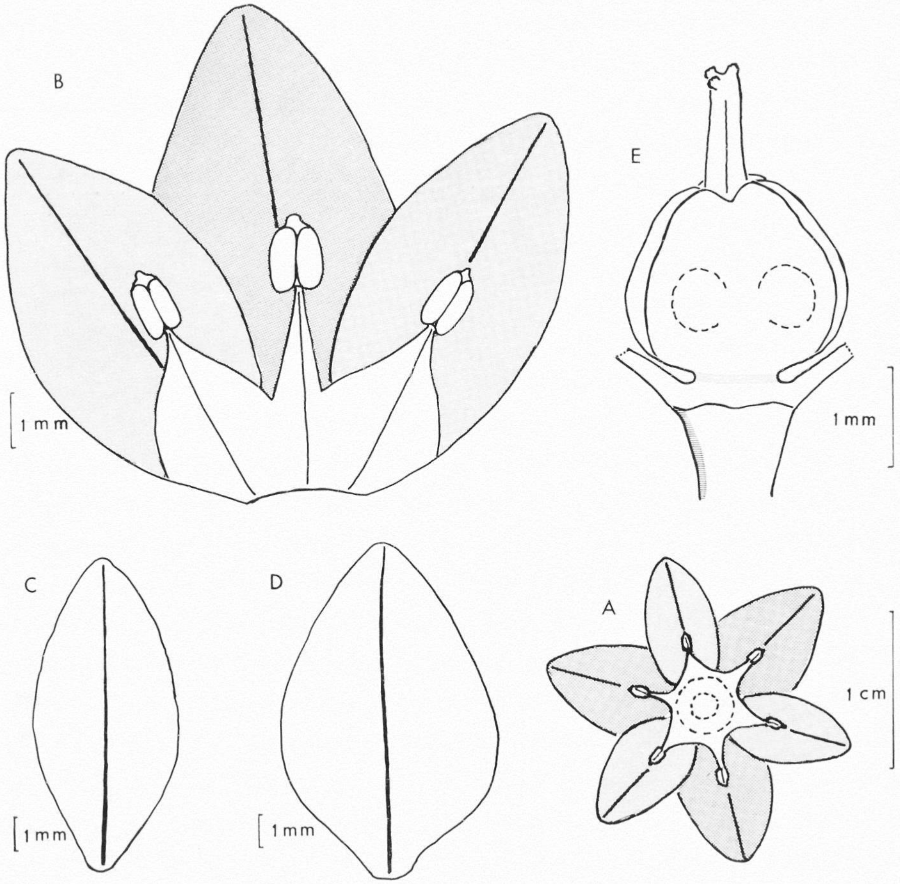

Fig. 4. *Allium oreophilum* C. A. Mey. — A. Flower, ovary removed. — B. Filaments and tepals. — C. Inner tepal. — D. Outer tepal. — E. Ovary with style and parts of tepals and pedicel, dotted lines indicate position of seeds.

Fig. 3. Diagrams of the bulb and the inflorescence of *Allium oreophilum* C. A. Mey. A—E. *p*, protective leaf; *s*, storage leaf; *sp*, sprout leaf; *f*, foliage leaf; *st*, stalk of increase bulb; *pr*, prophyll; *i.b.*, *v*, *x*, *y*, *z*, increase bulbs; *u*, renewal bulb; *m.b.*, main bulb. — A. Diagram of a plant at the time just before flowering; the internodes have been elongated to show the individual leaves. — B. The place of cross section cr. in C. ×0.5. — C. Cross section of the same bulb. — D. Longitudinal section of the same bulb. — E. Increase bulbs. ×0.5. — F. Longitudinal section through spathe showing the relative size of flower primordia; only the first flower primordium in each bostryx primordium is marked. — G. Inflorescence primordium in F seen from above. The arrangement of bostryx primordia 1—5, *a*—*h*, *t*—*z*, A—E, *p*—*s*, 6—10 and *k*—*n*.

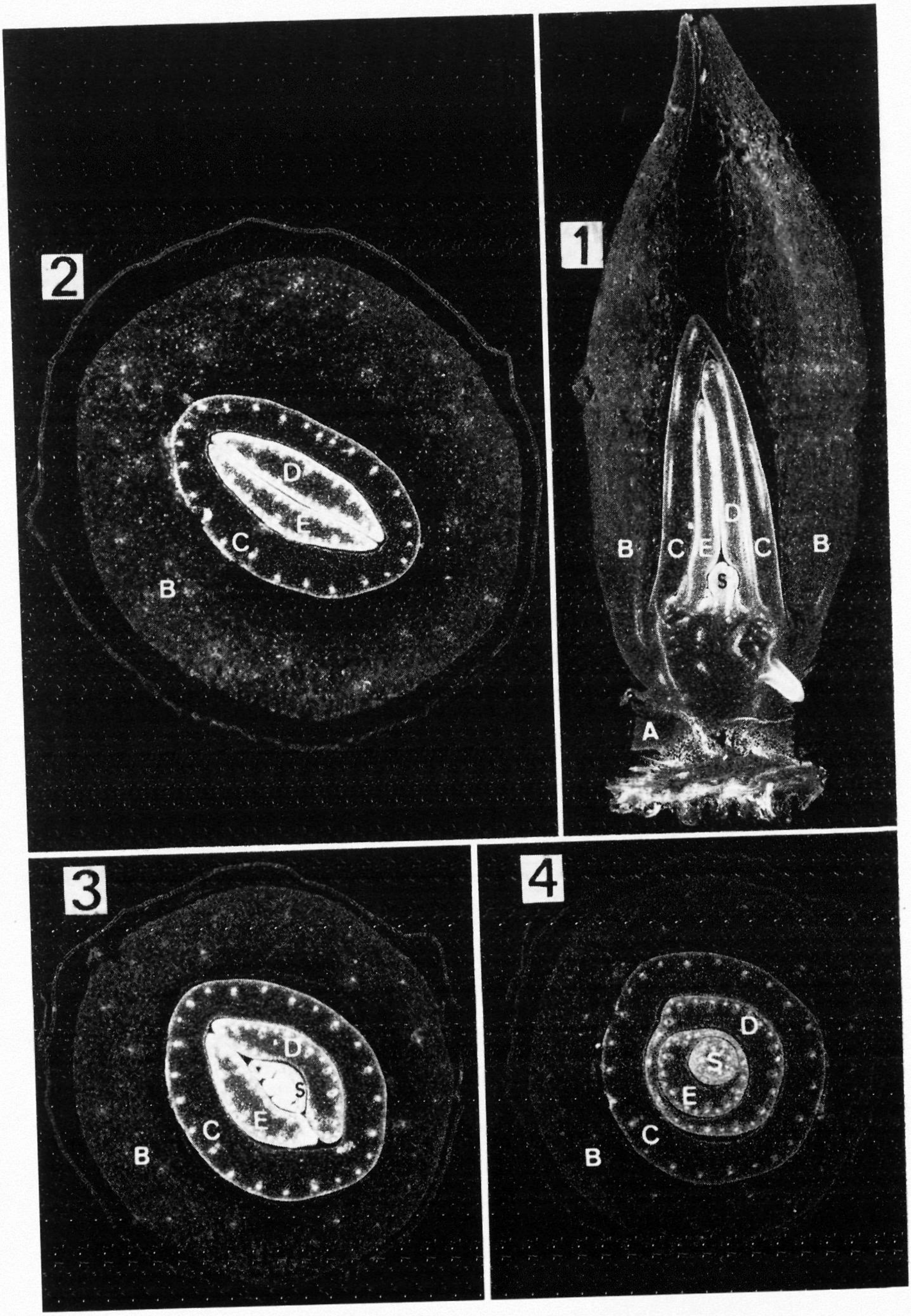

Fig. 5.

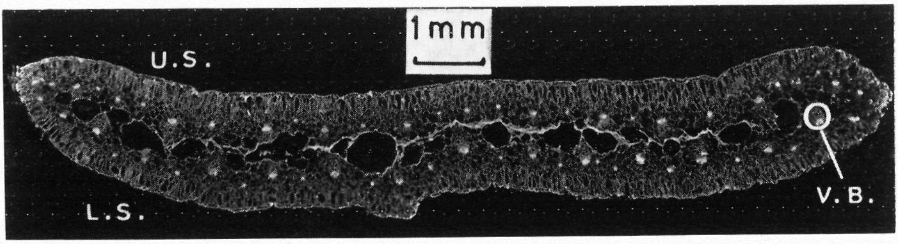

Fig. 6. *Allium oreophilum* C. A. Mey. Cross section through foliage leaf showing the organization of vascular bundles; V.B., vascular bundle; U.S., upper side; L.S., lower side. Photo: H. Rasper.

ALLIUM OREOPHILUM AND ITS SYSTEMATIC POSITION

Subgenus **Molium** (Koch) Wendelbo

Sect. **Porphyroprason** Ekberg, sect. nov. (Figs. 3—8).
Typus sectionis: *Allium oreophilum* C. A. Mey. (Fig. 8).

Bulbus cataphyllis penariis binis; bulbilli laterales pedunculati ± numerosi. Folia applanata, vernatione plana. Tepala magna et lata, post anthesin immutata. Filamenta connata et perigonio per dimidiam longitudinem adnata, lata. Ovarium loculis biovulatis, foveolis nectariferis nullis. Stigma trilobum.

Anatomical studies were made on material of *A. oreophilum* procured from the firma of C. G. van Tubergen of Haarlem, Holland.

The organization of the bulb and of the inflorescence is illustrated (Fig. 3) in the same way as Mann (1959 p. 767, 1960 p. 737) has done for other species. In subgenus *Melanocrommyum* and sect. *Molium* there is only one true storage cataphyll, whereas there are two in sect. *Porphyroprason*. However, there are two sprout leaves in the subgenus

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Fig. 5. Bulb of *Allium oreophilum* C. A. Mey. A, first storage leaf (removed); B, second storage leaf; C, sprout leaf; D, E, primordia of foliage leaves; S, spathe or scape primordium. — 1. Longitudinal section through bulb at the start of growth. Between the foliage leaf primordia E and D are the scape and spathe primordia. Between S and D at base is increase bulb primordium. ×15. — 2. Cross section of bulb at a level above spathe primordium. ×10. — 3. Cross section through the bulb at level of spathe primordium showing in the centre the spathe primordium S, enveloping the flower primordia. ×10. — 4. Cross section through bulb at a level below spathe primordium showing in the centre the scape primordium. ×10. — Photo: H. Rasper.

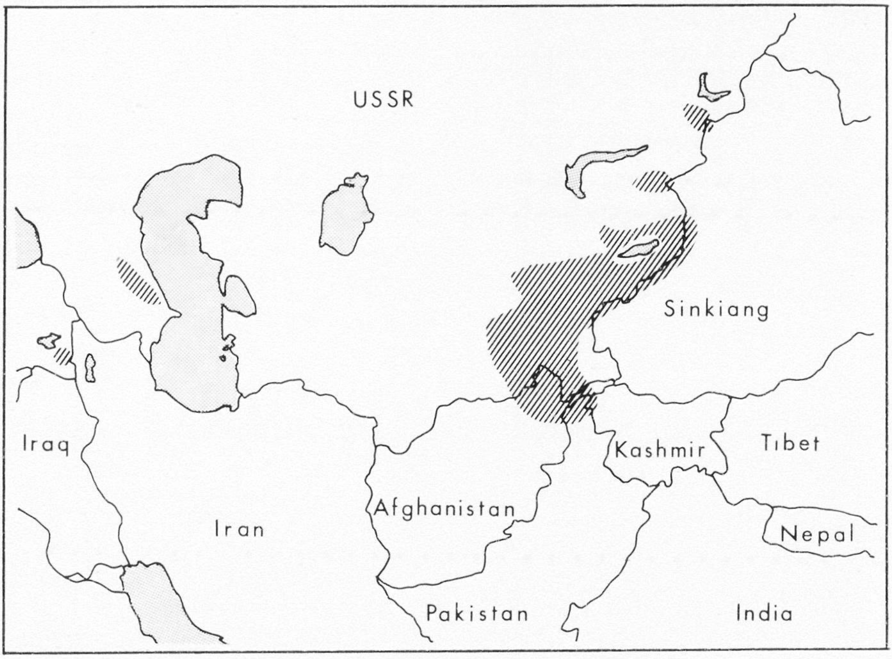

Fig. 7. *Allium oreophilum* C. A. MEY. General distribution. Based on information from Fl. Kavkaza 2 p. 141, distr. map 169; Fl. Tadjik. SSR. 2 p. 340; Fl. SSSR 4 p. 256 and herbarium material.

Melanocrommyum with no real storage function. The first of these sprout leaves could perhaps be compared with the second storage leaf in sect. *Porphyroprason*. In the sections *Molium* and *Porphyroprason*, but not in the subgenus *Melanocrommyum*, two respectively one protective cataphylls surround the renewal bulb. The increase bulbs of *A. oreophilum* show many similarities to those of species of sect. *Molium*. *A. giganteum* REGEL and *A. aflatunense* B. FEDTSCH. are the only species of sect. *Megaloprason* in which I have found increase bulbs. In the latter species these bulbs are developed much later during the vegetative period and are arranged asymmetrically. In *A. oreophilum* the increase bulbs occur symmetrically at the start of growth. The vernation of the young foliage leaves and the structure of the bulb are shown in Fig. 5. There is one dorsal and one ventral row of vascular bundles in the foliage leaf (Fig. 6). The same pattern is found in the subgenus *Melanocrommyum*.

A. oreophilum, the only species of sect. *Porphyroprason*, grows on

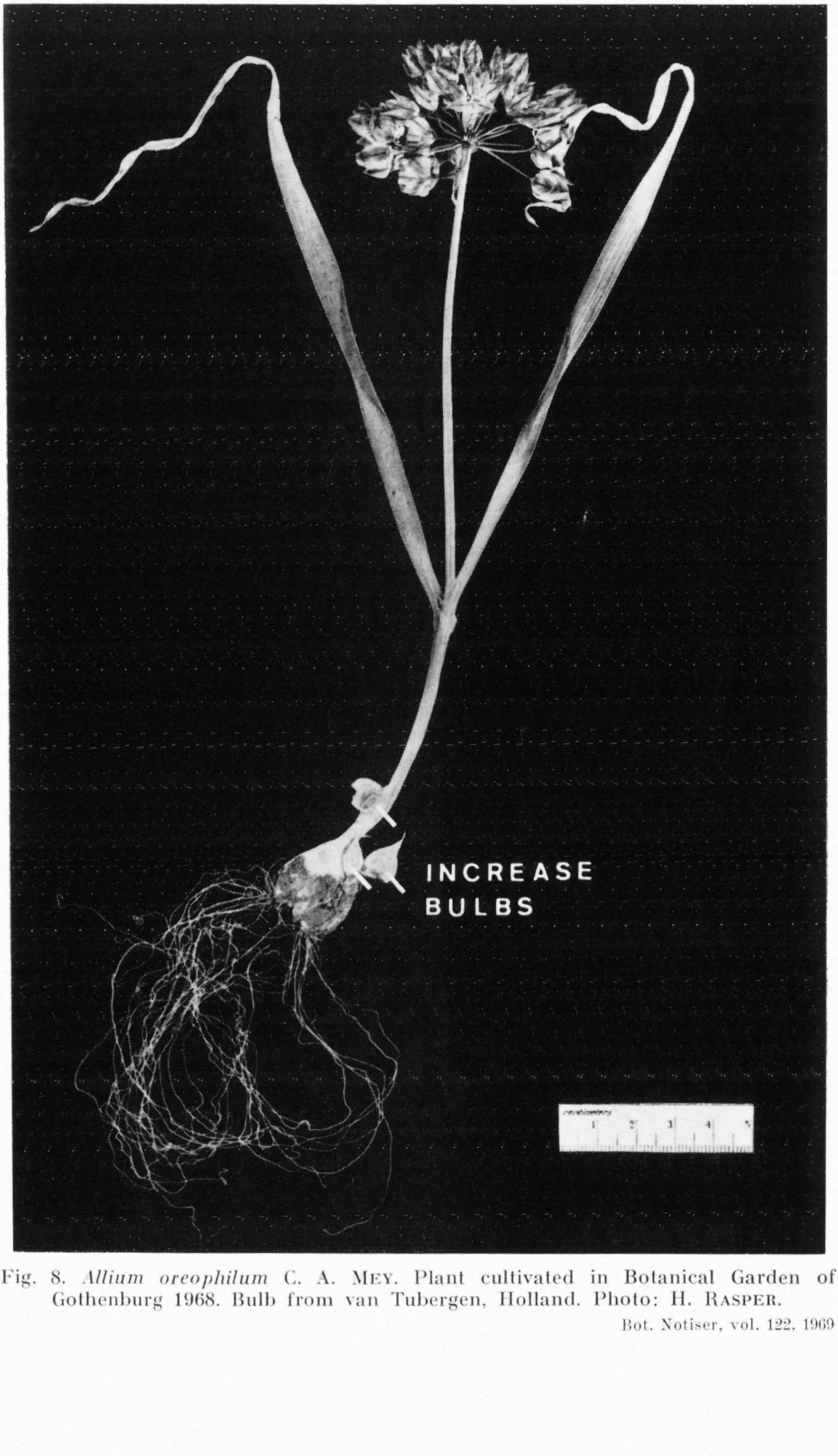

Fig. 8. *Allium oreophilum* C. A. Mey. Plant cultivated in Botanical Garden of Gothenburg 1968. Bulb from van Tubergen, Holland. Photo: H. Rasper.

stony slopes at high altitudes, ca. 3—4000 m. As shown in Fig. 8, there are large gaps in the distribution of the species between E. Turkey, E. Caucasus and the mountains of Central Asia. This would indicate that the species may have had a much larger distribution range in previous periods. The separate populations have received different names, but obviously it is not possible to distinguish taxonomically between them (cf. VVEDENSKY 1963 p. 338). The type of *A. oreophilum* comes from the Caucasus, *A. platystemon* KAR. & KIR. (1842 p. 514) was described from 'Alatau' and *A. ostrowskianum* REGEL (1881 p. 545) from 'Turcestania occidentalis'. The only locality of *A. oreophilum* known in Turkey is İspiriz Dağ, Başkale, province Van (DAVIS 23758!).

ACKNOWLEDGEMENTS

I am much indebted to Professor K. H. RECHINGER who has translated my descriptions into Latin, to Professor N. HYLANDER and Dr. W. T. STEARN for valuable suggestions, and to the head of my department, Professor P. WENDELBO, for criticism and help.

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The Genus Luzula in Australia

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ABSTRACT

Five species of *Luzula* DC. have been distinguished in the studied material from Australia, all of them belonging to the *campestris-multiflora* complex of the subgenus *Gymnodes*. The five studied species are as follows: *L. meridionalis* sp. nov. with three varieties, 2n=12, one variety with aneuploids in addition; *L. australasica* STEUDEL, pseudo-polyploid with 2n=24; *L. oldfieldii* HOOKER FIL. with two varieties, 2n=12; *L. alpestris* sp. nov.; and *L. acutifolia* sp. nov., 2n=12. *L. meridionalis* and *L. oldfieldii* have earlier been treated as varieties of *L. campestris* (L.) DC. A key for the identification of the species is given.

The occurrence of natural hybrids have been discussed.

INTRODUCTION

During spring and summer 1957—58 I had the opportunity to visit Australia. During this stay I collected material of *Luzula* from the southern and eastern parts of the continent, mainly in the regions around Melbourne, Adelaide, Canberra, and in the Snowy Mts., N.S.W., as well as in Tasmania. The collected material was brought to Sweden as seeds and as herbarium specimens, duplicates of the ones deposited in the herbaria which I visited. Herbaria where my material is found are: Herbarium Australiense, C.S.I.R.O., Canberra (CANB), and State Herbarium of South Australia, Adelaide (AD).

All the material of the genus *Luzula* found in Australia belongs to the *campestris-multiflora* complex of the subgenus *Gymnodes*. The basic chromosome number of this complex is x=6, with all chromosomes of about the same size (NORDENSKIÖLD 1951, 1956). True diploidy has been found to be the most common chromosome pattern among the previously studied taxa of the complex, and so is also the case with the Australian ones. True polyploidy occurs in the complex, but it has not been found in the Australian material. As the genus *Luzula* is considered to possess diffuse or polycentric centromeres, other types of chromosomal changes also are to be expected. In the *campestris-multiflora* complex a certain type of aneuploidy as well as endonuclear or pseudo-polyploidy has been found, and these types of changes in the chromosomal patterns have also been observed among the Australian *Luzula* (NORDENSKIÖLD 1961). Both the aneuploidy and the pseudo-polyploidy is considered to be a repatterning of the chromosome matter of the diploid set. In the aneuploid taxa the chromosomes always have two distinct sizes, one large one corresponding to the normal size found in true diploids and one small one of about half that size. The half-sized chromosomes always occur in pairs in the haploid set of a balanced taxon and they seem to originate from the normal sized ones by fragmentation. If all the twelve chromosomes of the nucleus are broken into two parts we obtain a taxon with the tetraploid chromosome number of 2n=24, a phenomenon named endonuclear polyploidy or pseudo-polyploidy. These pseudo-polyploid taxa have still chromosome complements of the diploid level and they also easily cross with the true diploids.

MATERIAL AND METHODS

The seeds brought to Sweden have been planted in greenhouse. Their chromosome numbers have been determined, usually in three plants from each collection. The plants have been studied cytologically and morphologically, and compared with the originally collected specimens. During this study four main taxa have been distinguished among the collected material. The investigated collections are demonstrated in Table 1, where their original localities, their chromosome numbers, and their collection and herbarium numbers are stated. They have been named and arranged according to the taxonomic disposition given below.

For the distinguishing of the taxonomic units of Australian *Luzula*, I have mainly used my own collections, specimens from nature as well as the cultivated plants. In order to obtain a check and better information about the distinguished taxa and their distribution I have used herbarium specimens from the Australian herbaria. By this study I have had the opportunity to cooperate with Dr. ELIZABETH EDGAR, D.S.I.R., Christchurch, New Zealand. She has studied the specimens of *Luzula* of the *campestris-mutiflora* complex from Australia in the Australian and the New Zealand herbaria and determined them according to my keys. The keys have worked well and from her determinations I have obtained the distributions of the taxa. Specimens quoted by F. BUCHENAU as well as other critical material I have had sent to me for study. Among the herbarium specimens studied, I have found one taxon, which I have not had in my cultures. In this way the number of main taxa of *Luzula* in Australia reaches five.

The herbarium specimens, from AD, CANB, CHR, MEL, NSW, and WELT ((the abbreviations follow Index Herbariorum 1964) have been cited with their herbarium numbers. When two numbers are given for a specimen, the second one in brackets indicates specimen studied by the author.

THE TAXONOMIC UNITS OF THE CAMPESTRIS-MULTIFLORA COMPLEX IN AUSTRALIA

The rank of the taxa of the *campestris-multiflora* complex always has been problematic. Many of the taxa were at first described as varieties of the European *L. campestris,* but later on raised to specific rank, on the other hand many of them have been described as species and later on reduced to varieties. As the physiological and genetical differences between taxa of geographically remote areas seem to be clearly marked, it has been found most correct to give the taxa, originating from distinct geographical regions, specific rank. Consequently, I have not found it just to treat any of the Australian taxa as varieties of the European *L. campestris,* and, thus, I have given specific rank to the five main taxa found in the studied material of Australia.

Key to the species

1.. Distinctly rhizomatous; inflorescence congested, distinctly elongated .... *L. australasica*
1.. Loosely tufted; inflorescence congested or umbelloid, not distinctly elongated
  2. Inflorescence umbelloid (rarely reduced to one head); caruncula well developed .... *L. meridionalis*
  2. Inflorescence congested; caruncula minute
    3. Young leaves and bracts with pointed tips .... *L. acutifolia*
    3. Leaves and bracts with obtuse-callous tips
      4. Leaves broad, 3—7 (—10) mm; inflorescence globose .... *L. oldfieldii*
      4. Leaves very narrow, 1—3 mm; inflorescence conical or globose *L. alpestris*

Luzula meridionalis NORDENSKIÖLD sp. nov.

L. campestris (L.) DC. var. *bulbosa* BUCH.; BUCHENAU 1890 p. 165; 1898 p. 218; 1906 p. 95. — *L. campestris* (L.) DC. var. *migrata* BUCH.; BUCHENAU 1906 p. 94, non 1898 p. 220. — *L. migrata* (BUCH.) OSTENF.; OSTENFELD 1921 p. 16.

Caespitosa, caules 15—40 cm, raro 50 cm alti. Folia plana, dense vel disperse ciliata. Inflorescentia umbelloides (raro simplex). Flores 2—3 mm longi, tepala aequilonga, membranaceo-marginata, externa medio dorsi castanea. Fructus perigonium aequans, nitidus, castaneus, ferrugineus vel stramineus. Caruncula seminis magna. Semen c. 1 mm, caruncula 0.3—0.6 mm longa.

Table 1. Localities of collection, collectors, herbarium and chromosome numbers of th

Species	Locality of collection
L. meridionalis v. *meridionalis*	Near road Cape Jervis — Victor Harbour, S.A.
„ „	Southern Mt. Lofty Range, near Mt. Jagged, S.A.
„ „	Southern Mt. Lofty Range, W. of Mt. Compass, S.A.
„ „	Upper Sturt Road, before turnoff to Ironbank, S.A.
„ „	Waterfall Gully, 9 km SE. of Adelaide, S.A.
„ „	Southern Mt. Lofty Range, nr. Torrens Gorge Road, S.A
„ „	Mt. Lofty Range, between Ashton and Marble Hill, S.A.
„ „	Five miles E. of Cranbourne, Vic.
„ „	Knocklofty, W. of Hobart, Tasmania.
„ v. *flaccida*	Five Crossings, Brindabella Road, A.C.T.
„ „	Works Road, below Bull's Head, A.C.T., c. 4000 ft.
„ „	Mt. Ginini, A.C.T., c. 4000 ft.
„ „	Mt. Gingera, A.C.T., c. 5000 ft.
„ „	Canberra, A.C.T.
„ „	Wilson's Valley, Snowy Mts., N.S.W., 4700 ft.
„ „	Boggy Plain, Snowy Mts., N.S.W., 5200 ft.
„ „	Ferntree Gully, near Melbourne, Vic.
„ „	Seaford, near Melbourne, Vic., (at sea level).
„ „	Mt. Macedon, Memorial Cross, Vic., 3300 ft.
„ „	Mt. Macedon, 1 mile N. of Cross, Vic., 3100 ft.
„ „	Five miles S. of Trentham, Vic.
„ „	Breona, near shore of Great Lake, Tasmania, 3400 ft.
„ „	Breona, hillside W. of Great Lake, Tasmania.
„ „	Taroona, 2 miles S. of Hobart, Tasmania.
„ „	Bellerive, near Hobart, Tasmania.
„ v. *densiflora*	Uriarra Crossing, Murrumbidgee River, A.C.T.
„ „	Three miles SW. of Uriarra on Brindabella Road, A.C.T.
„ „	Paddy's River, Tidbinbilla District, A.C.T.
hybrid product	Near road Cape Jervis — Victor Harbour, S.A.
„ „ „	One mile S. of Fairlight near Uriarra, N.S.W.
„ „ „	Two miles SW. of Uriarra on Brindabella Road, N.S.W.
L. australasica	Mt. Ginini, A.C.T., c. 4000 ft.
„	Mt. Ginini, A.C.T., c. 4000 ft.
„	Mt. Gingera, A.C.T., c. 5000 ft.
„	Snowy Mts., near Mt. Kosciusko Hotel, N.S.W., c. 5000 ft
„	Snowy Mts., Wilson's Valley, N.S.W., 4600 ft.
„	Snowy Mts., Boggy Plain, N.S.W., 5100 ft.
„	Bogong High Plains, Vic.
„	Breona, near shore of Great Lake, Tasmania, 3400 ft.
„	Derwent Bridge, Tasmania, 2600 ft.
„	Snowy Mts., near Spencers Creek, N.S.W., c. 1750 m.
L. oldfieldii v. *oldfieldii*	Summit of Mt. Wellington, Tasmania, 4165 ft.
„ „	Bogong High Plains, Vic.
„ „	Ramshead Range, Snowy Mts., N.S.W., 1900 m.
„ „	Mt. Northcote, N. of Mt. Kosciusko, N.S.W.
„ v. *angustifolia*	Spencers Creek, Snowy Mts., N.S.W., 1750 m.
„ „	W. slope of Trapyard Creek, Snowy Mts., N.S.W., 1750 m.
L. acutifolia	Near Mt. Townsend, Australian Alps, N.S.W., 7000 ft.
„	Bogong High Plains, near Frying Pan, Vic., c. 1780 m.
„	Bogong High Plains, Vic.

material, which has been cultivated and determined as to its chromosome numbers.

Collectors and collecting nos.	2n	Herbarium nos.
Hj. Eichler 14317 & Author S7	12	AD 95804023
,, 14326 ,, S9	12	AD 95804021
,, 14327 ,, S10	12	AD 95604020
D. E. Simon ,, S11	12	
Hj. Eichler 14330 ,, S12	12	AD 95804019
,, 14343 ,, S14	12	AD 95804018
,, 14345 ,, S15	12	AD 95804017
Author S38	12	
W. D. Jackson & Author S44	12	CHR 172137
N. T. Burbidge, M. Gray 4370 & Author S20	12	
,, ,, 4373 ,, S21	12	
,, ,, 4378 ,, S23	12	CANB 39096
,, ,, ,, S26	12	
M. Gray 4358	12	
Author S32	12	CANB 39101
,, S34	12	CANB 39102
,, S6	12	
,, S39	12	
,, S40	12	CHR 172120
,, S41	12	
,, S42	12	
,, S54	12	
,, S55	12	
,, S50a	12	
,, S49	12	
M. Gray 4365 & Author S16	12	CANB 39093
,, ,, S19	12	CANB 39095
Hj. Eichler 13250	16	AD 95743002
,, 14323 & Author S8	12	AD 95804022
M. Gray 4366 & Author S17	16	CHR 172132
,, 4367 ,, S18	12—15	CANB 39094
N. T. Burbidge, M. Gray 4381 & Author S22	24	CANB 39098
,, ,, 4383 ,, S24	24	CANB 39100
,, ,, ,, S25	24	CANB 39099
Author S29	24	
,, S31	24	AD 96306062
,, S33	24	
T. J. Carr	24	
Author S53, S57	24	AD 96603061
,, S51	24	AD 96306063
Hj. Eichler 13633	24	AD 95753006
W. Curtis & Author S45	12	CHR 172125
T. J. Carr	12	
Hj. Eichler 13509	12	AD 95742011
A. B. Costin	12	CANB 49981
Hj. Eichler 13638	12	AD 95743005
,, 13499	12	AD 95736008
A. B. Costin 0044	12	CANB 58222
Hj. Eichler 14641	12	AD 95829016
T. J. Carr	12	

Loosely tufted, sometimes with a swollen or bulbous base; fruiting stem (10—) 15—40 (—50) cm high; *leaves* grass-like, flat, linear, 2—5 mm wide, ciliate with long white hairs at the edges and especially towards the base, tips obtuse; flowers light to dark brown, in ovoid or globular clusters, 1 rarely 2 clusters sessile, and 0—6 clusters, rarely more, on unequal branches; 1—4 leaf-like *bracts* beneath the inflorescence; *flowers* 2—3 mm long; *tepals* 6, brown with transparent, membranous, light margins, acuminate and equal in length; *capsule* light to dark brown, usually equalling the perianth, obovoid; *seeds* c. 1 mm long, with well developed basal *caruncula. Chromosome numbers:* 2n=12, 14 or 16.

Distribution: Widespread in New South Wales, Victoria, and Tasmania from sea level to about 6000 ft. in the mountains, as well as in south-eastern Queensland, southern districts of South Australia and western districts of West Australia.

This widespread species is very variable. In the material I have investigated the following three varieties have been distinguished:

1. Flowers large (3 mm long), fruiting stem 20—50 cm, capsule brown .... var. *meridionalis*
1. Flowers small (2.5 mm long), fruiting stem 15—40 cm
    2. Inflorescence flaccid, clusters loose, margins of leaves only sparsely hairy, capsule yellowish to light brown .... var. *flaccida*
    2. Inflorescence erect, clusters dense, margins of leaves and bracts thickly hairy, capsule reddish to dark brown .... var. *densiflora*

L. meridionalis var. meridionalis

Caules 20—50 cm alti, basis caulis bulboso-incrassata. Flores majores (3 mm longi). Tepala castanea vel ferruginea. Fructus ferrugineus.

Typus: MEL 10607, Swan River, Western Australia, PREISS (Fig. 1 A).

Loosely tufted with a bulbous base; fruting stem 20—40 (—50) cm high; *leaves* 2—3 (—5) mm wide, with villose margins and with evenly narrowing but obtuse tips; *inflorescence* umbelloid, clusters 1—6 (—10) with a diameter of 6—8 (—10) mm; *flowers* c. 3 mm long, brown with light brown, transparent margins; *fruit* brown to dark brown, equalling the perianth; *seeds* c. 0.9 mm, *caruncula* 0.3—0.4 mm, white or yellowish (Fig. 5 A). *Chromosome number:* 2n=12.

Habitat: Dry open forest and grassland.

Distribution: South-eastern New South Wales, Victoria, southern

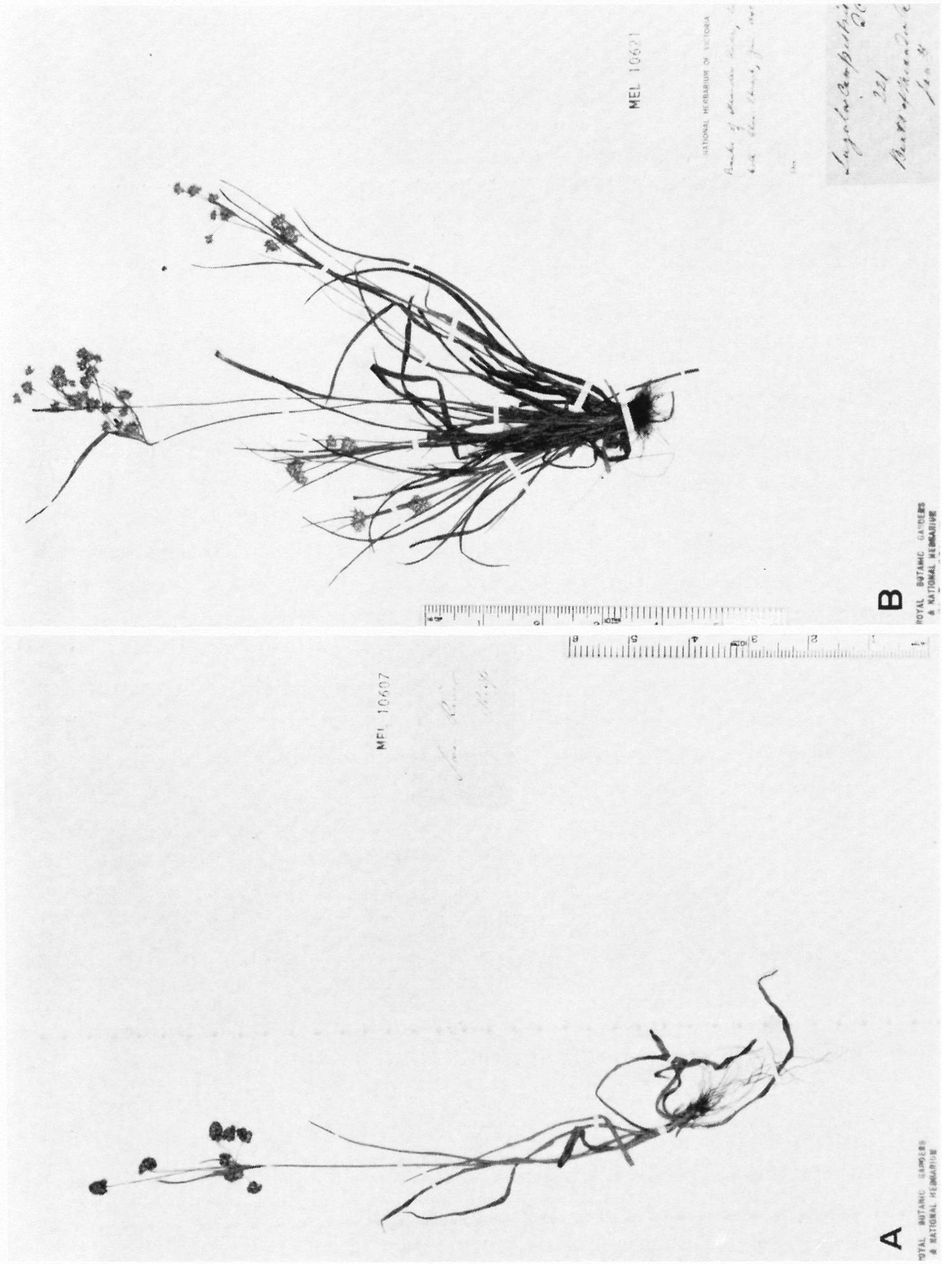

Fig. 1 A: *Luzula meridionalis* var. *meridionalis*. MEL 10607. Swan River, Western Australia, PREISS. — B: *L. meridionalis* var. *flaccida*. MEL 10621. Banks of Meander River, Tasmania, Jan. 1848, CHAS. STUART 221.

districts of South Australia, western districts of West Australia, and Tasmania.

Representative specimens studied: AD 95804019, Mt. Lofty Rn., Waterfall Gully, S.A., 29.10.1957, Hj. Eichler and H. Nordenskiöld; AD 95804021, Southern Mt. Lofty Rn., near Mt. Jagged, S.A., 29.10.1957, Hj. Eichler and H. Nordenskiöld; MEL 10588, Western Australia, J. Drummond 337.

L. meridionalis var. **flaccida** (Buch.) Nordenskiöld comb. nov.

L. campestris (L.) DC. var. *flaccida* Buch.; Buchenau 1906 p. 92.

Lectotypus: MEL 10621, Banks of Meander River, Tasmania, Jan. 1848, Chas. Stuart 221 (Fig. 1 B).

Loosely tufted; fruiting stem 15—25 cm, rarely 30 cm high; *leaves* 2—3 (—4) mm wide, sparsely ciliate with thick callous, obtuse tips; *inflorescence* umbelloid, clusters 1—6, rarely more, dispersed on flaccid branchlets, or occasionally reduced to one sessile cluster; *flowers* 2.0—2.5 mm long, yellowish to light brown, perianth with brown stripe, equalling or shorter than the yellowish to light brown, in sunny positions brown, *capsule*; *seeds* c. 1.0 mm long, with a white *caruncula* of 0.3—0.5 mm (Fig. 5 B). *Chromosome number*: 2n=12.

Habitat: Shady to open positions, in dry or moist situations, from sea level to about 5000 to 6000 ft. altitude in the mountains.

Distribution: South-eastern Queensland, eastern New South Wales, Victoria, south-eastern South Australia, and Tasmania.

Representative specimens studied: MEL 10675, Thredbo River, Snowy Mts., March 1890, W. Bauerlen 133; CANB 39096, Mt. Ginini, A.C.T., 6.11.1957, H. Nordenskiöld, N. T. Burbidge, and M. Gray; CHR 172120, Mt. Macedon, Victoria, 28.11.1957, H. Nordenskiöld; seen as photos: CANB 156411, Near Delegate, N.S.W., W. Bauerlen; NSW 72351, Circular Head, Tasmania, 25.11. 1836, R. C. Gunn 340.

L. meridionalis var. **densiflora** Nordenskiöld var. nov.

A var. *meridionalis* his notis differt: flores minores, 2—2.5 mm longi, capitula inflorescentiae densiflora, folia et bracteae marginibus dense villosa.

Typus: MEL 10592, Upper Barwon River, Victoria, Nov. 1882, B. Wilson, (Fig. 2 A).

Loosely tufted, with a bulbous or swollen base; fruiting stem 25—40 cm high; *leaves* 2—3 mm wide, margins thickly covered with white hairs; clusters of the *inflorescence* dense, one single and/or several dispersed on uneven rigid branches; 1—2 *bracts* ciliate along the whole

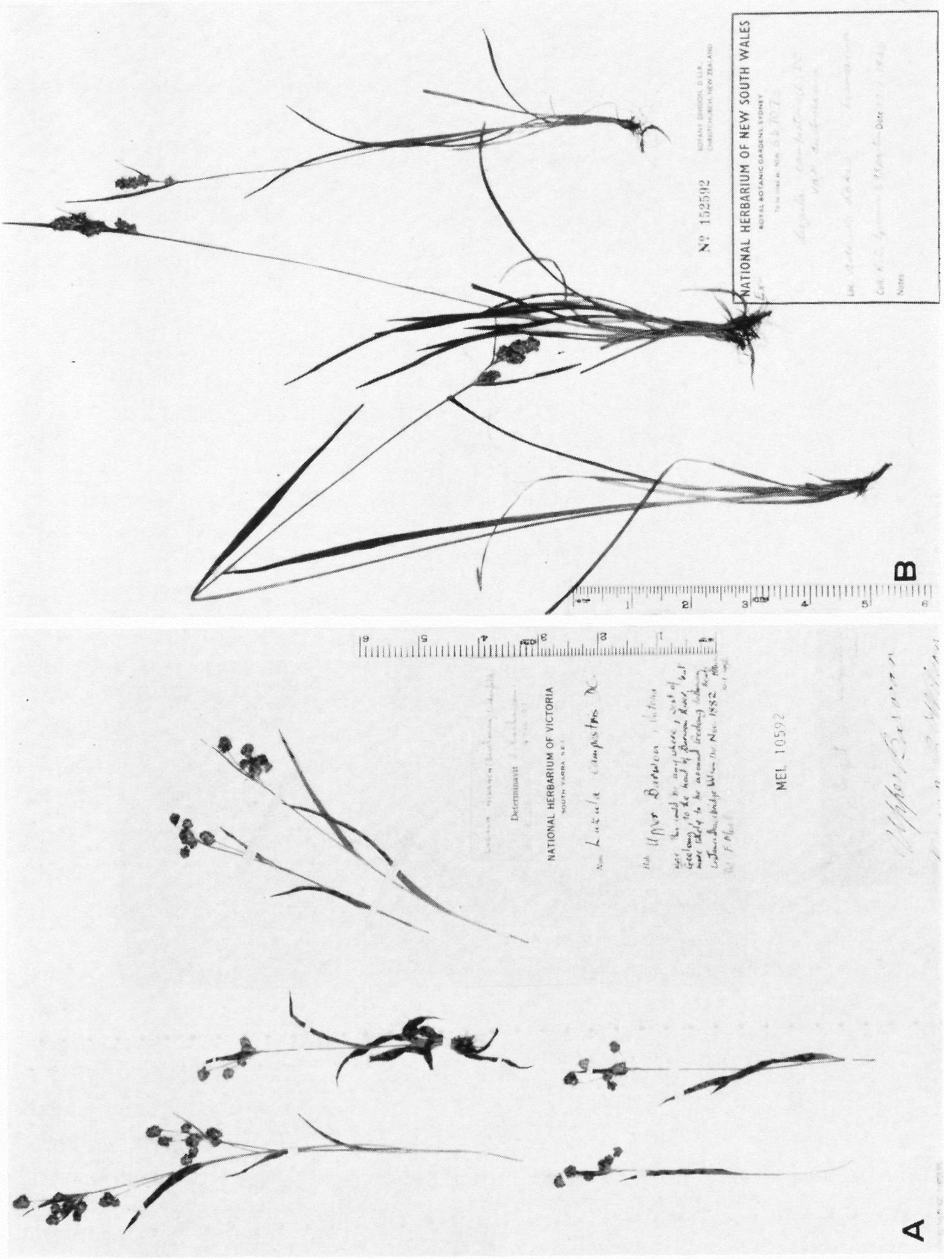

Fig. 2 A: *Luzula meridionalis* var. *densiflora*. MEL. 10592. Upper Barwon River, Victoria, Nov. 1882, B. Wilson. — B: *L. australasica*. NSW 65707, (CHR 152592), Arthur's Lake, Tasmania, 17 Jan. 1845, R. C. Gunn 598.

margin; *flowers* 2—2.5 mm long, perianth dark with a narrow light margin; *fruit* brown to dark red-brown, equalling or exceeding the perianth; *seeds* c. 0.9 mm long, with a large white *caruncula* of 0.4—0.5 mm (Fig. 5C). *Chromosome numbers:* 2n=12, 14 (NSW 77825, S. of George's Plains, S. of Bathurst, N.S.W., 11.10.1964, L. A. S. JOHNSON), or 16.

Habitat: Dry open forest or grassland.

Distribution: Eastern New South Wales, Victoria, south-eastern South Australia, and Tasmania.

Representative specimens studied: CANB 39093, Uriarra Crossing, Murrumbidgee River, A.C.T., 5.11.1957, H. NORDENSKIÖLD and M. GRAY; NSW 72358, Macquarie (Plains), Tasmania, 1842, C. R. GUNN 340 (portion); MEL 10619, South Esk River, Tasmania, probably Nov. 1849, C. STUART 724.

Concerning BUCHENAU's names of *L. campestris* var. *bulbosa* and *L. campestris* var. *migrata,* EDGAR (1966 pp. 170—171) has worked out and cleared up the varying conceptions, which BUCHENAU has given them in his three works on *Luzula* (1890, 1898 and 1906). He first describes from Australia and Tasmania *L. campestris* var. *bulbosa* with a bulbous or swollen stem base, narrow leaves and large caruncula (BUCHENAU 1890 p. 165). This taxon is now treated as *L. meridionalis.* Later on (1898 p. 220) he describes from "Neuholland, Tasmania, Neuseeland" *L. campestris* var. *migrata* with wide leaves and small caruncula. Here he indicates no type locality or type specimen. According to EDGAR there are, however, two specimens labelled *L. campestris* var. *migrata* by BUCHENAU's hand in Dominion Museum, Wellington, New Zealand. One is WELT 12608, Mt. Sedgwick, Tasmania, 1893, T. B. MOORE. It is immature and difficult to determine. The second specimen, WELT 12612, Mt. Egmont, New Zealand, is more mature, and it has been designated as lectotype for *L. migrata* of New Zealand by EDGAR (1966). This is, as I see it, correct, as BUCHENAU's description (1898) well fits the New Zealand species with its small caruncula and its decomposed or umbelloid inflorescences, whereas among the Australian taxa only the high alpine ones (*L. oldfieldii, L. alpestris* and *L. acutifolia*) have small caruncula and these species have all congested and not umbelloid inflorescences. For that reason the name "*migrata*" must be used for the New Zealand species. In the same article, where he originally describes *L. campestris* var. *migrata* he also mentions *L. campestris* var. *bulbosa* (BUCHENAU 1898 p. 218). Here he is hesitant, whether the bulbous growth is a character appropriate for distinguishing taxa, especially as he found that some of the Australian specimens he studied had no well developed bulbs. This is quite true as he has named BAUERLEN's specimen no. 276, MEL 10626, "*L. campestris* DC. var. *bulbosa* FR. B.", which is proved by his own handwriting dated 1894. This specimen, MEL 10626 (seen as photo), has no bulbous base and has in the present study been assigned to *L. meridionalis* var. *flaccida*. In his last publication (1906 p. 94) BUCHENAU has found that the name "*bulbosa*" was already occupied by a North American species *L. campestris* var. *bulbosa* WOOD (1863). He then alters his conception of *L. campestris* var. *migrata* and applies this name to the Australian plants, which he earlier had named var. *bulbosa* ("Formen, welche ich früher "var. *bulbosa*" nannte"), and the description is changed according to the Australian material giving it narrow instead of wide leaves and large instead of small caruncula. This alteration of conception can, however, not change the fact that the name "*migrata*" was at first used for a New Zealand species. In a note on the next page (1906 p. 95) he denies the existence of a distinct taxon with bulbous stem base and asserts this character to occur in most *Luzula* taxa growing in arid habitats. In the same article BUCHENAU (1906 p. 92) gives the description of still another Australian taxon of the complex, *L. campestris* var. *flaccida*. About this taxon he states as follows: "Die typischen Pflanzen von Tasmania (STEWART) und Hunter's Island auf den Fidji-Inseln (ATKINSON); ähnliche Formen aus New-South-Wales (BAUERLEN) weichen durch etwas breitere Blätter (bis 3 mm) und kleinere Perigonblätter, aber grössere Früchte ab." This name "*flaccida*" has here been used for the non-bulbous variety of the species.

Luzula australasica STEUDEL

STEUDEL 1855 p. 394 non sensu BUCHENAU 1890 p. 154 nec *L. campestris* (L.) DC. var. *australasica* BUCH.; BUCHENAU 1898 p. 216; 1906 p. 92. — *L. modesta* BUCH.; BUCHENAU 1906 p. 80.

Neotypus: CANB 39098, Mt. Ginini, A.C.T., 6.11.1957, H. NORDENSKIÖLD, N. T. BURBIDGE, and M. GRAY.

Horizontal rhizomes; fruiting stem 15—40 cm high; *leaves* 3—7 mm wide, margins sparsely ciliate with long hairs, flat with an obtuse-callous apex; *inflorescence* erect, consisting of one to four sessile, small clusters, forming an elongated, sometimes almost conical inflorescence, 1—2 (—3) cm long; *flowers* 2—3 mm long; *tepals* equal in length, light to dark brown with a white, transparent margin; perianth equalling the capsule; *fruit* brown or yellowish brown; *style* short (c. 0.2 mm), stigma long (c. 1 mm); *seeds* c. 1 mm long, dark brown with a large *caruncula* of c. 0.6 mm (Fig. 5 D). *Chromosome number*: 2n=24, pseudo-polyploid.

Habitat: Subalpine, often growing in *Sphagnum* bogs.

Distribution: In the mountains of New South Wales and Victoria at 4000 to 5500 ft. altitude and in Tasmania at an altitude of about 3000 ft.

Representative specimens studied: AD 96306063, North of Derwent Bridge, Tasmania, 12.12.1957, H. NORDENSKIÖLD; seen as photos: NSW 65707 (CHR 152952), Arthur's Lake, Tasmania, 17.1.1845, R. C. GUNN 598 (Fig. 2 B); MEL 10666, Snowy Mts., 6000 ft., March 1890, W. BAUERLEN 102.

Luzula oldfieldii HOOKER FIL.

HOOKER 1858 p. 68. — *L. austalasica* STEUDEL sensu BUCHENAU 1890 p. 154 non sensu orig. — *L. campestris* (L.) DC. var. *australasica* BUCH.; BUCHENAU 1898 p. 216; 1906 p. 92.

Loosely tufted, sometimes with spreading growth; fruiting stem 8—20 (—25) cm high; *leaves* broad, 3—7 (—10) mm wide, with a pale nerve-like margin, furnished with white hairs, and of about the same length as the flowering stem; flowers in clusters, usually congested into a single globose *inflorescence*; *flowers* c. 2.5 mm long, *tepals* brown with a white, transparent margin; *fruit* brown to dark brown, equal to or shorter than the perianth; *seeds* 1—1.2 mm long, *caruncula* minute to small (c. 0.1 mm).

Habitat: Alpine.

Distribution: Tasmania at 4000 to 4500 ft. and in the mountains of Victoria and New South Wales at 5000 to over 7000 ft. altitude.

In this alpine species a somewhat deviating variety has been distinguished. It is characterized by narrower leaves compared with the main species and a many-clustered inflorescence. It has here been described as *L. oldfieldii* var. *angustifolia*.

L. oldfieldii var. **oldfieldii**

Typus: Kew (Herb. HOOKER), "Wet places, summit of Mt. Wellington", OLDFIELD 138 (Fig. 3 A).

Loosely tufted, sometimes with spreading growth; *leaves* broad, 4—7 (—10) mm wide, with a pale nerve-like margin, and of about the same length as the fruting stem of 10—20 cm; *inflorescence* congested into a single globose head, *bracts* broad, usually exceeding the inflorescence; *tepals* brown with a broad, white transparent margin; *fruit* brown, equal to or shorter than the perianth; *seeds* c. 1 mm long, *caruncula* minute (Fig. 5 E). *Chromosome number:* 2n=12.

Habitat: Alpine, in exposed rocky places.

Distribution: In the mountains of Tasmania, Victoria, and New South Wales. Type locality: Summit of Mt. Wellington (4165 ft.), Tasmania.

Representative specimens studied: NSW 65719 (CHR 152591), Mt. Hothan at 6000 ft., Victoria, 17.1.1913, R. H. Cambage 3706; CANB 49981, Mt. Northcote, north of Mt. Kosciusko, N. S. W., 21.1.1958, A. B. Costin; CANB 97886, Kosciusko area, N. S. W., 21.1.1958, D. Moore; AD 95742011, Snowy Mts., Ramshead Range, at ca. 1900 m alt., 25.1.1957, Hj. Eichler 13509.

L. oldfieldii var. **angustifolia** Nordenskiöld var. nov.

Folia basalia angusta (3—6 mm lata), caule breviora; inflorescentia multicapitata, saepe contracta; caruncula basilaris fere parva.

Typus: CANB 165568 (CHR 150292 A), Etheridge Ridge, near Mt. Kosciusko, N.S.W., at base of ridge near road, slate rock country, 10.11.1966, M. Gray 5903.

Loosely tufted, *leaves* narrow (3—6 mm wide), with a pale nerve-like margin, and usually shorter than the tall fruiting stem of 15—25 cm; *inflorescence* composed of many clusters on unequal branchlets, more or less contracted; *tepals* brown with a narrow, white transparent margin; *fruit* dark brown, usually shorter than the perianth; *seeds* 1—1.2 mm long, *caruncula* small but usually larger than that of var. *oldfieldii* (Fig. 5 F). *Chromosome number:* 2n=12.

Habitat: Alpine to subalpine, in rocky country.

Distribution: In the mountains of New South Wales and Victoria at 5000 to 7000 ft. altitude.

Representative specimens studied: AD 75736008 (CHR 153218), Snowy Mts., western slope above Trapyard Creek, alt. ca. 1750 m., 25.1.1957, Hj. Eichler 13499; CANB 165564 (CHR 150288), Perisher Range (southern end), Kosciusco District, N.S.W., Snow Gum assoc. in sheltered gravel pit area, 10.11.1966, M. Gray 5909; AD 95743005 (CHR 153216), Snowy Mountains, Near Spencers Creek, between Adams Hut and Snowy River (ca. 8.5 km ENE of Mt. Kosciusko), N.S.W., alt. ca. 1750 m, 4.2.1957, Hj. Eichler 13638.

The specimens referred to this taxon and recorded above, originate all from the same area, i.e. Mt. Kosciusko District, and they seem to be fairly uniform. However, I have seen some other specimens, which might be referred to the same taxon. One NSW 65717 (CHR 152622), which is an isotype of the one described as *L. novae-cambriae* by GANDOGER (1899 p. 392). The other is a critical specimen, AD 96109026 from Mt. Wellington, Tasmania. This last mentioned one is very close to the main species in spite of its composed head, while GANDOGER's specimen is clearly intergrading into *L. meridionalis* var. *flaccida.* These facts indicate the possibility of a hybrid origin for these specimens as individuals of hybrid swarms from the cross *L. oldfieldii* var. *oldfieldii* and *L. meridionalis* var. *flaccida.* The intermediate size of the caruncula as well as the reduced fertility and flaccid inflorescence of NSW 65717 are other characters giving further grounds for this statement.

Concerning the two names *L. australasica* STEUDEL and *L. oldfieldii* HOOKER FIL., there has been great confusion. The main reason is STEUDEL's vague description together with his failure to give any distinct type locality. Only the abbreviated name "N. Holl." is stated. Moreover, his type specimen seems to have disappeared during the Second World War. The most evident character given by STEUDEL for *L. australasica* is the congested head. There are, however, other taxa from Australia and Tasmania with congested head-like inflorescences, which have been described. One is *L. oldfieldii* HOOKER FIL. and another one is *L. modesta* BUCH. Both these taxa have been possible to identify in my material. They are morphologically distinct and they do not have the same chromosome patterns. The first mentioned is a diploid with $2n=12$ and the latter is a pseudo-polyploid with $2n=24$. However, already BENTHAM (1878 p. 122) combined *L. australasica* with *L. oldfieldii* and from that time the two names usually have been used as synonyms (BUCHENAU 1890 p. 154, 1898 p. 216, and 1806 p. 92). BUCHENAU (1806) describes *L. modesta* from Tasmania as a new species with a congested head but distinctly different from *L. oldfieldii.* The question then must arise if STEUDEL's description of *L. australasica* corresponds to *L. oldfieldii, L. modesta* or perhaps another taxon with congested inflorescence. The two last words of STEUDEL's description says: "Praecedenti simillima", i.e. very similar to the immediately above described species, which is *L. chilensis* NEES. This remark gives an indication that his specimen ought to have had an inflorescence similar to that of *L. chilensis,* the inflorescence of which is distinctly elongated.

Fig. 3 A: *Luzula oldfieldii* var. *oldfieldii*. From the original sheet of HOOKER's herbarium, Kew. — B: *L. alpestris*. From the collection of AD 95736030 (CHR 153215). Near Bett's Creek, ca. 9 km ENE of Mt. Kosciusko, EICHLER 13471.

L. modesta is a taxon with such an elongated inflorescence, whereas *L. oldfieldii* has a globose head. Of my two new species described below, *L. alpestris* has a somewhat conical inflorescence, but it is a much smaller plant than the one described by STEUDEL, and the high alpine species *L. acutifolia* also has a congested inflorescence, but not the characteristic elongated or conical head found with *L. modesta* and *L. chilensis*. On that account, I have kept STEUDEL's name *L. australasica* for the 24-chromosomal species occurring in the subalpine regions in the mountains of Victoria and New South Wales, as well as in Tasmania. HOOKER's name *L. oldfieldii* with its distinct type locality (Mt. Wellington, Tasmania) has been used for the 12-chromosomal alpine species with the globose, congested inflorescence.

The two names *L. oldfieldii* and *L. australasica* have, moreover, been used for a taxon in New Zealand. HOOKER (1864) had specimens from New Zealand which he referred to *L. oldfieldii*. Since BUCHENAU (1890 p. 154) identified this name with *L. australasica*, CHEESEMAN (1925) applied BUCHENAU's later combination of that name *L. campestris* var. *australasica* (STEUDEL) BUCH. (BUCHENAU 1898 p. 216) to the New Zealand species. This taxon has now been treated as *L. rufa* by EDGAR (1966). She has also proved that the New Zealand species is distinct from the Australian one, here treated as *L. oldfieldii,* but by EDGAR (1966) designated as *L. australasica* (=*L. oldfieldii*). This fact is demonstrated by a table (EDGAR 1966 p. 168), where it is stated that *L. rufa* var. *rufa* usually is taller but has a thinner stem than is the case with the Australian *L. oldfieldii.* The heads of the inflorescences and their flowers are smaller in *L. rufa* and the shapes of their tepals are different. The capsule equals the tepals in *L. rufa* but is usually shorter than the tepals in the Australian *L. oldfieldii.* Thus, the two taxa really are different, and not only originating from two separate areas.

Luzula alpestris NORDENSKIÖLD sp. nov.

Caespitosa, caules erecti, 5—9 cm alti. Folia valde angusta, 1—3 mm, plerumque canaliculata, lamina basi longe ciliata. Inflorescentia congesta, obovata. Bracteae 1—3, inflorescentiam superantes. Flores parvi, 2 mm longi, ferruginei. Fructus fusco-ferrugineus, perigonio brevior vel aequilongus. Semina anguste-ovata, c. 1 mm longa, caruncula basilaris parva.

Typus: AD 95736030 (CHR 153215), Near Bett's Creek, south of the Paralyser (c. 9 km ENE of Mt. Kosciusko), alt. 1750 m., 24.1.1957, HJ. EICHLER 13471 (Fig. 3 B).

Tufted; *leaves* very narrow (1—3 mm), furrowed with a pale nerve-like margin, at the base furnished with long white hairs; fruiting stem 5—9 cm high; *flowers* 2 mm long; *inflorescence* congested in obovoid to conical heads; *bracts* usually spreading horizontally or downwards, very long, the lowest one, two or four times exceeding the head; *tepals* brown with a white transparent margin; *fruit* dark brown, shorter or equalling the perianth; *seeds* narrow, reddish brown, c. 1 mm long with a minute *caruncula. Chromosome number:* Undetermined.

Habitat: Alpine, around swampy places.

Distribution: In the mountains of New South Wales and Victoria at 5500 to 7000 ft. altitude.

Representative specimens studied: MEL 10534, Bogong High Plains, at Pretty Valley, Victoria, alt. 5500 ft, 27.12.1958, HELEN I. ASTON 186; NSW 65712 (CHR 15281), Mt. Kosciusko (tree line to 7000 ft.), N.S.W., Jan. 1899, J. H. MAIDEN and W. FORSYTH.

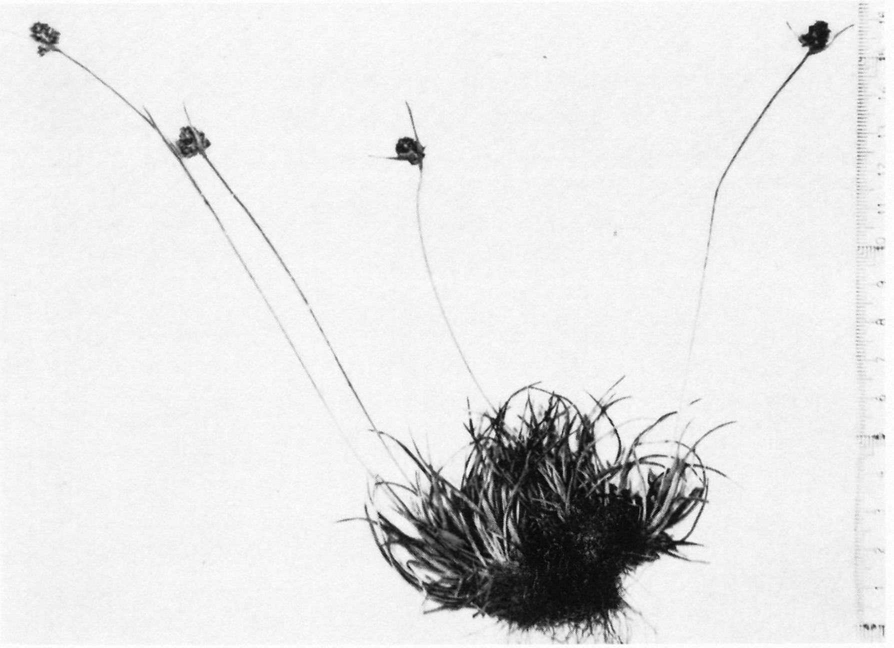

Fig. 4. *Luzula acutifolia*. From the collection of AD 95829016 (CHR 153214). Bogong High Plains, Australian Alps, Victoria, EICHLER 14641.

Luzula acutifolia NORDENSKIÖLD sp. nov.

Caespitosa, caules erecti, 10—20 cm alti. Folia basalia caule breviora, angusta plus minus canaliculata, disperse ciliata, acuminata, apice callosa. Inflorescentia composita congesta, bracteae 2—5, inflorescentiam multo superantes, apice acuminatae. Flores c. 2.5 mm longi, casteneo-nigri. Fructus nitidus, castaneus vel nigro-castaneus, perigonium aequans. Semina c. 1 mm longa, caruncula basilaris seminis parva.

Typus: AD 95829016 (CHR 153214), Bogong High Plains, Australian Alps, Victoria. Above Fall's Creek Ski Village, near Frying Pan (above ski lift from Skyline Lodge), ca. 1780 m., 31.1.1958, HJ. EICHLER 14641, (Fig. 4).

Loosely tufted, sometimes spreading; fruiting stem 10—20 cm high; basal *leaves* short, 1—2 mm wide, furrowed and very sparsely ciliate, apex of young leaves with pointed tips; inflorescence congested, consisting of 1—4 sessile clusters; *bracts* very long, 1—5 (—9) cm, with pointed tips; *flowers* c. 2.5 mm; *tepals* equal in length, dark brown with narrow, light margins; *style* short, c. 0.5 mm, stigma long, c.

2 mm; *fruit* dark brown to black, equalling the perianth, *seeds* c. 1 mm with a small, inconspicuous, white *caruncula* of about 0.1 mm (Fig. 5 G). *Chromosome number:* 2n=12.

Habitat: Alpine, in wet places near snow patches.

Distribution: In the mountains of New South Wales and Victoria at about 5000 to 7000 ft., and in Tasmania.

Representative specimens studied: CANB 165565 (CHR 150286), Mt. Kosciusko, N.S.W., semi-permanent snow area just below summit, 1966, M. GRAY 5905; CANB 58222 (CHR 153202), Near Mt. Townsend, Australian Alps, N.S.W., ca. 7000 ft. below snow patch, 1958, A. B. COSTIN; NSW 19611 (CHR 152580), Mt. Stilwell, Kosciusko, N.S.W., alt. 6500 ft., 18.1.1951, L. A. S. JOHNSON and E. CONSTABLE; MEL 10636, Mt. Kosciusko, 7000 ft, Feb. 1890, W. BAUERLEN 56.

This alpine species is characterized by the congested inflorescence, very long bracts and pointed tips of the young leaves and the bracts. This pointed apex of the leaves is a character regularly found in the *spicata-racemosa* group of the subgenus *Gymnodes* of the genus *Luzula*. Still, this taxon certainly belongs to the *campestris-multiflora* complex and it is easily crossed with the other members of the complex. The subalpine taxon of New Zealand *L. rufa* var. *albicomans* also is characterized by this callous but pointed leaf tip (EDGAR 1966).

OCCURRENCE OF NATURAL HYBRIDS

All taxa of the *campestris-multiflora* complex are able to hybridize artificially, and the investigated F_1-hybrids between the taxa of Australia usually are fertile. Thus, natural hybrids may occur in an area where the different taxa meet in nature. These F_1-hybrids ought to be fertile, but they will give rise to hybrid swarms, the individuals of which may have a varying degree of fertility.

In my cultivated material of the varieties of *L. meridionalis* three collections were found to be of hybrid origin (Table 1). Hybrids between *L. meridionalis* var. *densiflora* and var. *flaccida* are found in my collections nos. S17 and S18, corresponding to CHR 172132 and CANB 39094 respectively. A collection of the hybrid *L. meridionalis* var. *meridionalis* and var. *flaccida* is very likely found in no. S8 (AD 95804022, EICHLER 14323).

In the investigated herbarium material some of the studied specimens also must be interpreted as hybrid products between the varieties of *L. meridionalis*. During her study of the Australian material Dr.

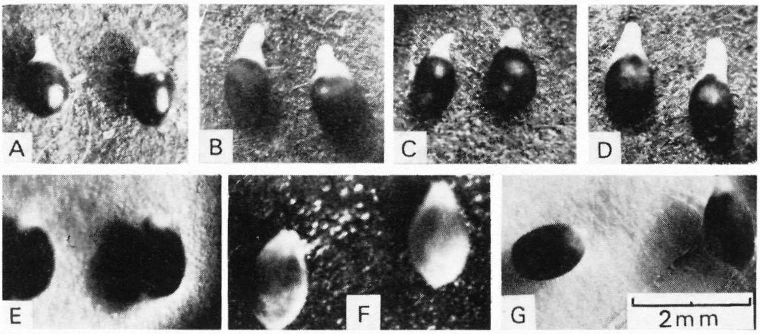

Fig. 5. Seeds of Australian *Luzula*. A: *L. meridionalis* var. *meridionalis*. Fleurien Peninsula, South Australia. — B: *L. meridionalis* var. *flaccida*. Breona, Tasmania. — C: *L. meridionalis* var. *densiflora*. Five Crossings, Brindabella Road, N.S.W. — D: *L. australasica*. Breona, Tasmania. — E: *L. oldfieldii* var. *oldfieldii*. Snowy Mountains, N.S.W. — F: *L. oldfieldii* var. *angustifolia*. Snowy Mountains, N.S.W. — G: *L. acutifolia*. Bogong High Plains, Victoria.

E. Edgar found several morphologically intermediate specimens. An interesting matter about the occurrence of those hybrids is the fact that their numbers are increasing with time, i.e. they are almost failing in the collections made before 1890 and most frequent in the ones made during the twenties and the thirties (Table 2). This increase with time of the occurrence of hybrids is statistically significant. During the Second World War almost no collections were made, and after that time the number of intermediate specimens was lowered again, and only about 10 per cent is found during the period 1940—1959. The explanation must in this case be the fact that in the old days collections were made from undisturbed areas, whereas in the first decades of our century there were much more populated areas to collect from. And those areas were not avoided as they are at the present time.

It seems very probable that hybrids between the alpine or subalpine species also may occur, but the studied alpine material is much smaller than that from lower altitudes. However, as reported above, some of the specimens referred to *L. oldfieldii* var. *angustifolia* very likely have a hybrid origin.

Certain individuals which I have studied as herbarium specimens are morphologically intermediate between *L. alpestris* and *L. meridionalis* var. *flaccida*. They are from Bogong High Plains, Victoria, and have nos. MEL 10090, MEL 10501, collected by J. H. Willis and NSW 90107 collected by N. C. Ford. The seeds of Dr. J. E. Willis' specimens have

Table 2. Number of specimens of *L. meridionalis* studied by Dr. E. EDGAR and the number of intermediates between its varieties found among them, tabled with respect to their collecting dates.

Time for collcetion:	before 1840	1840—59	1860—79	1880—99	1900—19	1920—39	1940—59	Total
Studied specimens	5	12	14	91	31	25	41	219
Intermediate specimens	0	0	0	4	4	10	4	22
Interm. specimens per cent:	0	0	0	4.4	12.9	40.0	9.8	10.0

too small caruncula to be classified as *L. meridionalis* var. *flaccida* and the last mentioned specimen is part of the same collection as NSW 65713, which in the present study has been treated as *L. alpestris*. I have here studied the sheet of CHR 152582, where both specimens of this collection are mounted on the same sheet. Two other specimens, MEL 10506 and MEL 10088, also originating from Bogong High Plains, Victoria, are morphologically intermediate between *L. oldfieldii* and *L. acutifolia*, why they probably are of hybrid origin.

Hybrids with the pseudo-polyploid *L. australasica* and the diploid species are possible to produce artificially but no presumable hybrid of that kind has been found in the studied material.

INTRODUCED TAXA

Neither the morphological investigation of the Australian taxa of *Luzula* nor the cytological examination of them have given evidence for an introduction of any European species into Australia. As such introduced material seems to be common in New Zealand (EDGAR 1966), it is a very surprising fact that no such material has been found in Australia as yet.

ACKNOWLEDGEMENTS

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Reproductive Drift, a Neglected Principle in Reproductive Biology

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ABSTRACT

Random deviations from expected frequencies in connection with the reproduction of the individual species in a plant community are discussed. The term reproductive drift is proposed for this phenomenon. The significance of numerical deviations for species occurring in very low numbers in a plant community is theoretically evaluated. It can be shown that such species are exposed to a great risk of random elimination in successive generations.

Experimental proof of the importance of reproductive drift in nature is still lacking. However, evidence of its consequences is demonstrated by material from the central Aegean archipelago in Greece in two instances: (1) for the establishment of species introduced by long-range dispersal in large plant communities and (2) for the species composition in small, isolated plant communities.

INTRODUCTION

The reproduction of a species in a plant community is controlled by biological and environmental factors, but is also influenced by a random factor. The significance of the random factor will be discussed in two instances: (1) for long-range migration and (2) for the species composition of small, isolated plant communities.

LONG-RANGE MIGRATION

In this paper the term long-range migration is restricted to such cases in which the dispersal of diaspores to a given locality is a single event that based on a high degree of probability will not be repeated for a long time.

Successful long-range migration is dependent on the effectiveness of the following factors: (1) the dispersal of diaspores, (2) the establishment of individuals in a new locality, and (3) the survival of the introduced species in future generations.

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The probability for an introduction of diaspores in suitable new localities depends on: (1) the number of diaspores produced by the parental population, (2) the dispersal efficiency of the diaspores, (3) the number and size of suitable localities that can be reached by the diaspores, and (4) the direction of the dispersal (it may be at random or directed, e.g., for water plants downwards along a river system).

The probability that diaspores introduced into a suitable locality will give rise to adult plants depends on: (1) the reproduction system of the plant community; (2) the competitive ability, especially in the seedling stage, compared to diaspores of previously established species; and (3) a random factor.

A species which has been established in a new locality as a single or very few individuals, i.e., the normal conditions in case of long-range migration, is dependant for its survival in successive generations on (1) the competitive ability compared to representatives of other species in the locality and (2) a random factor.

WEBB (1966), in a review of migration, discussed dispersal and establishment of plant species. He stressed the lack of information that makes it difficult to evaluate different factors and the role of long-range migration as a whole.

The random factors mentioned above seem to have been neglected previously or have only been incidentally mentioned (e.g., by SAKAI 1965). Therefore, a theoretical analysis of this factor will be made, complemented by examples, which illustrate its role in nature.

THE RANDOM FACTOR

If 5000 white and 5000 black balls in a model experiment are carefully mixed and a random sample of 1000 balls is taken, one would theoretically expect to get 500 white and 500 black balls. Usually such a sample will, however, not give the exact figures expected, but maybe instead 497 white and 503 black balls. If the sample is repeated many times, there will be a number of different deviations, but also some cases where the expected values are exactly obtained. The deviations are not haphazard, but the probability of every individual deviation can be calculated mathematically. It can be shown that the probabilities for such deviations follow frequency polygons of the Poisson series if the sample is made from an infinite number of objects and approximately so if it is made from a large number of objects.

In a plant community the number of diaspores produced are much higher than the number of plants established in the following generation. Therefore, the situation is comparable to a sample in which the expected frequencies of each species depend on the number of diaspores and their competitive ability. However, as mentioned above, random variation will modify these frequencies. A new term, "reproductive drift", is proposed for this phenomenon.

Reproductive drift is in most cases of little consequence and thus negligible as it only leads to numerically small oscillations in the number of individuals of a species in a number of successive generations. However, when the expected number of individuals is small, deviations may be of importance. Thus, in two cases, reproductive drift is significant: (1) for species represented by very few individuals in a large plant community and (2) for all, or almost all, the species in very small plant communities. These two cases will be treated separately below.

Random variation around expected gene (or other genetic) frequencies has long been studied in population genetics, where it is known as genetic drift. Its evolutionary consequences were originally demonstrated by WRIGHT (1931).

For the mathematic basis of the calculations used in the present paper, the reader is referred to handbooks in population genetics, e.g., LI (1955).

SPECIES REPRESENTED BY VERY FEW INDIVIDUALS IN A LARGE PLANT COMMUNITY

In a large plant community an immigrant introduced by long-range dispersal will initially be represented by a single or very few individuals out of a very large number (e.g., 10,000 or 100,000) of individuals of already established species. The future of the immigrant will be discussed below on the basis of its competitive ability.

(1) *The immigrant is competitively equal to established species.* Theoretically the immigrant should be able to repeat exactly its number in successive generations. However, a random variation around this expected value, i.e., reproductive drift, will occur. This random variation will approximately follow the Poisson series. In Fig. 1, frequency-polygons for 1, 2, 3, and 6 initial individuals are shown. From the polygons it can be seen that the probability for elimination already in the next generation is 37 % if the species was initially represented by one individual and 13 % if it was represented by two

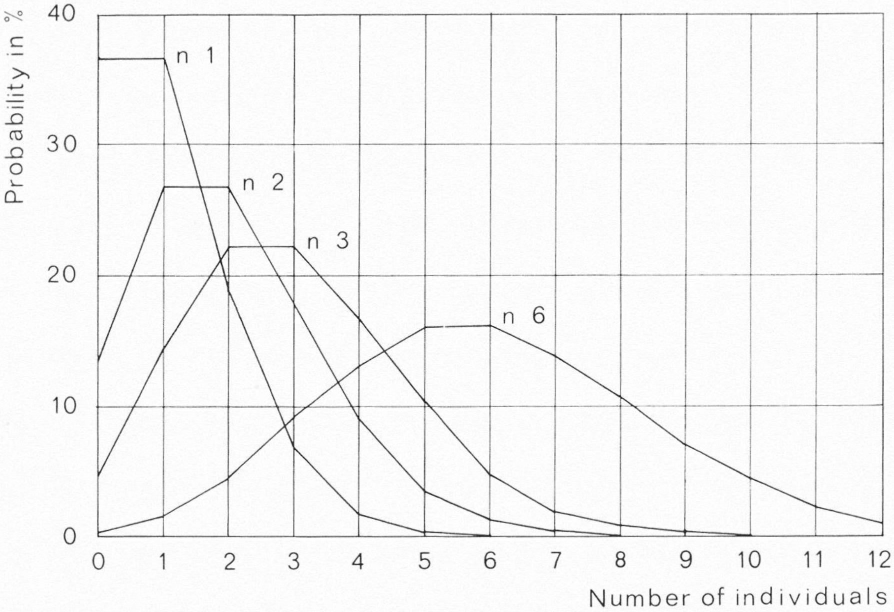

Fig. 1. The probability of a selectively neutral species initially occurring as 1, 2, 3, or 6 individuals in a large (theoretically infinite) plant community being represented in the following generation. On the horizontal axis, the number of individuals in the following generation is indicated, and on the vertical axis the probability percentage is given. The diagram represents frequency-polygons of the Poisson series.

Table 1. The probability percentage for the survival in a number of successive generations of a species that is initially represented by a single individual in a large (theoretically infinite) plant community. Values are given for two cases: (1) the species is competitively equal to previously established species and (2) the species is competitively 1 per cent superior to previously established species. The table is based on calculations by FISHER (1930).

Generations	No selective advantage	1 per cent advantage
1	63.2	63.6
2	46.9	47.4
3	37.4	38.0
4	31.2	31.9
5	26.8	27.5
6	23.5	24.3
7	21.0	21.8
–	–	–
15	11.3	12.2
31	5.9	6.9
63	3.0	4.1
127	1.5	2.7
–	–	–
∞	0	2.0

individuals. Even if it survives one generation, it will be subject to the same random process in successive generations. In Table 1 the probabilities for survival in a number of consecutive generations are tabulated for species initially represented by one individual. It is seen that the probability for survival after 5 generations is 27 %, after 15 generations 11 %, and after 127 generations 1.5 %.

A competitively neutral species, which has been introduced as a single or very few individuals, will therefore be randomly eliminated in most cases. Only rarely will it increase by the random mechanism to such an extent that it can be regarded as permanently established.

(2) *The immigrant is competitively slightly superior compared to established species.* Theoretically, such an immigrant should successively increase in number and finally eliminate species originally inhabiting the plant community. But even in this case the risk of random elimination is great. The probability of survival in the case of 1 % superiority has been calculated mathematically. From Table 1 it is seen that it is only slightly higher than for competitively neutral species.

(3) *The immigrant is comparatively markedly superior compared to established species.* Such immigrant species may also become randomly eliminated even if the risk decreases the more superior the species is. Markedly superior species can mainly be referred to three categories: (a) "colonizing" species inhabiting disturbed habitats (see e.g., BAKER & STEBBINS 1965), (b) species with stolons or subterranean propagules, and (c) species with a high competitive ability in the seedling stage. In case (b) the delimiting migratory factor apparently lies in the dispersal of the diaspores and in the successful introduction of the first individual. Case (c) mainly concerns species with heavy diaspores, with considerable amounts of food reserves, giving rise to vigorous seedlings. In this case the delimiting migratory factor apparently is the dispersal of the diaspores.

(4) *The immigrant is competitively inferior compared to established species.* Such an immigrant naturally is exposed to a great risk of selective and random elimination. If it by chance happens to be greatly increased in number, it will by competition decrease and again be exposed to the risk of random elimination. Such a species cannot therefore, be permanently established.

A consequence of the random process discussed above will be that a species in a plant community will be exposed to a great risk of elimination if it becomes reduced to one or a few individuals by disease or any other external factor. Reproductive drift is therefore certainly one of the main reasons for the common failure of protection of the last few individuals of a rare plant species in a given locality.

The evaluation of the probability for permanent establishment is not always dependent only on the competitive ability and the random process discussed above, but also other factors may interact. Thus, the introduction of a self-sterile species, only reproducing by seeds, as a single individual into a new locality can only end in failure. A similar failure of permanent establishment will occur in introduced species that are dependent on a pollinator that is lacking in the locality. During extreme years, e.g., with very low precipitation, species represented by few individuals in a plant community will be exposed to an increased risk of random elimination.

The random process operating on the establishment of the first individuals from diaspores successfully distributed to a new locality is theoretically equivalent to that of the reproduction of a species represented by a single individual in a plant community. However, the risk of random elimination is still greater, as the number of diaspores is normally very small, while an established individual usually will give rise to hundreds or thousands of diaspores. Even in this case the competitive ability in the seedling stage is surely an important factor. Species with diaspores possessing a large amount of reserve food will have a marked advantage in the seedling stage, providing them with a greater chance of being introduced.

The competitive advantage of species with large diaspores during the establishment of the first individuals and during the survival in successive generations may be the main reason for the remarkably low correlation between dispersal efficiency of diaspores and size of distribution areas in the angiosperms.

THE SPECIES COMPOSITION IN SMALL PLANT COMMUNITIES

In a small plant community, all, or almost all, the species are represented by relatively few individuals. Random deviations from expected numerical values therefore play an important role in the reproduction of the community. All, or almost all, the species run the risk of being randomly eliminated. Ultimately, reproductive drift ought to lead to elimination of all but one species. Such a consequence is certainly exceptional, as a plant community is usually an integrated system of a number of ecological "specialists" inhabiting different microniches.

As a consequence of the great importance of reproductive drift, the competitive ability of the species in a small community will play a subordinate role. A competitively superior species may very well be randomly eliminated, while an inferior species may survive. Thus, the species composition in a small plant community may not always truly reflect the habitat conditions.

An immigrant introduced by long-range dispersal into a small plant community will of course be exposed to reproductive drift in the same way as the established species. However, the probability for its establishment is considerably greater than in a large community. This advantage is in reality balanced by the normally much smaller area occupied by a small plant community, which makes successful dispersal to the actual locality less probable.

EXAMPLES ILLUSTRATING REPRODUCTIVE DRIFT

The existence of reproductive drift as a factor influencing the reproduction of the species in a plant community is evident. But is it negligible or significant compared to other factors operating during reproduction?

Experimental investigations of the different stages and the final result of introduction of various numbers of diaspores of a number of species in suitable, stable habitats, at present not occupied by the actual species, are planned by the author.

For lack of experimental data, the evidence of reproductive drift will be illustrated by examples of distribution areas in the flora of the central Aegean archipelago in Greece.

This archipelago has been intensely investigated by the author and a number of co-workers (B. BENTZER, R. VON BOTHMER, L. ENGSTRAND A. HANSEN, B. NORDENSTAM, S. SNOGERUP, A. STRID) in 1957—1968. About 35,000 herbarium numbers of vascular plants have been collected and c. 100,000 field annotations for individual species have been registered. Together with other records gathered in Flora Aegaea by RECHINGER (1943), these data form a fairly good base for a discussion on distribution areas in the region. Distribution maps for all indigenous species in the area are under preparation and are planned to be published in 1970—1971.

From this work, two cases have been selected illustrating the effect of reproductive drift: (1) the distribution pattern of species belonging to the phrygana vegetation and (2) the species composition in small, isolated habitats.

Some general comments on the distribution maps may be useful. The area investigated in detail is marked on all maps. The distribution in adjacent regions has been compiled from the literature (Halácsy 1901—1912; Rechinger 1943 a and b, 1949, 1961; Rechinger & Greuter 1967; Meikle 1954; Davis 1953; and Phitos 1967), but also c. 3,000 collections and numerous field annotations by the author and his co-workers have been used. Localities from the Turkish mainland have not been indicated. The distribution outside the marked area is partly incomplete as extensive areas are imperfectly known botanically, e.g., the west coast of Peloponnisos and many east Aegean islands.

To give the necessary base for an interpretation of the distribution areas presented, general trends in the Aegean phytogeography will be briefly reviewed. For a more complete discussion the reader is referred to Rechinger (1950, 1951).

OUTLINES OF THE AEGEAN PHYTOGEOGRAPHY

In the Pliocene, a land bridge existed in the central part of the Aegean connecting southern Greece and western Turkey. This land bridge was delimited in the north by a large lake covering most parts of the present North Aegean Sea and in the south by the Sea of Crete, which separated it from the south Aegean island chain. In the beginning of the Pleistocene, this land bridge was broken down, beginning with a separation from the Turkish mainland and later on also by a separation from the Greek mainland. The ultimate result was the present archipelago. For details and references see Creutzburg (1963, 1966).

Tectonic activity locally leading to considerable vertical movements may have occurred even lately, especially in the southern part of the central Aegean area (an active volcano still exists on the island of Thira).

During the Pleistocene, the sea level has fluctuated considerably with regressions up to 100—200 m during glacial periods and transgressions up to 35 m during interglacials (see Pfannenstiel 1951, 1954). These fluctuations have influenced the size of the islands only to a minor extent, as the coasts are mostly steep and the sea is deep. In single instances, regressions may have led to junctions of some islands, as Naxos and Paros, which are at present separated only by a shallow strait. Many small islands adjacent to larger ones may also have been connected with the larger islands. Transgressions have apparently also led to the disappearance of some of the smallest islands.

The geological formations are rather varied in the entire area, but also within the islands. Milos and adjacent islands and the greater part of the Thira area were formed from volcanic rock. The main rock in all the other islands is crystalline schist. Hard crystalline limestones also occur on all the large islands except Milos and Serifos. However, on the northern islands (Kithnos, Kea, Siros, Mikonos, Tinos, and Andros) the limestone areas are relatively small. Soft, marly limestones are rare and confined to the small islands south of Naxos and to Sikinos. Outcrops of granite occur on Naxos, Mikonos, and Tinos.

The central Aegean has a typical Mediterranean climate. The precipitation is low, 300—400 mm annually. No rain normally falls during the summer months. This is partly compensated for by the heavy dew during the nights. The temperature differences among the islands are small. The values for the annual temperature vary between 17.5° and 18.5°C. Local deviations occur within some islands owing to the broken topography with mountain peaks up to 1,000 m in height. Thus, north-eastern Andros, and probably also northern Ikaria, has a considerably higher precipitation compared to the normal values for the area. Generally, the water supply is the main factor for the distribution of different vegetation types, while the composition of the rock seems to be of subordinate importance.

On account of the floristic composition, the Aegean has been divided by RECHINGER (1943) into a number of phytogeographical regions (see Fig. 2):

(1) *The south Aegean region,* characterized by a very high endemism (c. 200 endemic species).
(2) *The east Aegean region,* with a strong Turkish flora element.
(3) *The west Aegean region,* with a flora similar to that of the Greek mainland.
(4) *The central Aegean region,* with a flora mainly agreeing with that of the Greek mainland but lacking many species common to the west Aegean region and the Greek mainland. Many species and species complexes that are abundant in the surrounding regions have only scattered localities in the central Aegean (cf. Fig. 17), and some are completely lacking (cf. Fig. 16).

The detailed investigation by the author and his co-workers have mainly been confined to the central Aegean area. All the c. 200 islands have been visited with the exception of the island of Youra and two adjacent islets, which for political reasons never seem to have been accessible to botanists. One of the east Aegean islands, Ikaria, has been included in the investigation. This island has a botanically unique position among the east Aegean islands. The Turkish element is relatively weak. Instead, the island gives from a floristic point of view an impression of being an old, isolated refugium.

DISTRIBUTION OF PHRYGANA SPECIES

The eastern facies of the Mediterranean garigue, the phrygana, is the dominating vegetation type throughout the central Aegean. In many of the smaller islands, as well as in some of the larger, isolated islands, as Astipalaia and Anafi, the phrygana probably represents the natural vegetation on dry habitats throughout the islands. On most of the larger islands, the phrygana has been greatly extended as a result of deforestation. Formerly, dry forests mainly of *Quercus coccifera* L., but possibly also of *Pinus halepensis* WILLD. certainly have played an important role in the vegetation. At present, only small patches of forests exist on some of the larger islands; viz., Naxos, Andros, and Kea. The degradation of the forests to phrygana is mainly a result of

Fig. 2. The subdivision of the Aegean into phytogeographical regions according to RECHINGER (1943, 1950). The geographical names are in accordance with The Times Atlas (BARTHOLOMEW 1956).

human activity (cutting of trees followed by intensive grazing). Extensive areas were formerly cultivated. As the agriculture is now in strong retrogression, especially on the medium-sized and small islands, vast areas of abandoned fields have been invaded by phrygana vegetation.

The conditions on very small islands are rather complex. Many of these islands have a normally developed phrygana, while others have a sublitoral element of a very special composition (see p. 119).

The phrygana is very rich in species. It is dominated by (often spiny) shrubs, geophytes, and annuals. Many of the phrygana species are widely distributed in the Mediterranean. Some species are endemic to the Aegean and adjacent regions — e.g., *Euphorbia acanthothamnos* Heldr. & Sart. and *Centaurea raphanina* S. & S. A few species are endemic to the central Aegean — viz., *Fritillaria tuntasia* Heldr., *Bupleurum aira* Snog., *Verbascum adeliae* Hal., *Dianthus cinnamomeus* S. & S., and *Hymenonema graecum* (L.) DC. (also doubtfully recorded from the Istanbul area).

Most species are indifferent to the composition of the rock, be it crystalline schist, limestone, or young volcanic formations. A few species are confined to siliceous rock — e.g., *Stipa bromoides* (L.) Brand. and *Alkanna tinctoria* (L.) Tausch., while a few others have only been found on limestone — e.g., *Lithospermum apulum* L. and *Helianthemum apenninum* (L.) Lam. & DC.

Many of the phrygana species are evenly distributed throughout the central Aegean, often with the exception of the small, distant "oceanic" islands between Astipalaia and Karpathos. However, a considerable number of species belonging to different life-forms are unevenly distributed in the area. Some examples of distribution areas are given in Figs. 3—14 and below.

Shrubs

Evenly distributed

Calicotome villosa (Poir.) Link
Cistus creticus L.
Coridothymus capitatus (L.) Reichenb. f.
Fumana thymifolia (L.) Verl.
Genista acanthoclados DC.
Sarcopoterium spinosum (L.) Spach (Fig. 3)
Satureja thymbra L.
Teucrium polium L.

Unevenly distributed

Anthyllis hermanniae L. (Fig. 4)
Cistus parviflorus Lam. (Fig. 5)
Euphorbia acanthothamnos Heldr. & Sart. (Fig. 6)
Fumana arabica (Jusl.) Spach
Hypericum empetrifolium Willd. (Fig. 7)
Phlomis fruticosa L.
Teucrium microphylium Desf.
Teucrium brevifolium Schreb.

Perennial herbs

Evenly distributed

Carex distachya Desf.
Carlina corymbosa L.
Centaurea raphanina S. & S. (Fig. 8)
Dactylis hispanica Roth
Eryngium campestre L.
Hypericum triquetrifolium Turra & Farset
Oryzopsis coerulescens (Desf.) Richt.
Reichardia picroides (L.) Roth

Unevenly distributed

Alkanna tinctoria (L.) Tausch. (Fig. 9)
Astragalus spruneri Boiss. (Fig. 10)
Centaurea spruneri Boiss. & Heldr.
Dianthus cinnamomeus S. & S.
Erysimum pusillum Chaub. & Bory
Stipa lagascae Roem. & Schult.
Stipa bromoides (L.) Brand
Thesium bergeri Zucc.

Geophytes

Most geophytes flower in autumn and winter. As the winter flora is still imperfectly known, reliable distribution maps cannot usually be prepared. Only a few species that are easily recognizable in spring and summer can be given as examples.

Evenly distributed	Unevenly distributed
Iris sisyrinchium L.	*Fritillaria erhartii* Boiss. & Orph. (Fig. 11)
Urginea maritima (L.) Bak.	*Fritillaria tuntasia* Heldr. (Fig. 11)

Annuals

Evenly distributed	Unevenly distributed
Astragalus hamosus L.	*Alyssum minus* (L.) Rothm.
Brachypodium distachyum (Tourn.) Pal.	*Alyssum umbellatum* Desf.
Bupleurum gracile Urv.	*Asteriscus aquaticus* (L.) Less. (Fig. 13)
Crepis multiflora S. & S.	*Crepis fuliginosa* S. & S.
Ononis reclinata L.	*Hypochoeris aethnensis* (L.) Benth. & Hook.
Silene nocturna L.	*Knautia integrifolia* (L.) Bert.
Stipa tortilis Desf.	*Nigella arvensis* L. (coll.)
Tordylium apulum L. (Fig. 12)	*Tordylium aegaeum* Run. (Fig. 14)

The number of unevenly distributed phrygana species in the central Aegean is over 50, geophytes with imperfectly known areas excluded. Most of these species occur in all the surrounding phytogeographical areas in the Aegean (cf. Figs. 4, 5, 6, 7, 9, 13).

The efficiency of diaspore dispersal can hardly be estimated with any accuracy for any of the individual species in the phrygana. However, if evenly and unevenly distributed or local species in the central Aegean are compared as groups, they can be regarded as equivalent in this respect. Both groups include species with heavy diaspores, apparently not well adapted for long-range dispersal, as well as species with light seeds having different adaptations for long-range dispersal. There is no reason to assume that unevenly distributed or local species would generally have a lower competitive ability compared to evenly distributed species, as they often occur abundantly if present on an island (cf. Figs. 4, 5, 6, 7, 8, 9, 11, 13, 14).

The uneven distribution areas cannot be explained by the present climatic and edaphic conditions. The climate is fairly similar in the whole area, and different kinds of rocks occur on almost all the islands. With

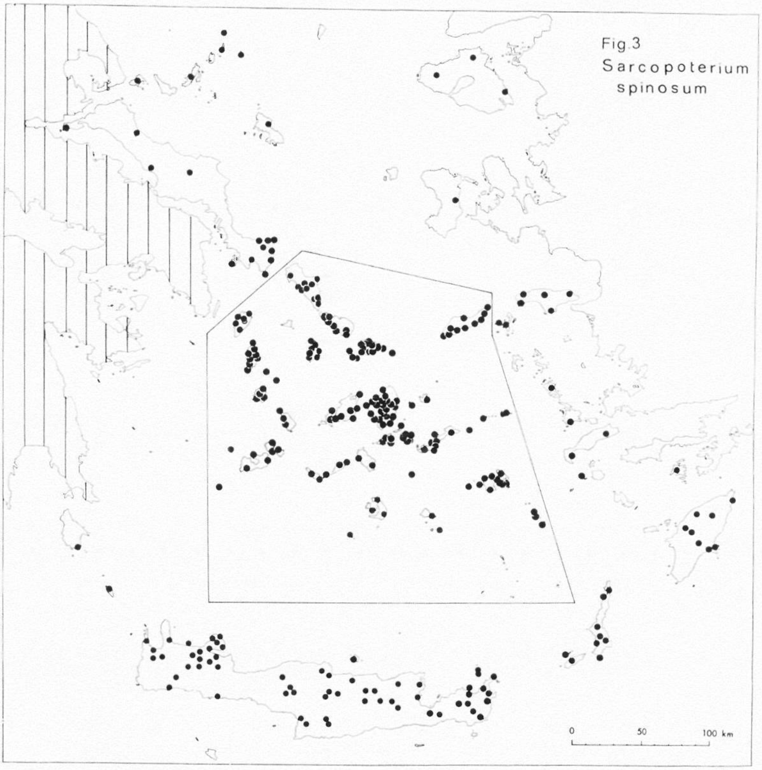

Fig. 3. The Aegean distribution of *Sarcopoterium* (*Poterium*) *spinosum* (L.) SPACH. The species is east Mediterranean, westwards reaching southern Italy and Sardinia. It is a thorny, strongly lignified, cushionlike shrub extremely common in the whole Aegean, and often a dominant component in the phrygana both on siliceous and calcareous ground. In the hatched area the species is frequent according to HALÁCSY (1901).

Fig. 4. The Aegean distribution of *Anthyllis hermanniae* L. The species is mainly east Mediterranean, westwards reaching the Balearic Islands. It is a strongly lignified shrub, in the central Aegean occurring mostly in coastal phrygana on siliceous ground.

Fig. 5. The Aegean distribution of *Cistus parviflorus* LAM. The species is east Mediterranean, westwards reaching southern Italy. It is a strongly lignified shrub, confined to the driest parts of the phrygana in the central Aegean, occurring on siliceous as well as on calcareous ground.

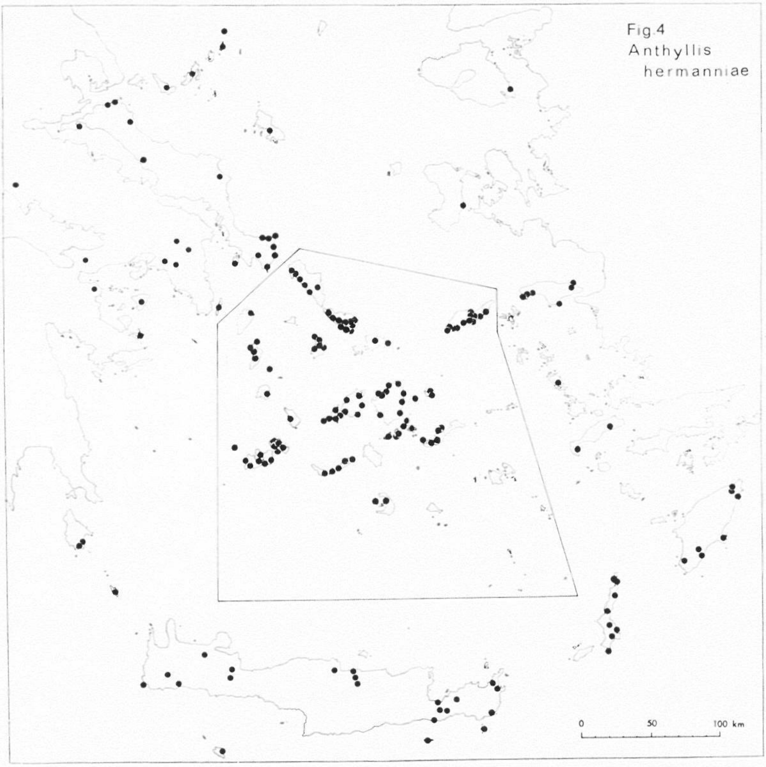
Fig.4 *Anthyllis hermanniae*

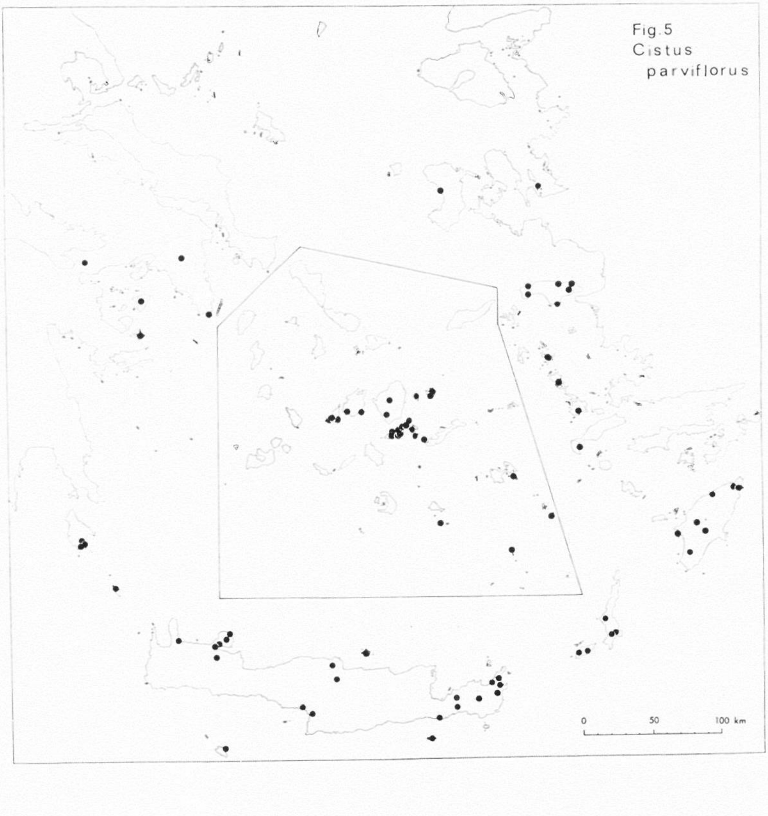
Fig.5 *Cistus parviflorus*

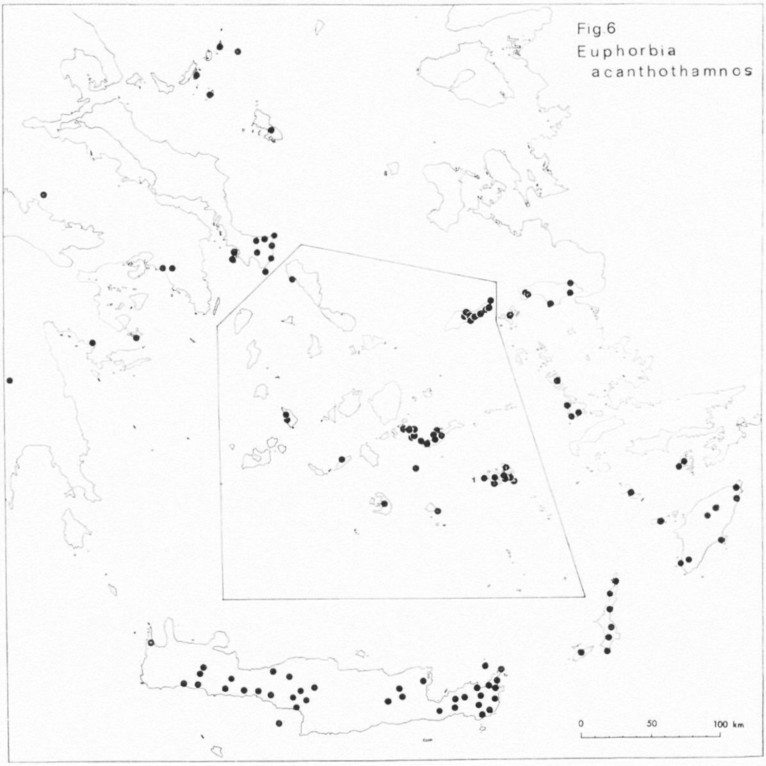

Fig. 6. The Aegean distribution of *Euphorbia acanthothamnos* HELDR. & SART. The species is endemic to the Aegean and adjacent regions. In the west Mediterranean it is replaced by the closely related *Euphorbia spinosa* L. The species is a thorny, strongly lignified shrub that locally dominates the phrygana both on siliceous and calcareous ground, but may also be found as a facultative chasmophyte.

Fig. 7. The Aegean distribution of *Hypericum empetrifolium* WILLD. The species is endemic to the southern part of the Balkan Peninsula (northwards reaching Albania), westernmost Turkey, and Cyrenaica. It is a small shrub occurring on siliceous as well as calcareous ground in phrygana vegetation, but sometimes also as a facultative chasmophyte.

Fig. 8. The Aegean distribution of *Centaurea raphanina* S. & S. The species is endemic to the Aegean region, the southern and central parts of the Greek mainland, and islands along the Greek west coast. Two mainly allopatric subspecies can be separated, ssp. *raphanina* occurring in the south Aegean region and ssp. *mixta* (DC.) RUN. on the Greek mainland. In the central Aegean the main part of the material randomly combines characters of the two subspecies (see RUNEMARK 1966). In the east Aegean region and in Turkey the species is replaced by the closely related *C. urvillei* DC. It is a perennial with a strongly developed tap root and spiny heads, occurring on siliceous and calcareous ground in phrygana vegetation, but also sometimes as a facultative chasmophyte.

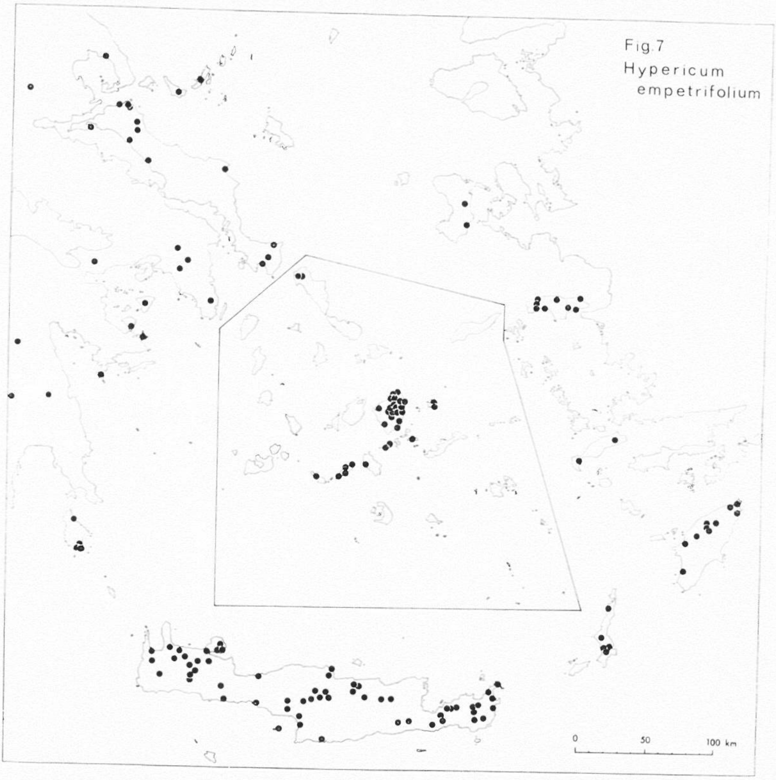
Fig.7
Hypericum
empetrifolium

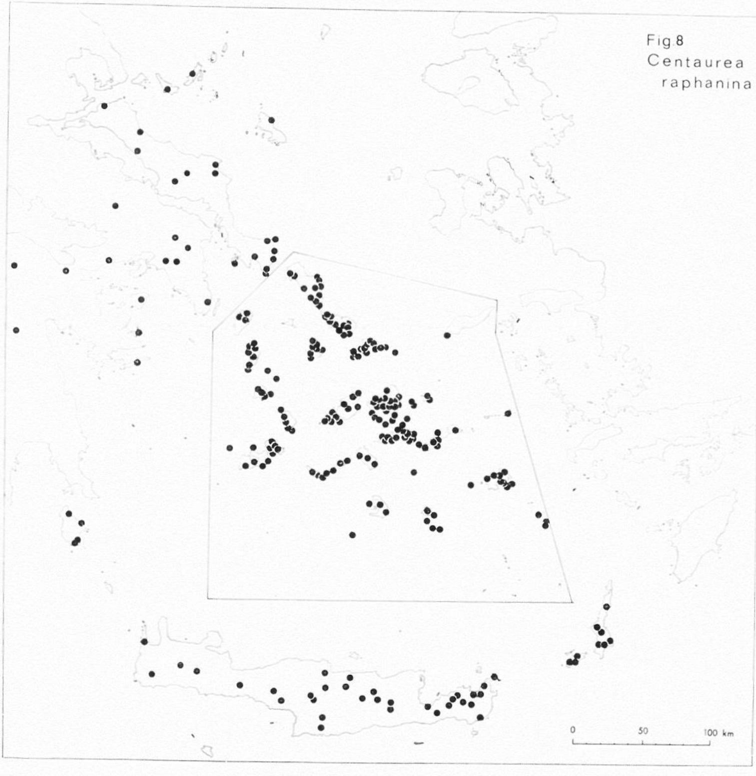
Fig.8
Centaurea
raphanina

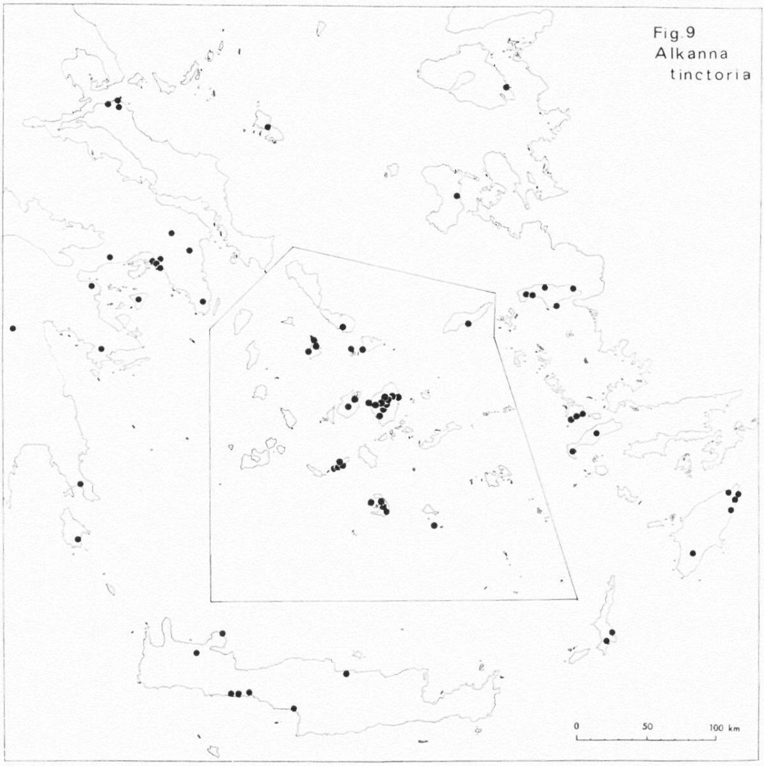

Fig. 9. The Aegean distribution of *Alkanna tinctoria* (L.) Tausch. The species is pan-Mediterranean. It is a rather small perennial that is confined to siliceous ground in phrygana vegetation in the central Aegean.

Fig. 10. The Aegean distribution of *Astragalus spruneri* Boiss. The species is endemic to the Aegean, eastern Greece, and northwestern Turkey. In Thessaly, Macedonia, and Bithynia it is represented by a morphologically deviating form series (v. *thessalus* Boiss.). It is a long-lived perennial with inflated pods that is confined to siliceous ground in phrygana vegetation in the central Aegean.

Fig. 11. The total distribution area of *Fritillaria erhartii* Boiss. & Orph. and *F. tuntasia* Heldr. As both species are extremely variable and a separation at the fruiting stage (most material was collected in the spring and summer) is uncertain, they have been represented on the same map. The two species are at least partly allopatric — *F. tuntasia* occurring in Kea, Kithnos, and Folegandros; *F. erhartii,* in Siros, Tinos, Mikonos, and on Euboea. Both species are long-lived geophytes, occurring only on siliceous ground in phrygana vegetation.

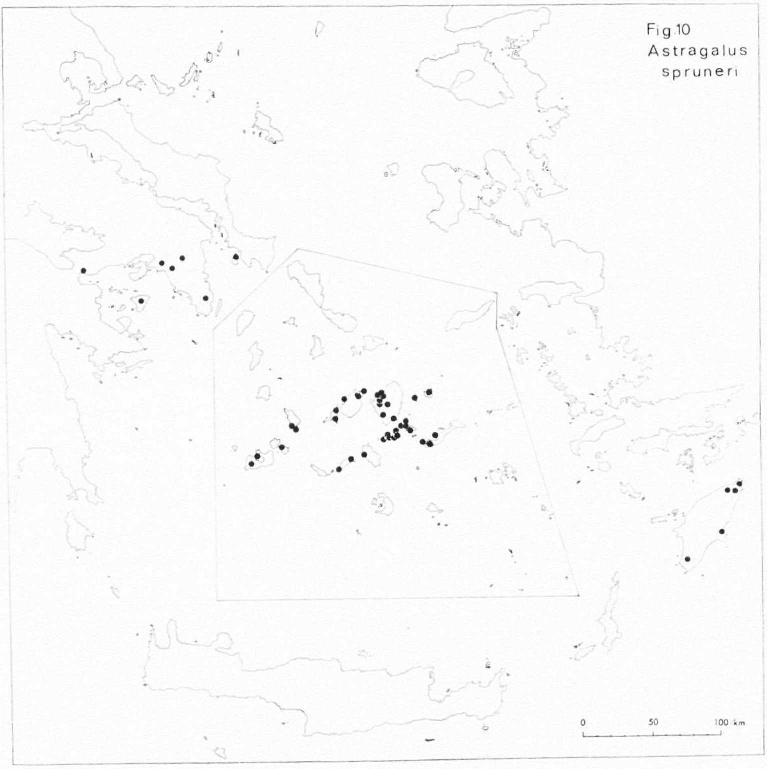
Fig.10
Astragalus
spruneri
0
50
100 km

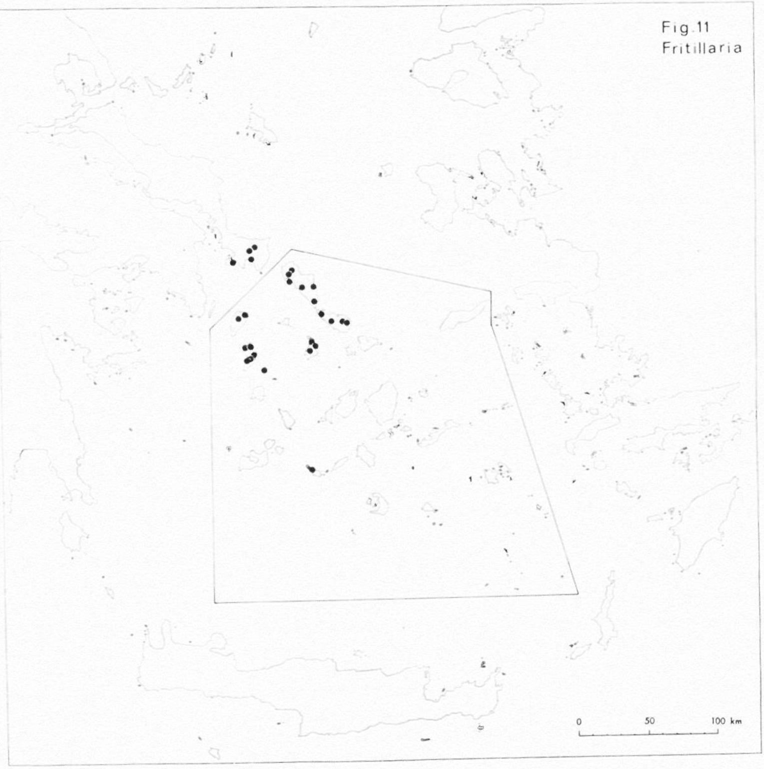
Fig.11
Fritillaria
0
50
100 km

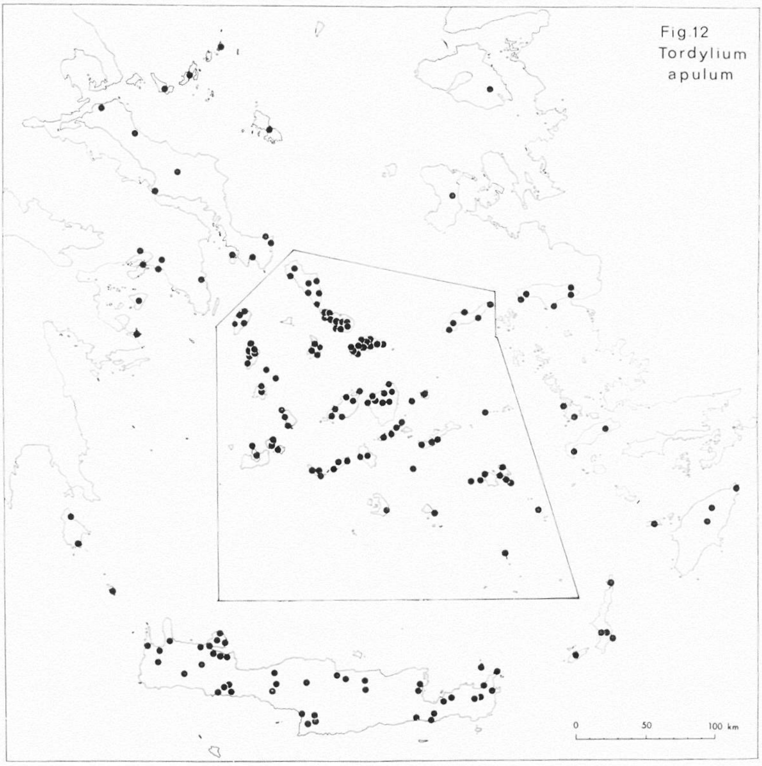

Fig. 12. The Aegean distribution of *Tordylium apulum* L. The species is mainly east Mediterranean, westwards reaching Algeria and southern France. The species is an annual, evenly distributed in the Aegean and abundant on siliceous as well as calcareous ground in phrygana vegetation, but also in localities influenced by human activity.

Fig. 13. The Aegean distribution of *Asteriscus aquaticus* (L.) LESS. The species is pan-Mediterranean, westwards reaching the Canary Islands. It is an annual, and in the central Aegean confined to dry coastal phrygana on siliceous as well as calcareous ground. The Aegean material has often been referred to a separate species, *A. citriodorus* HELDR. & HAL., but the differentiating characters often are randomly combined in single populations, making a separation impracticable (cf. RECHINGER 1961, RECHINGER & GREUTER 1967). In the hatched area the species is frequent according to HALÁCSY (1902).

Fig. 14. The total distribution area of *Tordylium aegaeum* RUN. The species is an annual, occurring on siliceous as well as calcareous ground in the phrygana vegetation.

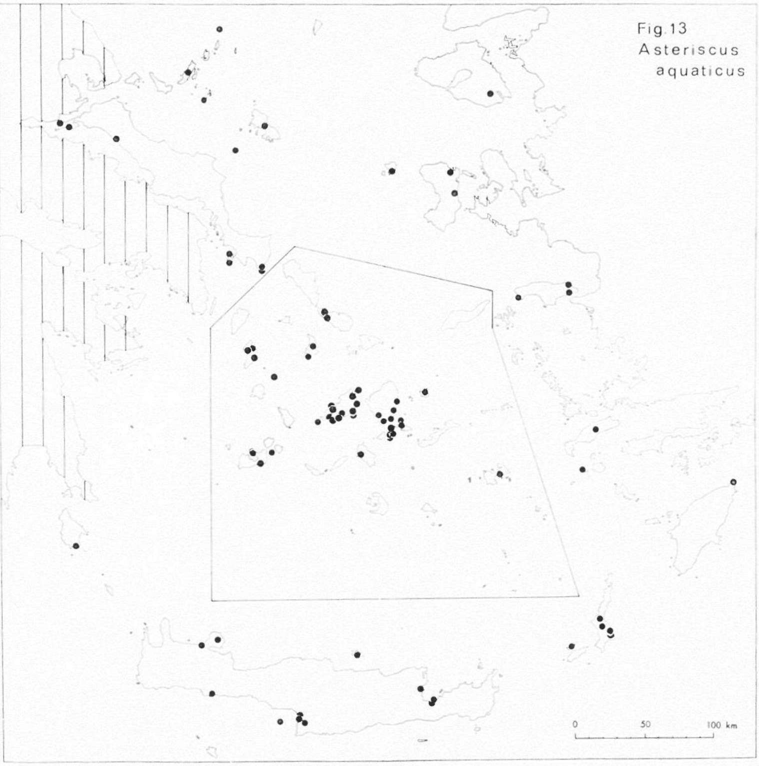
Fig.13
Asteriscus
aquaticus
0
50
100 km

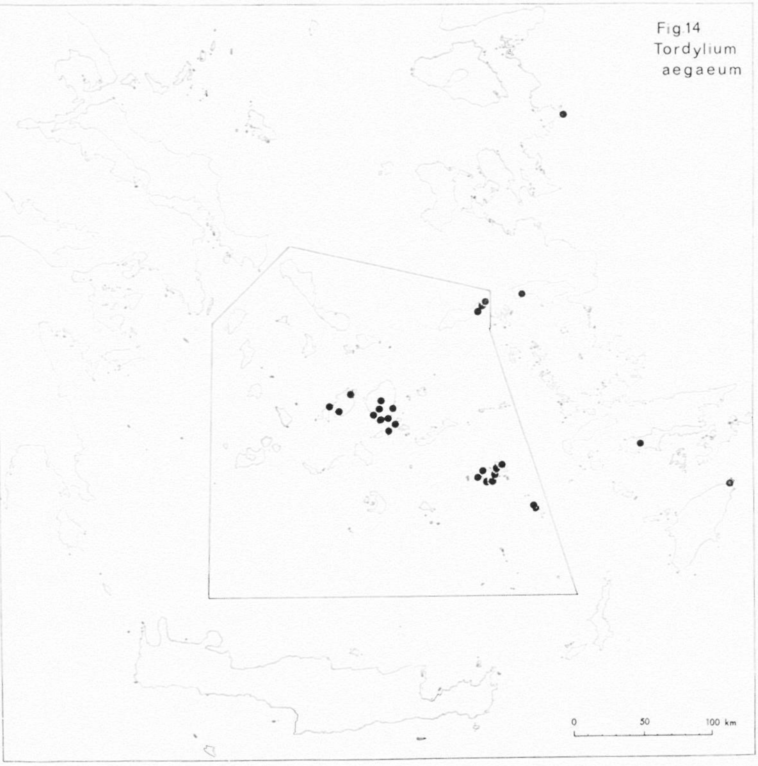
Fig.14
Tordylium
aegaeum
0
50
100 km

the exception of possible invasions of single species into the area in the Pleistocene, the present uneven distribution areas must be interpreted as the result of extinction of the actual species on many islands in connection with climatic fluctuations. Especially pluvial periods (corresponding to glacial periods in northern Europe) must have been critical for the phrygana element. The unevenly distributed species have apparently not, or only to a minor extent, been able to reinvade the islands which they have earlier occupied. A strong support for such an interpretation is the present scattered distribution areas, which cannot be fitted into any geographical or ecological patterns, but seem to be just at random (cf. Figs. 4, 5, 6, 7, 9, 11, 13, 14).

The distance between two adjacent central Aegean islands never exceeds 40 km. In most cases the large islands are only separated by straits of 5—20 km. It is remarkable that these short distances have been effective barriers to migration, even for species with light seeds, easily spread by wind — e.g., *Hypochoeris aethnensis* (L.) BENTH. & HOOK. and *Crepis fuliginosa* S. & S.

The uneven distribution areas presented can only be explained by a migratory situation in which reproductive drift has played an important role; i.e., most successful introductions of diaspores have failed. If they by chance have given rise to a single or a few individuals, these have in most cases been randomly eliminated in successive generations.

THE SPECIES COMPOSITION IN SMALL, ISOLATED PLANT COMMUNITIES

Isolated plant communities with a relatively small number of individuals have been studied in the central Aegean mainly in the following biotopes: (1) small islands, (2) cliffs, and (3) gravelly ground periodically flooded in winter and spring. The last-mentioned community with a plant composition dominated by west Mediterranean—west European species, i.a., *Radiola linoides* ROTH and *Isoëtes hystrix* BORY will be treated in a separate paper. The two other communities are briefly discussed below.

CLIFFS

The islands of the central Aegean have a very broken topography with many cliffs from a few metres up to big cliff systems 700 m high on eastern Amorgos. In the adjacent phytogeographical regions the conditions are similar. Thus, the biggest cliff systems in the Aegean are those of Karpathos, which are over 1,000 m high, and the enormous gorges and cliffs along the coast of south-western Crete.

The number of obligate chasmophytes among the angiosperms in the central Aegean is over 60, of which c. 50 are confined to hard, crystalline limestone cliffs. Most of these chasmophytes are highly lignified shrubs, often with a taxonomically isolated position (cf. DAVIS 1951).

The discussion will be confined to the flora of limestone cliffs in coastal areas, as they are especially rich in chasmophytes (c. 45 species in the central Aegean area). The distribution of limestone cliffs in the Aegean is indicated in Fig. 15.

Most of the species on such "maritime" cliffs are Aegean endemics. A few species are endemic to the central Aegean, viz., *Helichrysum amorginum* BOISS. & ORPH., *Pimpinella pretenderis* ORPH., *Centaurea oliveriana* DC., *Campanula heterophylla* L., *Campanula calaminthifolia* LAM., and *Silene adelfiae* RUN. (sp. nov. ined.). However, most of the species also occur in the south Aegean region, especially on Crete. Some species are also met with in the east Aegean region, while very few have been found in the west Aegean region or along the coasts of the Greek mainland.

The distribution areas, the confinement to limestone cliffs, and the taxonomic isolation of many species give the impression that the element is the last remnant of a cliff flora that inhabited the coasts of the Sea of Crete in the Pliocene. The great age of the element is also supported by the pronounced local differentiation found in many species — e.g., *Senecio bicolor* (WILLD.) TOD., *Dianthus fruticosus* L., *Lactuca acanthifolia* (WILLD.) BOISS., *Scorzonera araneosa* S. & S. (= *eximia* RECH. F.), and *Erysimum* sect. *Cheiri* (see SNOGERUP 1967 a and b).

None of the obligate chasmophytes are evenly distributed over the cental Aegean. The most widespread species are *Dianthus fruticosus* L. s. lat. (Fig. 18) and *Scrophularia heterophylla* WILLD. All other species have variously scattered distribution areas, which do not follow any geographical or ecological patterns (cf. Figs. 19, 20, 21, 22, 23).

The present Aegean distribution areas cannot be generally explained by the competitive ability of the species. Thus two complexes, which are aggressive and dominating members of almost all cliff communities in the surrounding phytogeographical regions, — viz., the *Inula candida* complex (Fig. 16) and *Campanula* subsect. *Quinqueloculares* (Fig. 17) have a very restricted distribution in the area investigated.

No correlation between dispersal efficiency of diaspores and size of

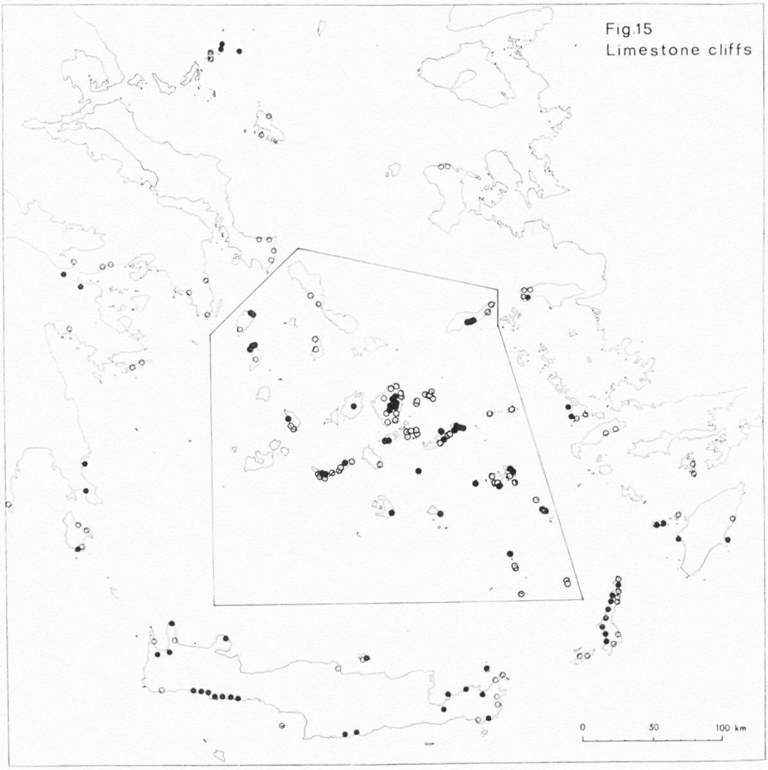

Fig. 15. The distribution of limestone cliffs in coastal areas in the Aegean. The map gives a correct representation of such cliffs in the detailedly investigated area marked on the map. Outside this area the records are based mainly on the observations of the author and his co-workers during different journeys in the Aegean, and are therefore very incomplete. Black dots indicate big cliff systems, rings minor cliffs.

Fig. 16. The Aegean distribution of the *Inula candida* complex. The complex is represented by seven species in the area, all perennial, lignified chasmophytes that are mostly restricted to limestone cliffs. The single species within the detailedly investigated area is *Inula heterolepis* BOISS., a very common chasmophyte in the east Aegean islands, in Karpathos and westernmost Turkey. For further information see RECHINGER (1938).

Fig. 17. The Aegean distribution of *Campanula* subsect. *Quinqueloculares*. The whole subsection is confined to the Aegean and adjacent regions. All species are biennial or perennial chasmophytes occurring on limestone, as well as on siliceous cliffs. In the central Aegean three species occur: *C. celsii* DC. on the western islands, *C. laciniata* L. on the southern ones, and *C.* aff. *sporadum* FEER on small islands east of Naxos and Mikonos. Besides, in the single east Aegean island Ikaria included in the detailedly investigated area, the east Aegean *C. lyrata* LAM. is abundant. For further information see PHITOS (1966).

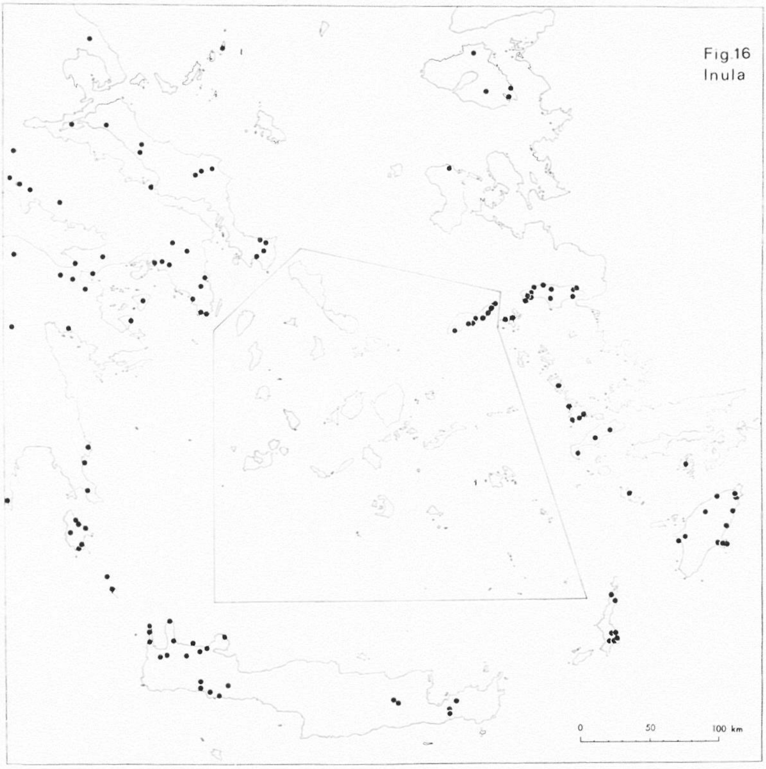

Fig.16
Inula

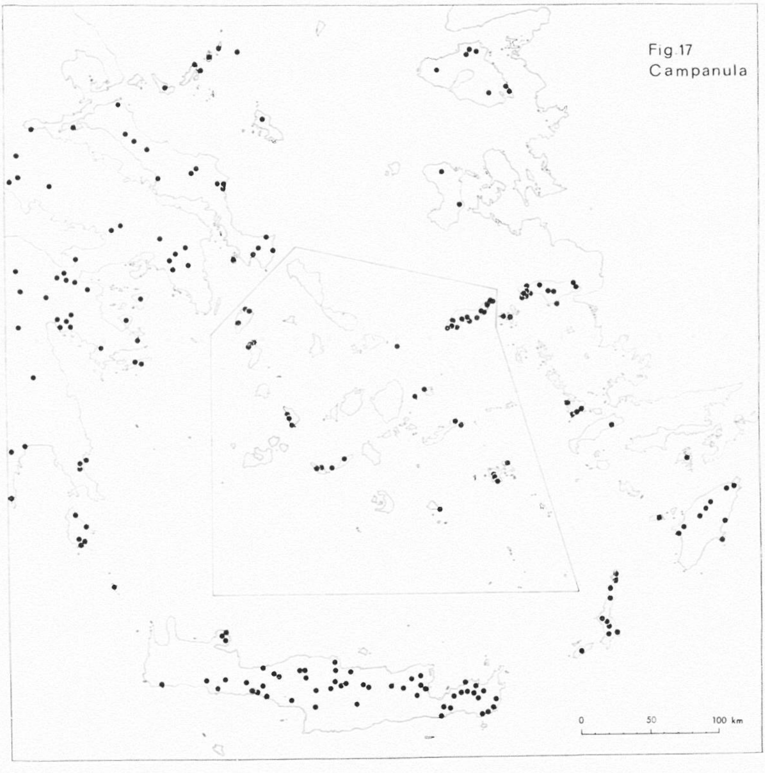

Fig.17
Campanula

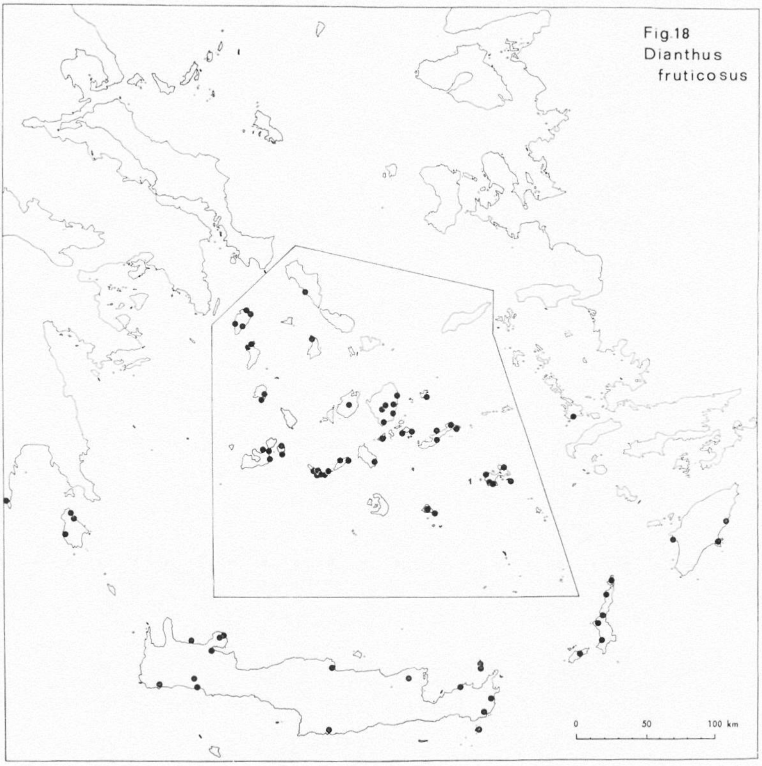

Fig. 18. The Aegean distribution of *Dianthus fruticosus* L. Outside this area the species has only been found in single localities along the coast of southern Peloponnisos and on the island of Kefallinia along the Greek west coast. The species is a strongly lignified shrub, in the central Aegean confined to limestone cliffs, with the exception of the Milos area where it grows on basaltic cliffs and Serifos where it is found on cliffs of hard crystalline schist. It displays strong local differentiation, and has been divided into three species: *D. fruticosus* s.str. in the western part of the central Aegean; *D. rhodius* RECH. F. in Rhodos; and *D. creticus* TAUSCH. (=*D. arboreus* auct. non L.) in the rest of the area. These species at most deserve subspecific rank (cf. DAVIS 1953).

Fig. 19. The total distribution area of *Helichrysum amorginum* BOISS. & ORPH. The species is a perennial, lignified shrub that is restricted to limestone cliffs. It is closely related to *H. doerfleri* RECH. F., a mountain chasmophyte in eastern Crete; *H. virgineum* (S. & S.) BOISS., growing on cliffs on the Athos peninsula in the northern Aegean; and to *H. taenari* ROTHM. from Cape Taenaron (Malea) in southern Peloponnisos.

Fig. 20. The total distribution area of *Asperula tournefortii* SIEB. The species is a perennial, lignified shrub that is restricted to limestone cliffs. It is related to *Asperula effusa* BOISS. and *A. asperrima* BOISS. from Spain.

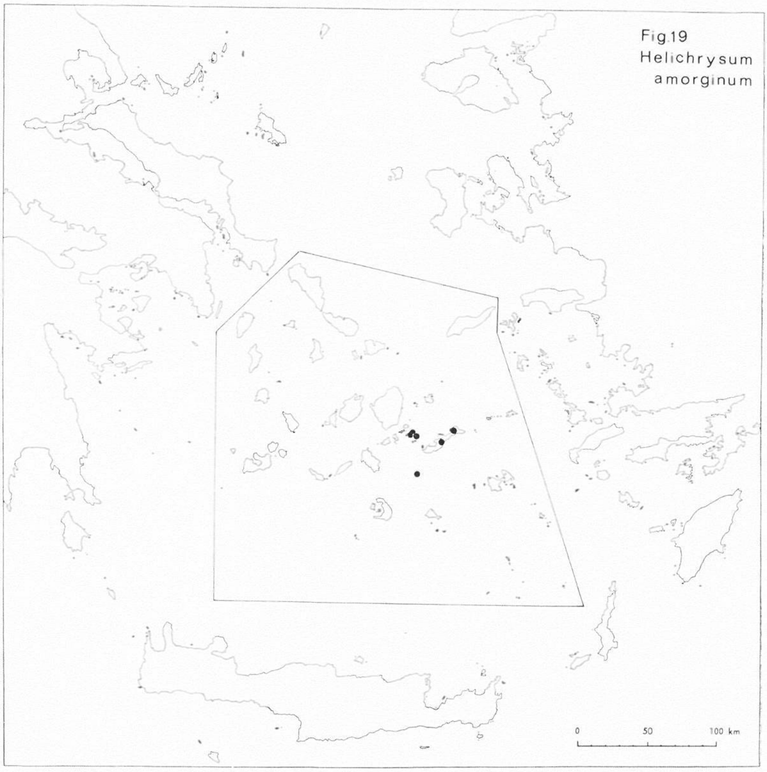
Fig.19 Helichrysum amorginum

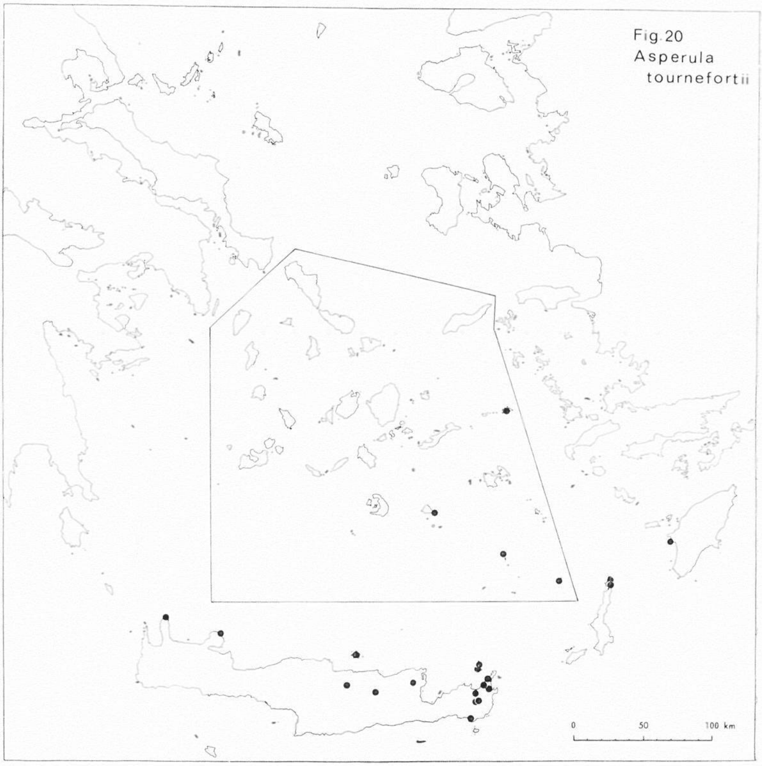
Fig. 20 Asperula tournefortii

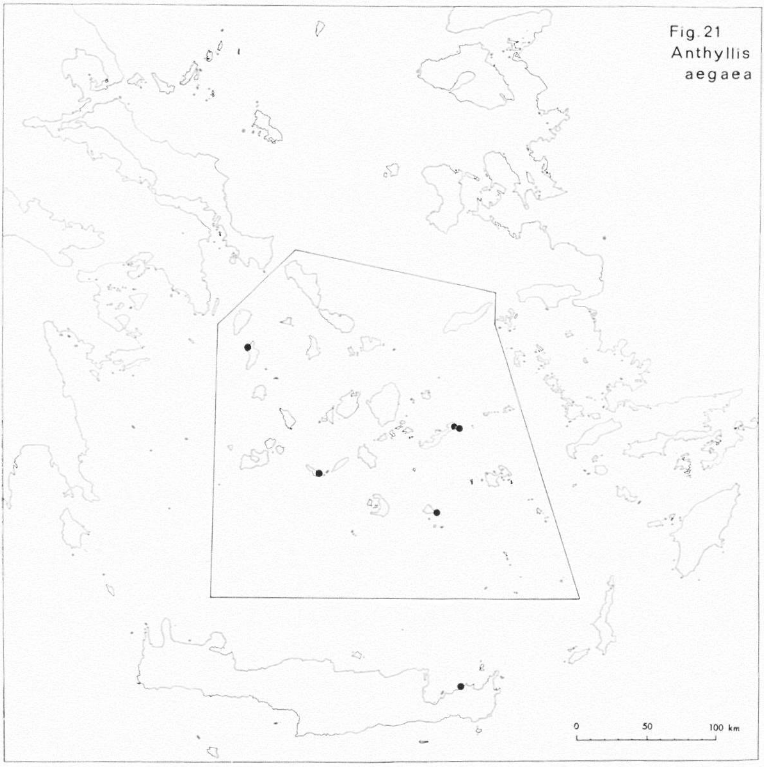

Fig. 21. The total distribution area of *Anthyllis aegaea* TURRILL. The species is a perennial, strongly lignified shrub that is confined to limestone cliffs. It is closely related to the west Mediterranean *A. barba-jovis* L.

Fig. 22. The Aegean distribution of *Seseli gummiferum* PALLAS ex. J. E. SMITH. The species is a long-lived monocarpic chasmophyte that is confined to limestone cliffs in the Aegean. The species has been divided into four subspecies by DAVIS (1953): ssp. *gummiferum* in the Crimea, ssp. *corymbosum* (BOISS.) P. H. DAVIS in south-eastern Turkey, ssp. *crithmifolium* (DC.) P. H. DAVIS and ssp. *aegaeum* P. H. DAVIS in the Aegean. The two Aegean subspecies, mainly distinguished by the presence or absence of pubescence on the basal leaves, hardly deserve to be separated.

Fig. 23. The Aegean distribution of *Senecio bicolor* (WILLD.) TOD. Outside the area, the species has been recorded from western Greece and Italy. It is a rather weakly lignified shrub, confined to limestone cliffs in the Aegean and showing a large local differentiation. The species is a member of the very polymorphic west Mediterranean *Senecio cineraria* complex.

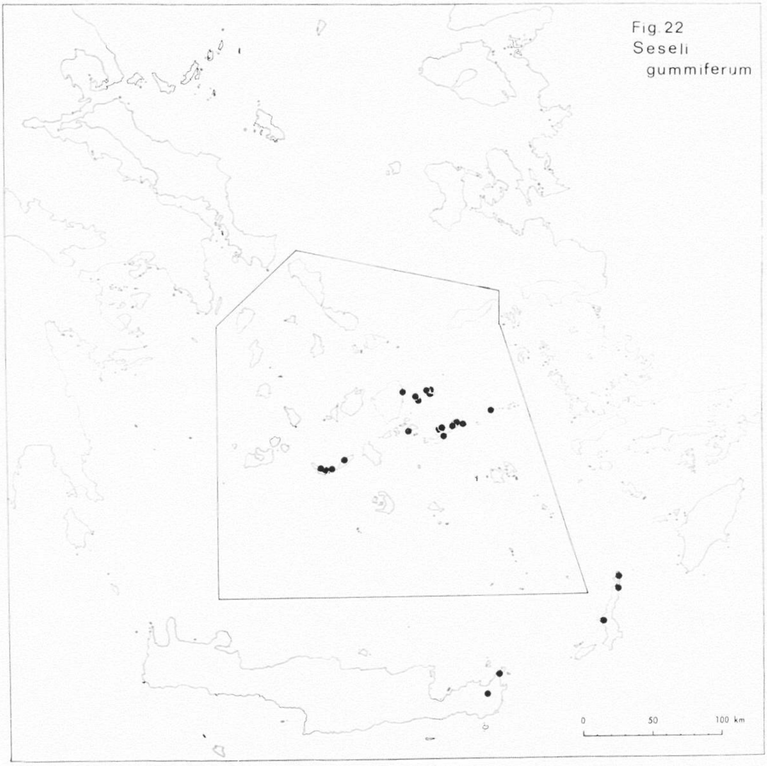

Fig. 22 Seseli gummiferum

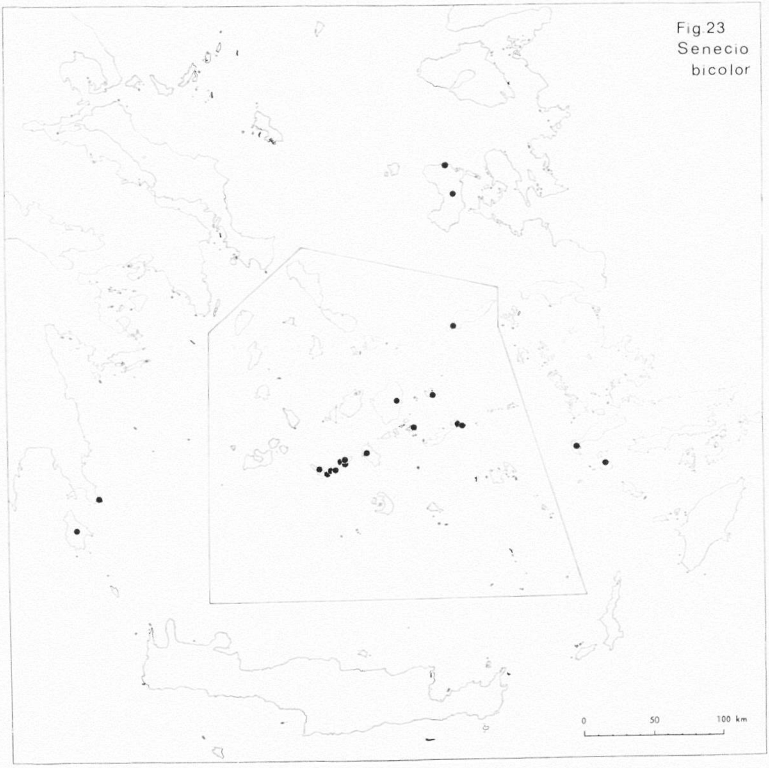

Fig. 23 Senecio bicolor

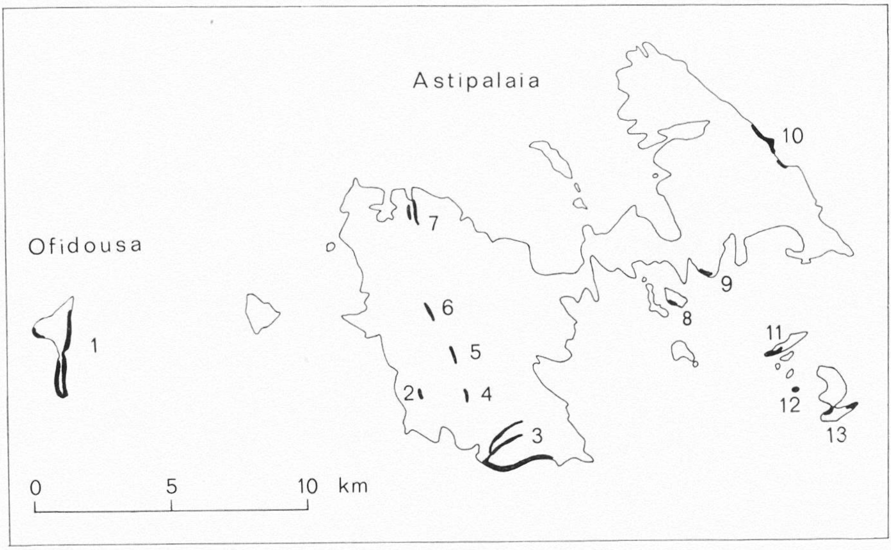

Fig. 24. The distribution of the limestone cliffs in the Astipalaia area. The figures refer to Table 2, where the occurrences of chasmophytes on the individual cliffs are tabulated.

Table 2. The distribution of obligately chasmophytic angiosperms on the different cliffs in the Astipalaia area. The numbers above refer to localities indicated in Fig. 24.

	1	2	3	4	5	6	7	8	9	10	11	12	13
Alyssum creticum L.	+	+	+	+	+	+	+	–	+	–	–	–	–
Amaracus tournefortii (Sibth.) Benth.	+	–	–	–	–	–	–	–	–	+	–	–	+
Arenaria muralis (Link) Sieb.	–	–	+	+	+	+	–	–	–	–	–	–	–
Brassica cretica Lam.	+	–	+	–	–	–	–	–	–	–	+	–	–
Campanula laciniata L.	–	–	+	+	+	+	–	–	–	+	–	–	–
Carum multiflorum (S. & S.) Boiss.	+	+	+	+	+	+	+	–	–	–	–	–	+
Dianthus fruticosus L.	–	–	+	–	+	+	+	–	–	+	–	+	–
Eryngium amorginum Rech. f.	+	–	–	–	–	–	–	–	–	+	–	–	–
Ferula chiliantha Rech. f.	–	+	+	–	–	–	–	–	–	–	–	–	–
Fibigia lunaroides (Willd.) S. & S.	–	–	–	–	–	–	+	–	–	+	–	–	–
Helichrysum orientale (L.) DC.	–	–	–	–	–	–	–	–	–	+	–	–	–
Lactuca acanthifolia (Willd.) Boiss.	–	+	+	+	+	–	–	+	–	+	+	+	+
Linum arboreum L.	–	–	–	–	–	–	–	–	–	+	–	–	–
Pimpinella pretenderis Orph.	+	–	–	–	–	–	–	–	–	+	–	–	–
Ptilostemon chamaepeuce (L.) Less.	–	–	–	–	–	+	+	–	–	–	–	–	–
Scorzonera araneosa S. & S.	–	–	+	+	–	–	+	–	–	+	+	–	+
Scrophularia heterophylla Willd.	+	+	+	+	+	+	+	+	+	+	–	–	+
Staehelina fruticosa L.	+	–	+	–	–	–	–	–	–	–	–	–	–
Symphytum creticum (Willd.) Run.	+	+	+	+	+	+	+	+	–	+	–	–	+
Number of species	9	6	12	8	8	8	8	3	2	12	3	2	6

the geographical areas can be demonstrated in the chasmophytes. Thus, *Helichrysum amorginum* BOISS. & ORPH. (Fig. 19) and *Senecio bicolor* (WILLD.) TOD. (Fig. 23), with small seeds and a well-developed pappus, have very restricted areas, while *Carum multiflorum* (S. & S.) BOISS. and *Brassica cretica* LAM. with large, heavy seeds are relatively extensively distributed. The strong local differentiation occurring in many chasmophytes is an indication of effective isolation. Long-range dispersal seems therefore to have played a rather insignificant role for the present distribution areas, apparently mainly because of the small area of the cliff systems making successful diaspore dispersal improbable.

Also within minor areas, the distribution of chasmophytes in different, isolated cliffs seems to be haphazard to a large extent, even if some correlation between the size of the cliff system and the number of chasmophytes can be demonstrated. This is illustrated in Table 2 where the big cliff systems in the Astipalaia area (localities 1, 3, and 10 in Fig. 24) have 9, 12, and 12, respectively, of the 20 chasmophytic angiosperms found in the area, while the other cliffs have between 2 and 8.

As the number of niches that can be used by plants, even in relatively big cliff systems, are very restricted, the number of individuals of every species is generally low. All, or almost all, chasmophytes in a cliff system are therefore subject to a considerable risk of random elimination.

SMALL ISLANDS

The central Aegean archipelago is composed of c. 200 islands of which c. 100 have an area of less than 1 km^2. In adjacent phytogeographical regions numerous such small islands also occur, of which c. 40 have been investigated by the author.

The islands always have a rocky ground consisting of crystalline schists, limestone, volcanic rock, or in a few cases granite. The composition of the flora on the small islands seems to be almost wholly independent of the substrate, possibly with the exception of granite.

Two distinct vegetation zones can be distinguished on the small islands: (1) a litoral zone inhabited by true halophytes and (2) a sublitoral zone, which is not washed by the sea even in stormy weather.

The halophytes in the litoral zone are mostly widespread Mediterranean species, occurring abundantly on all rocky shores of the Aegean — i.a., *Silene sedoides* POIR. (Fig. 25), *Lotus creticus* L., and *Frankenia*

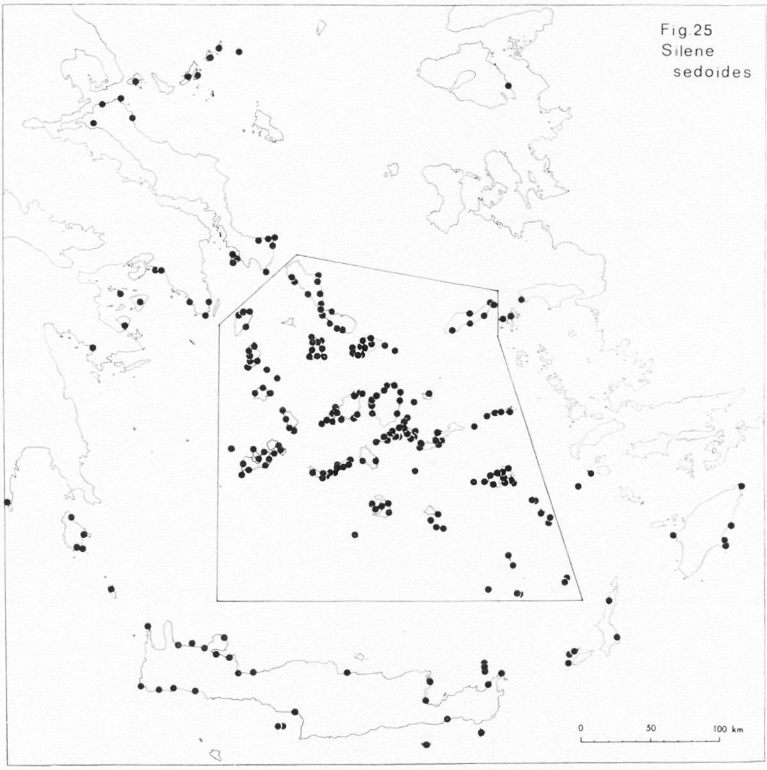

Fig. 25. The Aegean distribution of *Silene sedoides* Poir. The species is pan-Mediterranean. It is a small annual, occurring abundantly on rocky and stony shores, and to a less extent also on sandy shores throughout the Aegean.

Fig. 26. The total distribution area of *Arenaria aegaea* Rech. f. The species is a small annual, occurring on small islands and in a few cases also in the sublitoral zone of larger islands. It is a morphologically and ecologically distinct, diploid member of the *Arenaria serpyllifolia* complex, which in the Aegean is also represented by *A. leptoclados* Guss. (in the phrygana and localities influenced by human activity) and *A. serpyllifolia* L. s. str. in the alpine and subalpine zones of high mountains.

Fig. 27. The total distribution area of *Anthemis scopulorum* Rech. f. The species is an annual found on small islands and in a few instances also on screes below limestone cliffs on larger islands. It is extremely polymorphic in habit, leaf shape, size of the capitula, the development of the ligulae, and shape of the receptaculum, and displays a very strong local differentiation. Apparently, it has no close relatives.

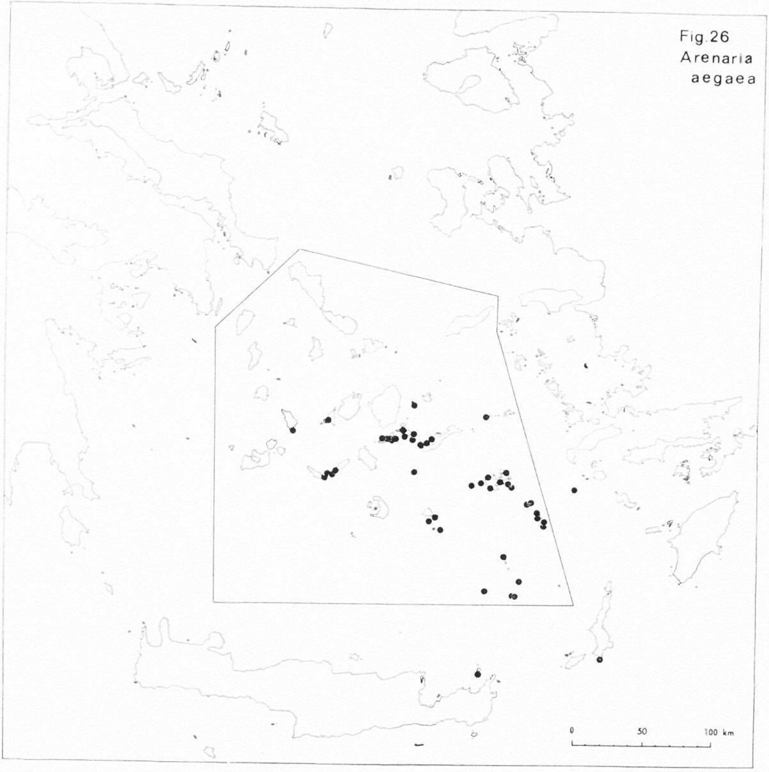
Fig. 26 Arenaria aegaea

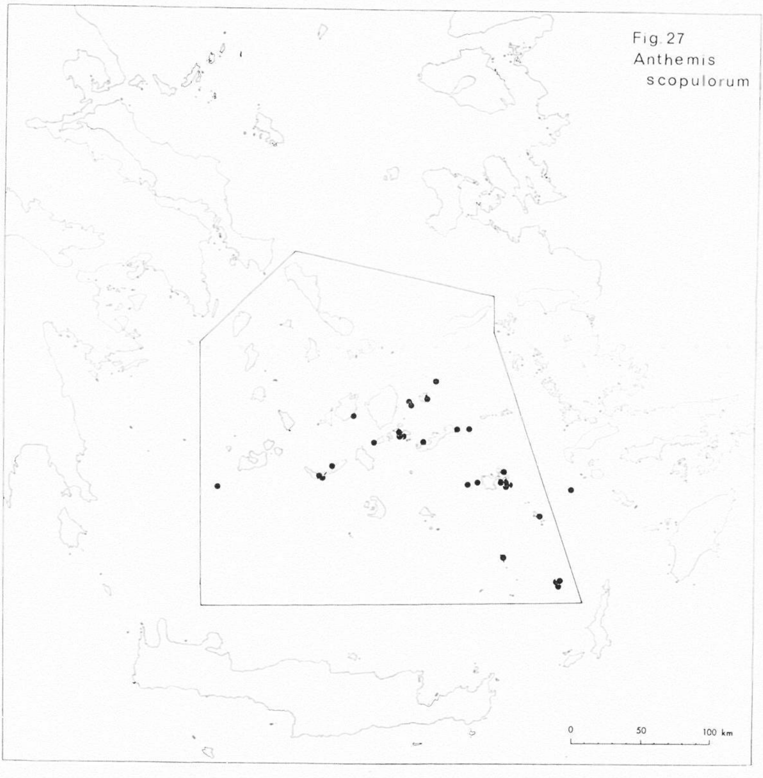
Fig. 27 Anthemis scopulorum

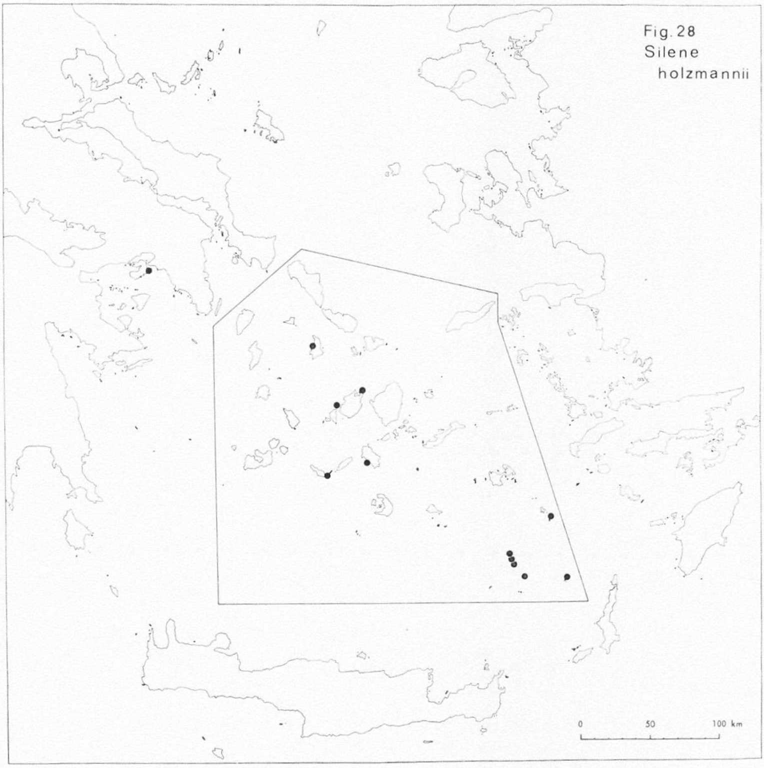

Fig. 28. The total distribution area of *Silene holzmannii* HELDR. The species is an annual that is entirely confined to small islands. It is related to *S. behen* L., a common weed in the Aegean, and *S. reinholdii* HELDR. on the Greek mainland.

Fig. 29. The total distribution area of *Salsola aegaea* RECH. F. The species is a lignified perennial that with few exceptions is confined to small islands. It is closely related to the west Mediterranean *S. vermiculata* L.

Fig. 30. The distribution of *Dactylis marina* BORRILL in the Aegean. The species is a perennial, which is known from three small islands in the central Aegean. It is a west Mediterranean species, morphologically mainly characterized by globose epidermal cells, and always confined to sea shores. The Aegean material deviates in being much more stout, with broader leaves, and may deserve to be taxonomically recognized as a separate species or subspecies.

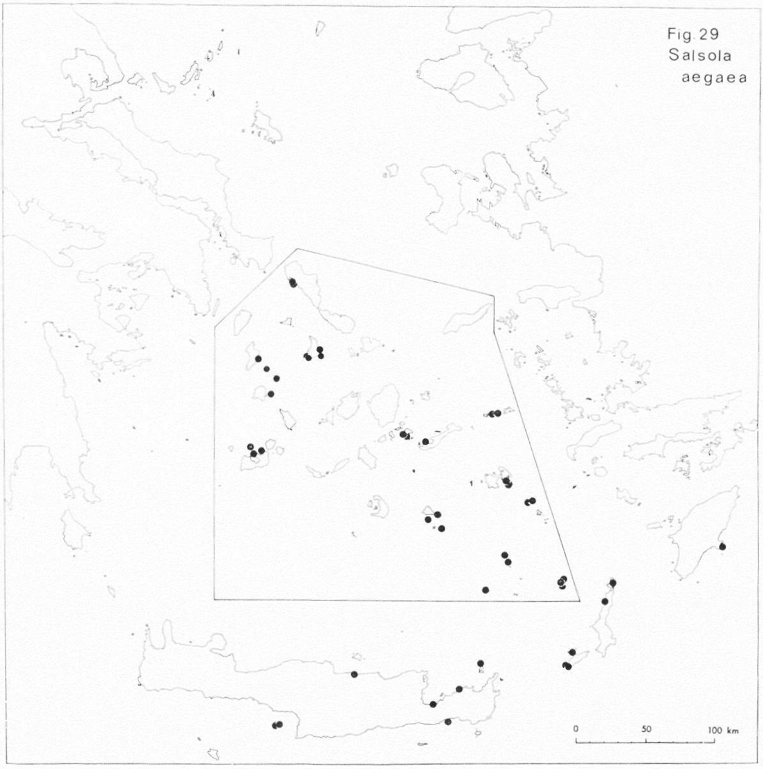

Fig. 29
Salsola
aegaea

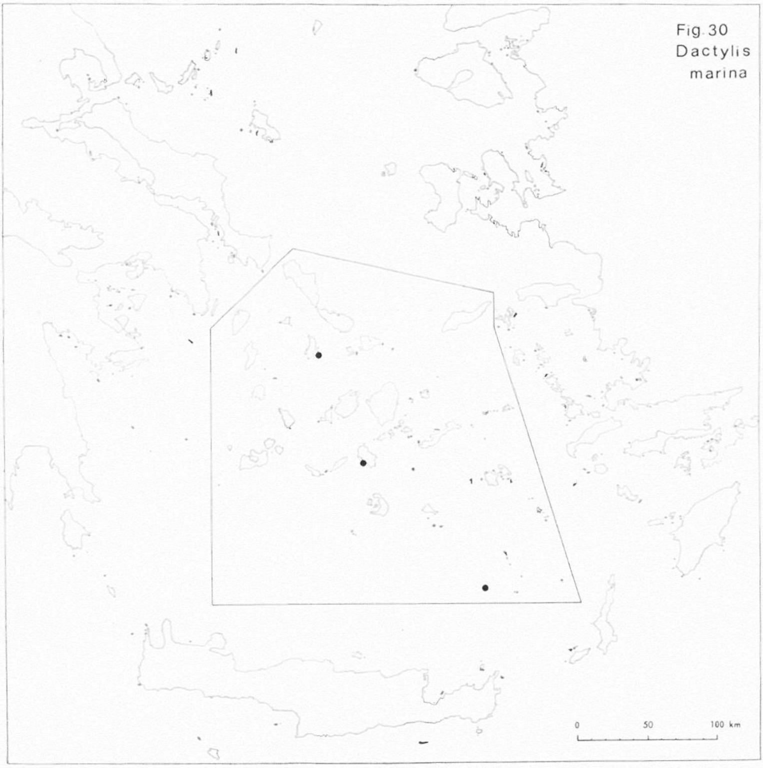

Fig. 30
Dactylis
marina

hirsuta L. Also a few Aegean endemics, some of which have very local distribution areas, occur, especially in *Limonium* and *Goniolimon*.

On many islands the sublitoral zone is inhabited by a phrygana vegetation poor in species. However, on c. 70 of the smallest islands, the phrygana vegetation is wholly lacking or only represented by very few species. Instead, a special sublitoral vegetation is found. Nine of the species belonging to this vegetation are wholly confined to small islands and 13 additional species are mainly confined to such islands but have rarely been found along the shores of larger islands.

The competitive ability of the sublitoral element is apparently low. It has apparently been substituted for a poor phrygana vegetation in many islets. Also on islands large enough to be used for grazing, it has almost always been replaced by phrygana vegetation. In extremely maritime localities on larger islands, e.g., narrow peninsulas, sublitoral species have been observed only in a few cases.

Ten of the sublitoral species are Aegean endemics while four are west Mediterranean with exclaves in the Aegean. The sublitoral element is almost wholly restricted to the central and south Aegean regions; only a few species have single localities in the west and east Aegean regions (cf. Figs. 26, 27, 28, 29, 30).

Dispersal of diaspores by the sea or birds would be expected to have played a significant role for the present distribution areas of the sublitoral species. However, several species e.g., *Anthemis scopulorum* Rech. f., *Trigonella rechingeri* Širj., *Atriplex recurva* Urv., and *Elymus rechingeri* (Run.) Run. (cf. Heneen & Runemark 1962) show a very strong local differentiation, indicating an effective isolation under present conditions. Long-range migration, therefore, seems to have played a rather insignificant role.

The distribution areas of the entire sublitoral element, the isolated occurrence of west Mediterranean species, and the strong local differentiation of many species give the impression that the small islands serve as refugia for the last remnants of a flora that occurred around the Sea of Crete in the Pliocene.

The distribution areas in the central Aegean for the individual sublitoral species are to a large extent haphazard (cf. Figs. 26, 27, 28, 29, 30). Also within minor areas the distribution of sublitoral species is often haphazard, which is illustrated in Tables 3 and 4, where the distribution of sublitoral species on small islands in the Paros and the Ios-Folegandros areas, respectively, are given.

The number of individuals of the sublitoral species on a small island

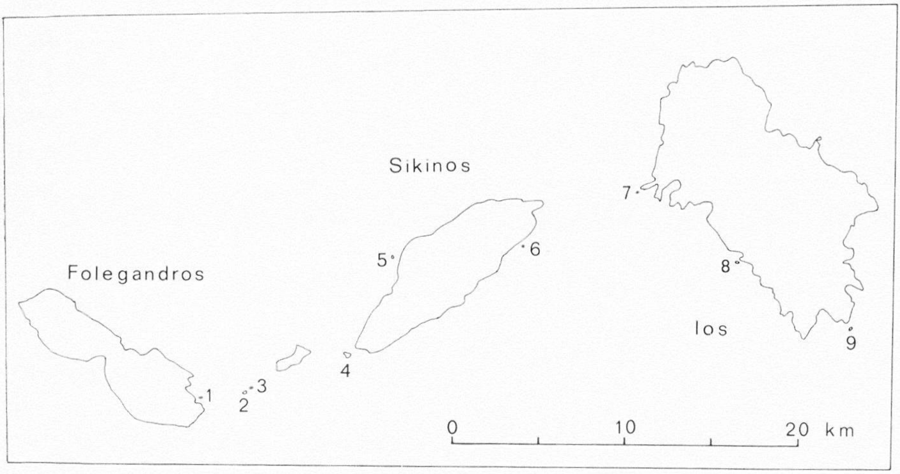

Fig. 31. The distribution of small islands inhabited by a special sublitoral flora in the Ios-Folegandros area. The figures refer to Table 3, where the occurrences of sublitoral species are tabulated for the individual islands.

Table 3. The distribution of sublitoral species on small islands in the Ios-Folegandros area. The numbers represent the islands with a sublitoral flora. Their positions are indicated in Fig. 31. Two of the species have been found in single cases on larger islands in the area — viz., *Lavatera arborea* and *Convolvulus oleifolius*.

	1	2	3	4	5	6	7	8	9
Anthemis scopulorum RECH. F.	+	+	+	–	+	–	–	–	–
Allium sp. (aff. *bourgaei* RECH. F.)	–	–	–	+	+	+	+	+	+
Arenaria aegaea RECH. F.	–	–	+	+	–	–	–	–	–
Atriplex recurva URV.	+	+	–	+	–	–	–	+	–
Convolvulus oleifolius DESF.	+	+	+	+	–	–	–	–	+
Dactylis marina BORRILL	–	–	–	–	–	–	–	+	–
Elymus rechingeri (RUN.) RUN.	–	–	+	+	+	+	+	–	–
Lavatera arborea L.	–	–	–	–	+	+	+	–	–
Silene holzmannii HELDR.	–	–	+	–	–	–	–	+	–
Suaeda fruticosa (L.) FORSK.	–	–	–	–	+	–	–	–	–
Trigonella rechingeri ŠIRJ.	+	+	+	+	–	–	–	–	–
Number of species	4	4	6	6	5	3	3	4	2

is usually low because of the small extension of the sublitoral zone. All, or almost all, the sublitoral species are therefore subject to a considerable risk of random elimination.

INTERPRETATION

The irregularly scattered distribution of chasmophytes and sublitoral species in the central Aegean can only be explained by a situation in which reproductive drift has played an important role through the random elimination of individual species on different cliffs and small islands, respectively.

This elimination process has certainly been accentuated by genetic drift, which can be assumed to have often resulted in accumulation of deleterious gene mutations and cytological aberrations, leading to a highly decreased viability and fertility of the individuals.

CONCLUSIONS

Experimental proof of the importance of reproductive drift in nature is still lacking. However, the demonstrated evidence is conclusive, in spite of being indirect, as it is based on a substantial material. Thus, the distribution areas in the central Aegean region of 50 phrygana, 45 chasmophytic, and 25 sublitoral species can only be explained by processes in which reproductive drift has played an important role.

The significance of reproductive drift apparently varies in different situations. It is of major importance in connection with long-range migration of species that are equal or only slightly superior in competition to permanently established ones, while it is a minor factor for species markedly superior to the original flora in the invaded habitat.

As a consequence, reproductive drift is generally of little significance for the migration within or to areas that do not yet possess a well-adapted vegetation. Thus, e.g., the reinvasion of areas covered by ice during glacial periods has certainly been little influenced by reproductive drift. Moreover, it is of minor importance for "colonizing" plants that invade disturbed habitats.

In areas, which have been subject only to minor climatic changes over extended periods, and therefore have floras that have long been well-adapted to the existing habitat conditions, e.g., the Mediterranean, parts of south Africa, and many tropical areas, reproductive drift is certainly one of the major factors affecting migration.

Successful long-range migration over long distances is certainly extremely rare in such areas even if a geological time scale is used. It presupposes a combination of very improbable events, as a successful dispersal of propagules to a suitable habitat and establisment in spite of reproductive drift. Moreover, a successful immigrant will have little genetic variability in the initial stage because of the small number of

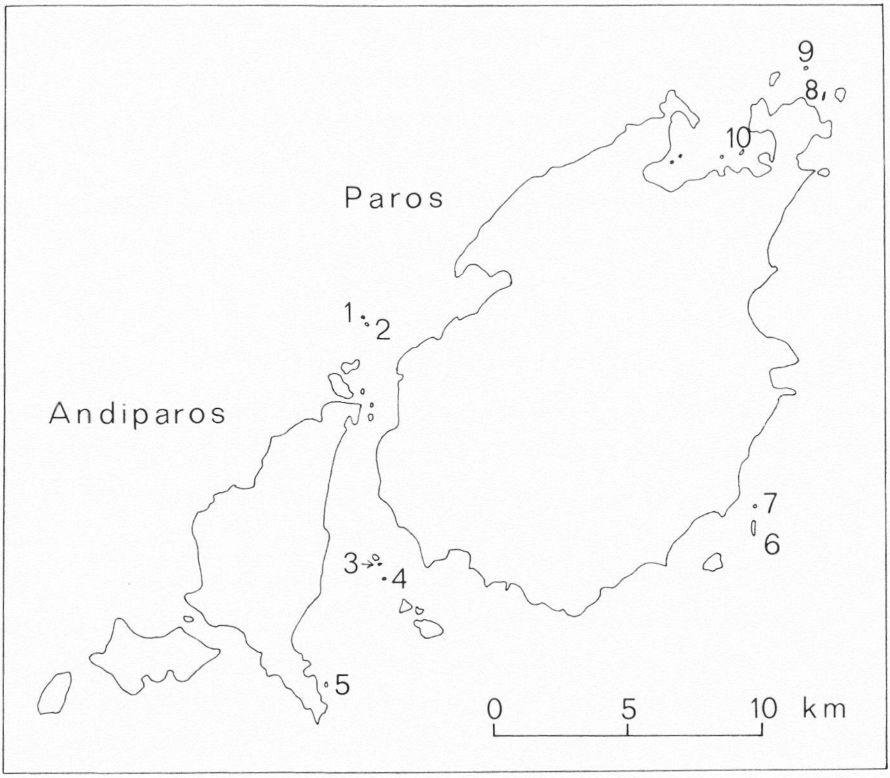

Fig. 32. The distribution of small islands inhabited by a special sublitoral flora in the Paros area. The figures refer to Table 4, where the occurrences of sublitoral species are tabulated for the individual islands.

Table 4. The distribution of sublitoral species on small islands in the Paros area. The numbers represent the islands with a sublitoral flora. Their positions are shown in Fig. 32. Only one of the species, *Allium* sp. (aff. *bourgaei*), has been found on a larger island in a single instance.

	1	2	3	4	5	6	7	8	9	10
Anthemis scopulorum RECH. F.	–	–	–	–	–	–	+	–	–	–
Allium sp. (aff. *bourgaei* RECH. F.)	+	+	+	+	–	+	–	–	–	–
Atriplex recurva URV.	+	+	–	–	+	–	–	–	–	–
Convolvulus oleifolius DESF.	–	–	+	+	–	–	–	+	–	+
Daucus gingidium VIS.	–	–	+	–	–	–	–	–	–	–
Elymus rechingeri (RUN.) RUN.	+	+	+	–	–	–	–	+	–	+
Lavatera arborea L.	+	+	–	+	–	+	+	–	+	+
Silene holzmannii HELDR.	–	+	–	–	–	–	–	+	+	–
Suaeda fruticosa (L.) FORSK.	–	–	–	–	–	+	+	+	–	–
Trigonella rechingeri ŠIRJ.	–	+	+	+	+	+	–	–	+	+
Number of species	4	5	5	4	2	4	3	4	2	4

individuals, giving little possibility for selective adaptation, and will also be exposed to the risk of deleterious effects of genetic drift.

In small, isolated plant communities random effects may be fatal, as non-adaptive processes may lead to the elimination of important constituents and in extreme instances to the extinction of the whole community. Thus, in the Aegean an original sublitoral flora has apparently been replaced by phrygana vegetation on many small islands, because of the combined deleterious effects of random fixation and elimination of species on the plant community level (i.e., reproductive drift) and of random fixation and elimination of genes on the population level (i.e., genetic drift).

Also in other small, isolated refugia, e.g., along the Norwegian coast and on high mountains during the last glaziation, reproductive drift has certainly played a considerable role, causing random elimination of many arctic and alpine species, which have not been able to reinvade earlier occupied areas.

ACKNOWLEDGEMENTS

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Aktuella problemställningar I
(Current Problems I)

Ekologiska problemställningar — med exempel från havsstrandängar

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ABSTRACT

A brief survey of various aims in analytical plant ecology with examples from Baltic sea-shore meadows is given. Difficulties encountered in studying problems of differentiation are treated first as the traditional approach of plant ecology. Many good correlations may be measured between different environmental factors and vegetation in the sea-shore meadows, where strong gradients are characteristic of the site and the vegetation is distinctly zoned. To separate the factor chiefly responsible for this zonal arrangement from secondary factors with similar gradients is a main problem of this ecological approach. Most edaphical gradients in the Baltic sea-shore meadows are directed by changes in the water-level of the sea. More continuous submersion produces poor aeration and lack of oxygen which is considered as the main reason for the zonal differentiation of the plant cover. Only species of the lower zones have aerenchymatous tissues, an anatomic adaptation to oxygen-deficiency. But reduced ability to take up water may possibly exclude these plants from the upper zones, at least in competition with non-aerenchymatous species. Horizontal gradients in salt concentration of the soil cannot explain the zonal arrangement of the plant cover, except in the uppermost parts of the shore-meadows. However, large osmotic concentrations are considered responsible for the exclusion of plants occurring in similar sites on the shores of fresh-water lakes. Halic conditions exert a powerful general selection of the diaspores reaching the shore-meadow, but oxygen and possibly water are chiefly responsible for the ultimate zonal arrangement of the plant cover.

Recent trends have stressed a more functional view of plant ecology, in which mineral circulation, organic matter turnover and interrelations between biotic and abiotic components in dynamic ecosystems are questions of considerable interest. Determination of net primary productivity is one of the basic problems of this ecological approach, and some of the difficulties encountered in shore-meadow ecosystems are discussed. The importance of experimental methods in quantitative ecology is exemplified with cropping and manuring experiments. The significance of treating the component species separately, at least in studying mineral circulation, is indicated by considerable differences

in the uptake of sodium and potassium between two important shore-meadow plants.

The dynamic concept of plant succession must always be considered, irrespective of the aims of ecological research. In Baltic sea-shore meadows, the isostatic land-upheaval is a powerful external force, promoting a fast and regular succession with complete zonal displacement within a few decades.

DIFFERENTIERINGSPROBLEM

Den traditionella växtekologiska målsättningen kan, visserligen med en ganska grov generalisering, karakteriseras som ett differentieringstänkande. Genom mätning av vissa ståndortsfaktorer som ansetts vara av betydelse, har man försökt att ge en förklaring till enskilda arters eller regelbundet återkommande artkombinationers, växtsamhällens, olikformiga fördelning inom ett område. Många samband mellan ståndortsparametrar och vegetationsgradienter har ofta kunnat påvisas, och där en diskontinuitet i växttäcket kunnat korreleras med en mätt ståndortsgradient har man, med rätt eller orätt, ibland ansett sig ha påvisat den för diskontinuiteten utslagsgivande ståndortsfaktorn. I vissa fall är det kanske den direkt på organismerna verkande faktorn som man lyckats spåra eller t.o.m. mäta. I andra fall är det mätvärden på en överordnad faktor som man erhållit. I ytterligare andra fall har man endast registrerat en sekundäreffekt, en indikation på en förändring av ståndorten.

Att bedöma betydelsen av ett påvisat samband mellan ståndort och vegetation kan vara synnerligen vanskligt och ofta får man nöja sig med att endast påvisa. Dessutom tillkommer konkurrensen mellan organismerna som en svårmätbar storhet och försvårar bedömningen ytterligare. Ett allmänt accepterat faktum är ju, att den realiserade, ekologiska amplituden hos en art normalt är väsentligt snävare än dess fysiologiska amplitud. Andra svårigheter bereder de temporala variationerna, som nödvändiggör långa observationsserier och många mätningar.

Av detta framgår, att den traditionella växtekologien har att brottas med ofta till synes oöverstigliga svårigheter. Men nödgas oftast nöja sig med att registrera olika samband mellan ståndort och vegetation och sedan mer eller mindre subjektivt bedöma värdet ur differentieringssynpunkt av dessa. För att statistiska metoder skall kunna tillämpas måste dels vissa principiella fordringar ställas på insamlingen av mätvärden, dels måste antalet observationer vara tillräckligt stort. Men inte ens om dessa förutsättningar är uppfyllda kommer man längre än till en siffermässig precisering av sambanden.

Låt oss nu mot denna bakgrund försöka analysera de påvisbara relationerna mellan ståndortsgradienter och vegetationsdifferentiering på havsstrandängarna vid Östersjön. Havsstrandängen är exempel på ett vegetationskomplex med ett växttäckte uppdelat i flera zoner av sällsynt konstant artsammansättning. De tongivande arterna är alla graminider, men dessutom förekommer åtskilliga mindre framträdade arter som är av stor betydelse för den floristiska karakteristiken och strukturbeskrivningen. Ehuru den fysionomiska skärpan i denna zonering huvudsakligen betingas av de dominanta graminidernas fördelning, har varje art sin givna amplitud inom komplexet, för somliga mycket vid, för andra snäv.

Ett zonerat vegetationskomplex av denna typ torde knappast kunna uppstå utan en stark, ensidigt riktad ståndortsgradient. En sådan ytterst betydelsefull gradient betingas av vattenståndsvariationerna i havet. Det fordras inga ingående undersökningar för att fastställa det självklara faktum, att strandängens undre delar oftare än de övre utsättes för översvämningar. Vattentillgången för växtligheten i de undre zonerna blir härigenom jämnare, och grundvattenytan ligger nästan permanent inom eller strax under rhizosfären, som härigenom aldrig torkar ut. Ett mycket gott samband mellan vattentillgång och vegetationszonering kan alltså lätt påvisas.

Belägg för att vattenståndsvariationerna vore oväsentliga för vegetationsdifferentieringen på havsstrandängen torde knappast kunna framläggas. Tvärtom utgör en översvämning en av de mest genomgripande förändringar av en miljö som kan ske. I brist på acceptabla alternativ nödgas man konstatera, att grunden till vegetationsdifferentieringen måste sökas i vattenståndsförhållandena. Emellertid är problemet därmed inte löst, knappast ens inringat, emedan många olika egenskaper hos miljön dirigeras av vattenståndsvariationerna och grundvattenytans läge. En maximal vattentillgång leder sålunda till försämrad genomluftning och en anaerob, reducerande miljö. Reducerande betingelser påverkar löslighetsförhållandena och därmed växttillgängligheten av flera mineralämnen, främst dock mikroämnena, nitrifikationen inhiberas, det organiska materialets nedbrytning försvåras och humifieringen ger delvis upphov till andra slutprodukter än under oxiderande betingelser. Svavlet fastläggs i närvaro av reducerat tvåvärt järn delvis som svårlöslig ferrosulfid eller avges i form av giftigt svavelväte.

Teoretiskt kan naturligtvis alla dessa egenskaper vara av betydelse för vegetationens zonala differentiering. Bristen på nitratkväve torde dock kompenseras genom tillgång till ammoniumkväve, som är stabilt i reducerande miljö. Att en gradient i tillgången på något mikroämne skulle orsaka differentieringen är teoretiskt möjligt men osannolikt, då det reella behovet av dessa ämnen torde vara mycket litet hos flertalet kärlväxter. Våra kunskaper om den naturliga vegetationens mikroämnesbehov är dock ännu ytterst obetydliga, varför ett motsatt påstående för närvarande inte skulle kunna vederläggas.

Bristen på syrgas är det som i naturen ger upphov till reducerande miljö. Syrgastillgången i marken är alltså en överordnad ståndortsfaktor som ger doseringen av flera andra markfaktorer. Men det är samtidigt en direkt på organismerna verkande ståndortsfaktor genom att respirationen utom hos vissa bakteriegrupper förutsätter tillgång på syre. Även rötternas tillväxt samt mineralämnes- och vattenupptagningen fordrar sålunda syre. Vid ett ingående studium av ståndortens abiotiska komponenter är det lätt att glömma organismerna, vilkas fördelning man söker orsaken till. I detta fall ger oss ett särdrag i deras anatomiska byggnad en direkt fingervisning om en ståndortsfaktor som kan vara utslagsgivande för den zonala differentieringen. Från skottens klyvöppningar ända ner mot rotspetsarna har de arter som kännetecknar de nedre zonerna på strandängen en lucker, luftförande vävnad, ett aerenkym, vars funktion torde vara obestridlig. Någon liknande vävnad förekommer inte hos de arter som endast uppträder i de övre zonerna. I markens syrgastillgång föreligger alltså en ståndortsgradient, som är korrelerad med en anatomisk struktur med en till denna faktor knuten funktion. Arter som saknar denna anpassning kan inte förutsättas ha existensmöjligheter i en övervägande anaerob miljö. Men på de övre zonernas bättre dränerade underlag tycks aerenkymväxterna ej klara konkurrensen med de arter som saknar dessa luftförande vävnader. Möjligt är att deras vattenupptagning försvåras redan vid en vattentillgång obetydligt under den maximala och att alltså även vattenfaktorn som sådan, likaväl som syrgasfaktorn, spelar en avgörande roll för differentieringen på havsstrandängen.

Ett liknande resonemang torde kunna föras kring vegetationsdifferentieringen på en insjöstrandäng. Och ändå är knappast en enda art gemensam för dessa båda för periodiska översvämningar utsatta vegetationskomplex, utom i den översta zonen närmast under högvattenlinjen. Havsstrandängen kännetecknas i betydande utsträckning av arter som ej förekommer i någon annan miljö eller först återkommer vid saltkällor eller på liknande mycket elektrolytrika ståndorter i Central- och Osteuropa. Vid översvämningarna tillförs havsstrandängen stora kvantiteter havssalter. Substratets acidoida lermineral mättas nästan fullständigt med metalljoner, främst av magnesium och natrium, och markvätskan får efter en långvarig submersion ungefär samma salthalt som havet med natrium- och kloridjoner som kvantitativt viktigaste komponenter. De höga salthalterna innebär att växternas vattenupptagning försvåras. I någon utsträckning kan de kompensera detta genom att öka sitt innehåll av osmotiskt aktiva sockerarter men endast till en viss gräns. För att övervinna markvätskans osmotiska sugkraft fordras sedan en upptagning av dess salter. Kärlväxterna på insjöstranden är tydligen inte så fysiologiskt rustade att de kan utvecklas med nämnvärt förhöjda salthalter i sina vävnader, något som de eljest så konkurrenssvaga havsstrandarterna däremot har anpassat sig till.

I samband med de ofta långvariga lågvattenperioder som infaller särskilt under början och mitten av vegetationsperioden kan markvätskans salthalt inom rhizosfären även i ett slutet växttäcke bli dubbelt så hög som östersjövattnets. Betingelserna för en saltanrikning kan förefalla mest gynnsamma i de övre zonerna, som sällan översvämmas, men härigenom blir också tillförseln av nya havssalter efter en urlakande nederbördsperiod mer sporadisk. Samspelet mellan tillförsel, anrikning och urlakning leder till att man oftast inte finner någon nämnvärd elektrolythaltsgradient mellan strandängens mellersta och undre zoner. Var salthaltsmaximum vid ett visst tillfälle uppträder beror av vattenstånds- och avdunstningsförhållanden under perioden före mättillfället. De naturliga temporala och regionala variationerna är inom varje zon så pass betydande, att salthaltsförhållandena inte kan ha någon avgörande inverkan på vegetationens zonala differentiering. Först i den översta, lågstarrdominerade zonen blir markvätskans elektrolythalt generellt så mycket lägre, att denna faktor kan tillmätas betydelse för differentieringen. Det är också först här som inslaget av arter, gemensamma med insjöstränder och andra glykiska miljöer, blir framträdande.

Differentieringsproblemet kan för havsstrandängarna vid Östersjön i korthet sammanfattas sålunda. De höga salthalterna utövar en stark selektion bland de diasporer som tillföres och begränsar urvalet till ett litet antal arter. Inom vegetationskomplexet torde det däremot främst vara syrgas- och vattenfaktorn som dirigerar den zonala fördelningen av dessa arter. I denna översikt har jag medvetet uteslutit de vegetationsfattiga sänkor med dålig dränering, som erbjuder sina speciella problem ur differentieringssynpunkt, och enbart skildrat förhållandena för den primära vegetationen.

De starka ståndortsgradienter som utmärker havsstrandängarna utgör ovanligt goda förutsättningar för differentieringsstudier. Att mer allsidigt belysa differentieringsproblemet med utgångspunkt från fastmarksängarna med deras utpräglat mosaikartade strukturegenskaper torde vara en mycket krävande uppgift, där delvis andra egenskaper hos miljön måste beaktas. Vattentillgången utgör även här en av de mest centrala ståndortsfaktorerna, som i fastmarksängar med lågt liggande grundvattenyta bör studeras i relation till exponeringsförhållandena. Att undersöka mätbara uttryck för markens syra-bas-status, såsom pH, metalljonmättnadsgrad och eventuell karbonathalt, framstår också som ytterst väsentligt vid ett studium av fastmarksängens gradienter.

PROBLEMSTÄLLNINGAR KRING DYNAMIK OCH FUNKTION

Inom nyare riktningar av växtekologien har helt andra tankegångar än de ovan skisserade kommit att ställas i förgrunden. I linje med tidens betraktelsesätt och kanske också tidens krav har den ekologiska målsättningen snabbt förändrats. Differentieringsproblemen har kommit att ägnas mindre intresse och betydelsen av det tidigare så fundamentala artbegreppet har av vissa forskare t.o.m. börjat ifrågasättas som nödvändig referens för ekologisk forskning. I förgrunden ställs nu funktionella och dynamiska aspekter på naturen.

Ekosystemen eller i vidaste bemärkelse miljön som helhet bildar alltså ramen för den moderna ekologien. I det ytterst komplicerade samspel som råder mellan levande och döda komponenter måste de enskilda organismernas uppgift i denna dynamik, deras funktion, vara det primära. Organismer med likartade uppgifter bör med detta betraktelsesätt, oavsett arttillhörighet, utan avsevärda nackdelar ofta kunna behandlas som en funktionell enhet. De tekniska framstegen inom fysikens och kemiens områden har underlättat den moderna ekosystemanalysen och i många fall skapat förutsättningar för en mätmetodik som tidigare var otänkbar. En ingående ekosystemanalys fordrar dock på längre sikt en tvärvetenskaplig samverkan mellan olika forskningsriktningar och resurser av en helt annan storleksordning än den traditionella växtekologien för att ge ett tillfredsställande resultat.

När funktionella och dynamiska aspekter lägges på havsstrandängarna vid Östersjön gör sig tydligen åtskilliga centrala frågeställningar gällande, frågeställningar som med det traditionella ekologiska betraktelsesättet inte på samma sätt behövde aktualiseras. Mineralämnescirkulationen mellan mark och vegetation, det organiska materialets uppbyggnad genom de primära producenterna, dess omhändertagande av konsumenter och destruenter, främst mikroflora och markfauna, och de mer eller mindre stabila slutprodukternas egenskaper är centrala problemställningar. Tidskrävande förrådsbestämningar av mängden cirkulerande och bundna mineralämnen och den organiska substansens fördelning på uppbyggnads-, nedbrytnings- och slutled tillhör det betydelsefulla första steget i analysen. De kvantitativa aspekterna måste sedan ställas i relation till en tidsfaktor för att ett mått på dynamiken i ekosystemet skall erhållas. Det fordrar långa och fullständiga observationer och det är här som de verkliga svårigheterna möter.

Av principiellt mycket stort intresse är sålunda ett mått på den primära produktiviteten, mängden ur koldioxid, vatten och solenergi syntetiserad organisk substans per tidsenhet, t.ex. ett år. Att med tämligen god precision mäta vikten av den under ett år nybildade ovanjordiska växtbiomassan bereder inga större svårigheter i strandängsekosystemen, där hela denna fraktion årligen förnyas. Felkällor kan betingas av svårigheter att skilja under året bildade men tidigt avdöende växtdelar från kvarstående förna från tidigare år liksom av förluster genom primär konsumtion, men dessa felkällor har i ett från kreatursbetning avskärmat strandängsekosystem tämligen ringa betydelse. Normalt nybildas årligen 0.2—0.3 kg skottmassa per m^2 och mängden ovanjordisk förna från tidigare år utgör på högsommaren 0.3—0.5 kg. Men mängden rotbiomassa+markförna utgör vid samma tid 5—7 kg/m^2 av vilket den förra fraktionen utgör en stor del. Vikten av humuskomponenten är av samma storleksordning. Minst nittio procent av växtbiomassan befinner sig alltså under markytan även när fältskiktet är som bäst utvecklat. Att med någon direktmetod mäta den årliga omsättningen av rotbiomassan är förenat med stora svårigheter. Om hela denna fraktion årligen förnyades skulle minst 3 kg/m^2 eller 30 ton/ha organisk substans nybildas varje år. Så är emellertid knappast fallet. Vikten av rotbiomassan är sålunda obetydligt mindre tidigt på våren än vid andra årstider. De grövre rötterna ersätts mycket långsamt, huvuddelen har en livslängd av åtskilliga år. Å andra sidan vet vi ännu ingenting om livslängden hos de finaste och mest aktiva rötterna eller rothåren. Mycket talar för att de förnyas flera gånger varje år och utgör en »dold» fraktion som ej kan mätas med konventionella metoder.

Ett intressant ekologiskt problem med praktisk anknytning är hur fältskiktsproduktionen påverkas av beskattning. Efter en fullständig skörd av strandängens fältskikt en enda gång under högsommaren minskar vikten av den under följande år bildade ovanjordiska skottmassan till hälften eller en tredjedel av fjolårsvärdet, oberoende av om försöksytorna gödslats med fosfor och/eller kväve (tillgången på växttillgängligt kalium är alltid mycket god). Samtidigt minskar graminidernas relativa andel till förmån för rosettväxter, ja, för den i de övre zonerna så kvantitativt framträdande rödsvingeln kan beskattningen bli förödande. En fullständig förlust av assimilerande skottmassa under den aktiva perioden verkar alltså tydligt nedsättande på strandängens primära produktivitet. Uthålligheten tycks vara beroende av att substanser transporteras från skottmassan till de underjordiska organen under eftersommaren och hösten. En viss utarmning av rotbiomassans rörliga organiska komponenter torde ske i samband med att skottmassan förnyas under försommaren. Transporterna av organiskt material mellan de olika fraktionerna av biomassan är en annan dynamisk aspekt vid ekosystemanalysen, som kanske inte får den uppmärksamhet den förtjänar.

Mineralämnesdynamiken på havsstrandängen måste vid ekosystemanalysen tillmätas särskilt intresse på grund av markens särpräglade egenskaper. De höga salthalternas betydelse för selektionen har tidigare berörts. Tillgången på och upptagningen av natrium, magnesium och klorid är väsentligt större än i andra ängsekosystem. Det rörliga kaliumförrådet är också mycket stort, vilket emellertid inte motsvaras av någon anmärkningsvärd överupptagning i förhållande till fastmarksängarna, i vilka följaktligen en väsentligt större del av det rörliga kaliumförrådet årligen cirkulerar. Fosfortillgången är däremot mycket knapp att döma av växttäckets obetydliga fosforinnehåll och den avsevärda ökningen i skottmasseproduktion som erhålles vid fosfatgödsling. En viss tröghet i mobiliseringen av växttillgängligt kväve är också märkbar. Växttäcket svarar på tillförsel av ammoniumkväve medan nitratkväve inte tycks ge någon effekt. I tillgången på mangan och järn finns betydande olikheter mellan zonerna. I de undre zonerna föreligger en del mangan som tvåvärd, utbytbar jon och en del järn, särkilt på våren, i reducerad tvåvärd och växttillgänglig form. Åtminstone i salttågbältet på strandängens mellersta del sker skottmassans järnupptagning huvudsakligen på våren och försommaren medan manganupptagningen i stället blir allt större under loppet av vegetationsperioden. Undersökningar över mineralämnenas frigörande ur förnamaterialet pågår och resultatet har ännu inte analyserats.

Ehuru de gröna växterna ur funktionell synpunkt tillsammans bildar den första trofiska nivån, det breda nedersta steget i den trappformade terrestra näringspyramiden, är dock skillnaden mellan de olika arternas mineralämnesupptagning ofta så stor även inom samma ekosystem att varje art bör analyseras separat. Redan en ringa förskjutning i proportionen mellan två kvantitativt framträdande arter kan leda till ändrade totalomsättningsförhållanden för enskilda element. Som exempel kan nämnas att salttågen (*Juncus gerardi*) vid måttlig elektrolythalt framstår som kaliumkonsument, medan gulkämpar (*Plantago maritima*) redan är en utpräglad natriumkonsument. I ett artrikt ekosystem blir dock ofta av tids- och kostnadsskäl säranalyser av varje art otänkbar, naturligtvis på bekostnad av i många fall väsentlig detaljinformation.

Ett studium av ekosystemens dynamik och funktion möjliggör och nödvändiggör experimentella metoder av en helt annan omfattning än vid studium av vegetationsdifferentieringen. Genom t.ex. gödslings- och beskattningsförsök kan värdefull information erhållas. Radionuklider av för vegetationen väsentliga element torde framdeles få stor betydelse, bl.a. när det gäller att följa upptagningen och omsättningen av enskilda ämnen och mäta omfattningen av återtransporter från skottmassa till rotsystem.

VEGETATIONSDYNAMIK

Vegetationsdynamiska problemställningar, successionsfrågor, måste alltid beaktas vilka utgångspunkter man än har för det ekologiska arbetet. Betingelserna för växtligheten är nästan alltid underkastade förändringar; det stabila slutstadiet är i ett kulturlandskap mera en hypotes än en realitet. De primära successionernas drivkraft, organismernas egen förändring av miljön, överflyglas sålunda oftast av sekundära drivkrafter. Fastmarksängarna utgör i allmänhet labila kulturprodukter, där förändringar i växttäcket snabbt inträder med förändringar i markanvändningen. Så länge en röjd ängsmark utnyttjas till regelbundet intensivt kreatursbete kan knappast några vedväxter förekomma, och fältskiktet präglas av betesresistenta arter, främst lågväxta graminider. Om betestrycket lättar något, får buskar som ogärna ätes av kreaturen bättre livsbetingelser och börjar återkolonisera. I skydd av buskinitialerna kan örter och småningom även enstaka beteskänsligare vedväxter, såsom lövträd och barrträd, växa upp. Om betningen upphör går sedan utvecklingen snabbt vidare mot ett slutet skogsstadium.

Trädlösheten på en fastmarksäng är sålunda av sekundär natur. Havsstrandängarna däremot är primärt trädlösa, och även om fältskiktets struktur och artsammansättning i viss mån betingas av kreatursbetning kan flertalet av zonationskomplexets olika ekosystem utvecklas utan påtagligt kulturinflytande. Det betyder emellertid knappast att de skulle utgöra några stabila och oföränderliga miljöer. På tidvattenkusterna bidrar vegetationens slamsamling effektivt till att höja underlaget och därigenom så förändra miljön, att nya arter kan kolonisera, varigenom en primär succession uppkommer. Den förlöper först snabbt men sedan allt långsammare tills ett stagnationsstadium inträder.

Inom Östersjöområdet är det i stället den isostatiska landhöjningen som utgör den viktigaste drivkraften för successionen. De olika zonalt utbildade successionsstadierna har i Mellansverige härigenom endast en varaktighet av några få årtionden och en kontinuerlig zonförskjutning är en förutsättning för strandängens fortbestånd. Ekosystemen befinner sig alltså ständigt på vandring nedåt. Något stagnationsstadium inträffar aldrig, utan så snart inte längre några högvatten når upp koloniseras den forna strandängsarealen snabbt av fastmarksvegetation.

Vegetationssuccessioner måste tydligen beaktas vid allt ekologiskt arbete på havsstrandängar liksom i många andra vitt skilda miljöer. Vegetationsdynamiska aspekter blir sålunda en del av den ekologiska analysen, oavsett om målet är en analys av växttäckets differentiering eller ekosystemets funktion.

Från Lunds Botaniska Förenings förhandlingar 1968

16 FEBRUARI. Professor Henning Weimarck informerade om hur långt arbetet med inventeringen av Skånes flora framskridit. Fältarbetet avsågs kunna bli i huvudsak avslutat under 1968. Professor Weimarck exemplifierade inventeringens resultat med en del utbredningskartor för växtgeografiskt särskilt intressanta arter.

Trädgårdsmästare John Kraft höll föredrag: »Om vresbokar och andra avvikande bokformer i Skåne». Föredragshållaren, som gjort en ingående inventering av dessa speciella bokformer, beskrev med hjälp av ett rikhaltigt bildmaterial deras viktigaste förekomster i Skåne.

8 MARS. Professor Dr. G. Wagenitz höll föredrag över ämnet »Probleme der Gross-Systematik bei den Angiospermen». Föredragshållaren berörde ett antal svårbemästrade systematiska problem, såsom avgränsning och inplacering av *Papaverales,* inordnandet av *Callitriche* m.fl.

29 MARS. Lunds Botaniska Förening firade sitt 110-årsjubileum.

Parentation hölls över föreningens bortgångna hedersledamot, professorskan Anna Murbeck.

Professor Arne Müntzing höll föredrag om »Principerna för experimentell taxonomi». Föredragshållaren gav en översikt över den experimentella taxonomiens arbetsmetoder och teoretiska bakgrund, samt gav exempel på undersökningsresultat. En riktig bedömning av dessa fodrar ett förhållandevis stort arbetsmaterial och en ingående kännedom om detta.

Professor Henning Weimarck gav historiska glimtar från föreningens 110-åriga verksamhet.

10 MAJ. Exkursion företogs till Glumslövstrakten under ledning av fil. dr Arvid Nilsson.

Vid Ålabodarna besöktes bl.a. sluttningen c. 600 m sydost om samhällets hamn. Här hade tidigare varit öppen mark med en del slånbuskar och vildrosor, och i vegetationen ingick då *Orobanche major, Campanula glomerata* och *Agrimonia odorata.* Nu hade trädskiktet blivit nästan helt slutet av uppväxande almar (dels *Ulmus carpinifolia,* som spritts från planterade exemplar, dels *Ulmus glabra*). Av den tidigare fältskiktsfloran återstår nästan enbart *Viola hirta.* I en glänta i övre delen av denna sluttning (kring en mindre odling) fanns *Equisetum telmateia* tillsammans med bl.a. *Epilobium hirsutum.*

Förflyttning skedde så till tegelbruket vid Hildesborg. I branten 1.4 km nordväst om samhället noterades bl.a. *Astragalus glycyphyllus, Centaurea scabiosa, Cirsium acaule, Filipendula vulgaris, Geranium sanguineum, Plantago* *media, Primula veris, Satureja acinos, Carex flacca* och *Helictotrichon pratense*. På toppen av kullarna c. 1.2 km nordväst om Hildesborg demonstrerade ARVID NILSSON de lämningar av förskansningar, som finns här. Området användes nu som betesmark.

Senare företogs en 600—700 m lång vandring längs kusten söderut från Hildesborgs tegelbruk. I den öppna gräsmarken fanns *Campanula glomerata* (bladrosetter) tillsammans med bl.a. *Primula veris*. I kanten av en dunge med planterad svarttall (*Pinus nigra*) växte *Vicia tenuifolia*. Lite längre söderut i lövskogsfragment hittades *Allium scorodoprasum* och *Corydalis pumila*. Inom området finns både *Ulmus glabra* och *carpinifolia* (den senare inplanterad men under spridning) och exkursionsledaren ARVID NILSSON har här funnit ett exemplar av hybriden mellan dess arter.

Vid ett sammanträde på Lantbrukshögskolan i Alnarp föredrogs revisorernas berättelser över granskningen av räkenskaperna för Opera Botanica och Botaniska Notiser. Föreningen godkände revisionsberättelsen och beviljade ansvarsfrihet åt berörda parter.

Dagen avslutades med en rundvandring i Alnarp. Denna avsåg att ge en belysning av den försöksverksamhet som Lantbrukshögskolan bedriver vid Institutionen för prydnadsväxtodling. Före rundvandringen med demonstration av försöksmaterial orienterade statshortonom SVEN ERIK LENANDER om försöksverksamheten. Laborator BÖRJE LÖVKVIST demonstrerade frilandsförsök med *Kniphofia*. Han berörde också odling av *Delphinium, Aquilegia, Erigeron* och *Buddleia* samt sortförsök med rosor och gödslingsförsök med nejlikor.

8 SEPTEMBER. Exkursion företogs till sydskånska sjöar. Route: Lund — S. Sandby — Silvåkra — Krankesjön — Revinge — Harlösa — Övedskloster — Veberöd — Skönabäck — Brodda — Svaneholm; Svaneholm — Börringe — Svedala — Staffanstorp — Lund. Första exkursionsmålet var Krankesjön, där fil. dr ASTA ALMESTRAND redogjorde för sjöns historia. Krankesjön sänktes 1892 och ytterligare sänkning skedde vid Kävlingeåns reglering på 1940-talet. Från en sjö med öppna, trädlösa stränder och med endast svagt utvecklad vegetation ute i sjön hade utvecklingen gått mot allt större igenväxning av stränderna och riklig vattenvegetation. Färden fortsatte till Vombsjön, där laborator NILS MALMER gav en orientering om dess historia. Enligt de nuvarande planerna skall sjön omvandlas till ett vattenmagasin samtidigt som vattenuttaget skall fördubblas, vilket kräver kraftiga ingrepp i det flacka landskapet, som omger sjön i väster, norr och öster. Vattenståndsamplituden kommer att röra sig om c. 3 m. Landskapsvårdsplanen går ut på att »återställa» den vegetation, som idag finns runt sjön, men på en högre nivå. Planen urskiljer 5 »zoner»: (1) Släntytorna på vallarna som skall sås med gräsfröblandning. (2) Den lägsta zonen där »sumpplantering» sker med *Phragmites*. (3) Våtzonen, som kommer att domineras av al och vide. (4) Mellanzonen, som planteras med pil, björk, fläder och hägg. (5) Torrzonen, som skall domineras av poppel med inslag av ros, rönn och vildapel. Hur Vombsjön, denna pärla i skånsk natur, kommer att planteras igen med poppel (av alla träd!) diskuterades livligt på höjderna vid sjöns sydvästra strand.

Dagens sista exkursionsmål var Svaneholmssjön. Docent SVEN BJÖRK erinrade om hur vattenståndssänkningar påverkar sjöarna och kan leda till igenväxning. Föredragshållaren berörde också hur sjörestaureringar kan genomföras. Därefter demonstrerades en vattengående slåttermaskin av dess konstruktör CRONQUIST.

Vid en exkursion med roddbåt demonstrerade fil. mag. FOLKE PERSSON vegetationen i Svaneholmssjön. Tidigare har sjön varit så gott som helt täckt av näckrosor, men större delen har de senaste åren rensats upp. Detta har lett till en ökad insolation, vilket medfört en kraftig ökning av *Ceratophyllum demersum*. Undervattensvegetationen utgjordes främst av *Potamogeton*-arter (*P. crispus, P. pectinatus, P. perfoliatus*). Fil. mag. GUNNAR ANDERSSON förevisade en del apparatur, bl.a. ljusmätare och vattenhämtare.

Fil. lic. ULF LETTEVALL redogjorde för fiskbeståndet i Svaneholmssjön. Både vikt och antal hos fiskarna (speciellt gädda) ökar, om man går från den täta vassvegetationen över den glesare näckrosvegetationen till det klippta området med *Ceratophyllum*.

27 SEPTEMBER. Museiintendent OVE ALMBORN höll föredrag om »Några glimtar ur Botaniska institutionens historia de senaste hundra åren».

Föredragshållaren berörde inledningsvis den botaniska forskningens och undervisningens utveckling i Lund under tiden från Universitetets grundande framtill mitten av 1800-talet. Med utgångspunkt från färdigställandet av den botaniska institutionen (Agardhianum) och den nuvarande botaniska trädgården med dess växthus för hundra år sedan gav han därefter en utförlig översikt över botanikens utveckling i Lund fram till våra dagar.

Docent HANS RUNEMARK talade om några aktuella forskningsriktningar vid institutionen för systematisk och ekologisk botanik.

17 OKTOBER. Sammanträde hölls i samarbete med Mendelska Sällskapet. Dr. JENS CLAUSEN talade över ämnet »Gen Ecology and Breeding».

15 NOVEMBER. Val av styrelse för år 1969 företogs. Valda blev: Docent HANS RUNEMARK, ordförande; docent SVEN SNOGERUP, vice ordförande; fil. lic. ARNE STRID, sekreterare; fil. kand. JIMMY PERSSON, vice sekreterare; samt fil. lic. FOLKE ANDERSSON, trädgårdsmästare JOHN KRAFT, docent SUNE PETTERSSON, docent SVEN OLOV STRANDHEDE, fil. kand. LENNART LINDGREN och fil. kand. ÖRJAN NILSSON. Till revisorer utsågs fil. mag. TORGNY VON WACHENFELDT och fil. mag. ULF OLSSON och till revisorssuppleanter fil. kand. MATS GUSTAFSSON och fil. kand. LENNART ENGSTRAND. Docent RUNEMARK tackade därefter de avgående styrelseledamöterna, särskilt prof. HENNING WEIMARCK för intresserat arbete till föreningens fromma.

Fil. lic. GERMUND TYLER höll föredrag om »Sydskandinaviska havsstrandängar». Föredragshållaren skildrade havsstrandängar från Bråviken i Östergötland, Öresundskusten vid Skanör samt södra Jyllands västkust.

9 DECEMBER. Fil. lic. GUNNAR WEIMARCK visade färgbilder och berättade om en resa på Grönland sommaren 1968.

Jan Ericson

Botanisk litteratur
(Botanical Literature)

KÅRE ARNSTEIN LYE: Moseflora. — Universitetsforlaget. Oslo 1968. 140 sid., 60 fig. i texten. Pris N. kr. 29.

Denna flora avser att täcka de norska skogsskolornas behov av en vägledning över de vanligaste norska mossarterna. Boken kan dock anses fylla även amatörbotanisternas behov av en lättfattlig fältflora över de vanligaste skogs- och myrmossorna — detta till stor del tack vare de utmärkta illustrationerna, huvudsakligen hämtade ur E. V. WATSON's »British Mosses and Liverworts» (ny upplaga 1968).

De första 38 sidorna ägnas åt en allmän del, där mossornas systematik, morfologi, fortplantning, ekologi, utbredning, ekonomiska betydelse etc. behandlas. Denna inledande del avslutas med en förteckning över de för skandinaviska förhållanden användbara, större mossflororna.

Speciellt värdefulla för nybörjaren torde artlistorna från olika, lättdefinierade biotoper vara. Dessa artlistor kompletteras med en tabell över olika mossors näringskrav.

Floran omfattar allt som allt 224 arter, varav de 60 vanligaste illustreras med såväl habitus- som detaljfigurer. Florans bestämningsnyckel är fördelad på de fyra huvudgrupperna (A) Levermoser, (B) Akrokarpe bladmoser (og sotmoser), (C) Pleurokarpe bladmoser och (D) Sphagnum — torvmoser. Nycklarna omfattar dock inte alla upptagna arter utan endast omkring 160. De arter, som uteslutits ur nycklarna, har av författaren betecknats som sällsynta och därmed mindre väsentliga i detta sammanhang. Recensenten finner dock detta arrangemang mindre lyckat. I artbeskrivningarna är den starka ekologiska betoningen värdefull. Det enkla och lättförståeliga språket i dessa beskrivningar gör också floran användbar för en bredare, nordisk publik.

Samtliga mossor har försetts med norska namn, t.ex. dronningmose, krokodilmose, tusenbeinmose, delvis nykonstruerade för ändamålet. Resultatet av dessa nykonstruktioner kan kanske diskuteras.

S. O. STRANDHEDE

LEIF RYVARDEN: Flora over kjuker. — Universitetsforlaget. Oslo 1968. 96 sid., 19 fig. i texten. Pris N. kr. 24.50.

»Kjuker» är den norska benämningen på tickor, eller danskarnas »poresvampe». Dessa basidiomyceter tillhör fam. *Polyporaceae* s.l., vilken emellertid ofta uppdelas i flera familjer och underfamiljer. Författaren gör ingen sådan uppdelning i sin flora, utan släktena och arterna är ordnade i bokstavsordning. Detta arrangemang kan sägas ha den fördelen, att det är lätt att hitta — om man vet åtminstone släktnamnet, men innebär en uppenbar olägenhet, om man bara har en »gruppkunskap» motsvarande ungefär underfamiljerna. Författaren menar sannolikt, att man tar sig fram till släktet via de nycklar, som finns i boken. Recensenten har haft tillfälle att pröva bestämningsnycklar och beskrivningar under hösten 1968 och funnit floran mycket användbar även i södra Sverige.

Släktuppfattningen inom *Polyporaceae* s.l. har alltsedan 1800-talet varit starkt divergerande. RYVARDEN följer i sin flora den uppfattning, vars förespråkare i Mellaneuropa speciellt är JAHN i »Mitteleuropäische Porlinge und ihre Vorkommen in Westfalen» (1963) och KREISEL »Die phytopathogenen Grosspilze Deutschlands» (1961). Författaren tar också hänsyn till de revideringar, som DONK publicerat så sent som 1967.

Det är med tacksamhet, man tar emot en flora, eller, som författaren vill kalla det, »dette forarbeid» till en flora över tickorna, denna svampgrupp, som normalt behandlas mycket summariskt i mindre svampfloror för fältbruk. Illustrationerna är kanske det, som vållat författaren de största problemen. I detta fall är materialet kanske ovanligt svårillustrerat, och resultatet har inte heller blivit särskilt bra, trots att den välkända och skickliga floraillustratören fru DAGNY LID bidragit med teckningar. Recensenten hoppas, att nästa upplaga av floran om möjligt skall ha både bättre och fler figurer, samt att den upplagan skall kunna betraktas som en nordisk flora över *Polyporaceae* och angränsande familjer.

Ett önskemål av en bredare publik är sannolikt, att få tickornas trivialnamn inte bara på norska utan även på övriga nordiska språk.

Denna flora är ett omtryck av författarens avhandling i Blyttia 1967 kompletterad med ett antal figurer.

S. O. STRANDHEDE

SUBHASH CHANDRA DATTA: An Introduction to Gymnosperms. — Asia Publishing House, London 1966 (publication date 11th May 1967). 168 pp., 62 figs. in the text. Price 22 s.

The author is a lecturer in botany at the University of Calcutta, and his book addresses chiefly to Indian students and teachers of botany. The treatment is rather conventional and opens with a chapter of the general features of *Gymnospermae*. In the following eight chapters a systematic treatment follows, and chapter ten gives a short review of fossil floras of India. In the following appendix, the author gives some aspects of paleobotany and "some important references", the last one from 1964.

The quality of the binding and especially of the boards is low.

S. O. STRANDHEDE

J. B. THOMAS: Einführung in die Photobiologie. — Georg Thieme Verlag. Stuttgart 1968. VIII + 320 pp. 84 figs. Paperback. Price DM 9.80.

This book is a translation of "Primary photoprocesses in biology", published in Amsterdam in 1965. The author is professor of biophysics at the University of Utrecht and is a specialist on photosynthesis. The translation has been prepared by Dr. G. SCHOSER of the University of Tübingen. This guarantees a correct treatment of the material, since Dr. SCHOSER is himself a well-known scientist in the field of photobiology. Except for the language the only change from the former edition seems to be in the physical appearance of the book. There has been no loss in quality of figures etc. in connection with the change to paperback.

The book consists of two main parts. In the first one the physical, chemical and biological background of photobiology is described. In the second one the various photobiological phenomena are treated separately: Photosynthesis, vision, movements induced or regulated by light, photomorphogenesis, and bioluminescence. Effect of UV (such as the processes taking place in skin, mutations or other damaging effects on macromolecules) are not treated, neither are photoreactivation or photodynamic action by visible light. The book describes our knowledge about the primary photoprocesses. It is not intended to provide any knowledge about the attatched biochemistry, physiology or ecology. Neither does it describe the experiments or methods by which the theories or opinions were derived. Thus it cannot be used as a guide to experimental technique of photobiology, but fortunately some other books of this type have appeared recently.

The volume is extremely compact and loaded with facts, and has a very valuable reference list. It must, however, be considered a drawback the most recent material in this new edition is still from 1964, and even from this year very little is included. Photobiology is a rapidly developing science (thanks to the author of the book among others). The book can be recommended to (among others) the specialized photobiologist who wants to broaden his knowledge.

LARS OLOF BJÖRN

JALAS, J. (ed.): Suuri Kasvikirja. — Otava. Helsingfors. I, 851 s. 1958. II, 893 s. 1965.

Suuri Kasvikirja (Stora Växtboken), vars två första band föreligger för anmälan, är avsedd att komplettera egentliga floror över Finlands inhemska och naturaliserade kärlväxter med en framställning av vårt vetande om arternas miljökrav, totala utbredningsområden, variation, kromosomtalsförhållanden, anknytning till människan etc. Verket är illustrerat med färg- och svartvitfotografier, detaljteckningar och kartor. Färgfotografierna är av finländskt ursprung, medan ett antal av de svartvita är svenska.

Bestämningsnycklar och vidlyftigare morfologiska beskrivningar av de behandlade arterna förekommer inte. Däremot presenteras utförligt nyare forskningsresultat och ges åtskilliga litteraturreferenser med tonvikt på finländska förhållanden. Ett författarteam har mellan sina medlemmar fördelat arterna, ett förfarande som medför goda möjligheter till initierad behandling men som bidrar till en i en del fall märkbar heterogenitet beträffande artiklarnas omfång och utformning. Det förefaller t.ex. väl generöst att tilldela släktet *Alchemilla* nästan 32 sidor, flertalet behandlande småarter inom *vulgaris*-gruppen.

Framställningen börjar direkt på släktnivå. Familjer anges endast i övre marginalen. I ett verk av detta slag vore en presentation i text av högre taxas karakteristika i högsta grad befogad för att ge läsaren inblick i systemets uppbyggnad och motivera den valda uppställningen.

Framställningen är intresseväckande och förefaller välavvägd. I samband med kromosomtalsuppgifterna anges ofta från vilket geografiskt område talet rapporterats. Fullständighet beträffande sådana uppgifter torde inte vara möjlig att uppnå i ett verk av detta slag. Med tacksamhet noteras också en sådan detalj som att i förekommande fall karakteristiska sjukdomsframkallande svampar tas upp till behandling under respektive värdväxter. Upplysningar av sådant slag kan vara av det största allmänbotaniska intresse.

Flertalet svartvitillustrationer fyller sitt ändamål. Dock har tyvärr några av prickkartorna, hämtade ur andra arbeten, utfallit olyckligt beträffande streckgrovlek och punktstorlek. De kartor i band II, vilka baseras på linjekartering, har f.ö. återgivits så små, att de minsta markeringarna inte kan urskiljas med full säkerhet. Annars ger just dessa kartor ett gott intryck.

Färgplanscherna gör däremot inte verket bättre. I band I är de genomgående murriga och orena. Endast någon enstaka bild har sluppit lyckligt genom klichéring och tryckning. Färgbilderna i band II har en helt annan karaktär och är mestadels alldeles för grälla. Den enda riktigt bra bilden sitter på skyddsomslaget. En jämförelse mellan Suuri Kasvikirjas färgbilder och planscherna — från 30-talets mitt — i Vilda Växter i Norden utfaller genomgående till de senares förmån trots deras väl stillsamma färgskala. Dessutom är färgbildsmaterialet i Vilda Växter i Norden betydligt rikligare och mera komplett.

Man frågar sig också huruvida illustrationernas värde motsvarar de dryga tryckkostnaderna. Snarast får man intrycket att urvalet varit beroende på vad som för stunden funnits tillgängligt. Vilken väsentlig information förmedlas av planschen i band II mot s. 624, föreställande »*Rosa* sp.»?

Slutomdömet om Suuri Kasvikarja måste bli i hög grad positivt trots de anförda anmärkningarna. Det är bara att beklaga, att verket genom sitt språk är otillgängligt för flertalet nordiska läsare. Något motsvarande beträffande kvalitet och utförlighet finns inte att tillgå inom vårt språkområde.

ANNA och GUNNAR WEIMARCK

STAFLEU, F. A.: Taxonomic literature. A selective guide to botanical publications with dates, commentaries and types. — Regnum vegetabile 52. Utrecht 1967. XX+556 pp. Price (for members of I.A.T.P.) Sw. Cr. 64:— (postgiro 43 35 39, Göteborg).

Several generations of botanists have considered PRITZEL, Thesaurus literaturae botanicae (ed. 1, 1847—1851; ed. 2, 1871—1877, reprint 1950) as an indispensable source of information concerning botanical literature (major works, not papers printed in journals) from ancient time till the 1870's. The need of a new edition and continuation up to our time of this repertorium has often been emphasized. The present volume, though smaller in size than the Thesaurus and with another scope, is a most welcome complement to PRITZEL's classical work.

Dr. F. A. STAFLEU (Botanical Museum, Utrecht, Holland) has for many years collected information on dates of publication of taxonomic botanical literature. For nomenclatural purpose it is often essential to know the exact or approximative date when a work was issued or available on the book-market. Every taxonomist has sometimes been obliged to investigate whether a description of a taxon predates or is predated by another name published in the same year. In many cases, especially in books issued in fascicles, the year of publication on the title-page is not reliable more than for a limited part of the work. Dr. STAFLEU is known as the leading expert of such questions (cf. a detailed survey of botanical publications issued in the turbulent years 1788—1792 in Taxon 12, 1963). It is a matter of course that such research needs much patience, talent for detective work and access not only to large botanical libraries but also to archives containing letters from or to the botanists concerned.

In his preface, STAFLEU stresses that the words "selective guide" in the subtitle should be taken seriously. The criterion for inclusion of a book or serial has been a certain importance for taxonomy to-day in combination with the availability of special information (often previously unpublished) about its publication. He also meets any criticism with the words "I hope nobody will ask me: Why did you not include such and such a publication?" . . . "Perfection or near-perfection is impossible to achieve in this work". The reader will soon find that the majority of the publications quoted are from the 18th and the 19th centuries, or from the first decades of our century. There is hardly any author now alive quoted. We can state a marked preponderance of literature from Central and Western Europe, as well as of literature on phanerogams. Many important authors on cryptogams have not been mentioned though they afford intricate bibliographical problems, e.g. TH. M. FRIES, G. W. KOERBER, W. NYLANDER and F. STEPHANI. No doubt, STAFLEU's work will stimulate and serve as a model to future research on such neglected fields of taxonomic botanic literature.

The biographic data of the authors quoted are mostly very brief: years of birth and death and a few words like "German physician" or "English gardener". A most valuable paragraph under each author is the statement "Herbarium and types", where we find information concerning the location of his main collections, isotypes etc. This is a welcome supplement to the "Index of Collectors" I (A—D) and II (E—H) in Regnum vegetabile 2 (1954) and 9 (1957). Many taxonomists have eagerly looked forward to a continuation of this series.

The following remarks are minor notes which might be useful to a forthcoming 2nd edition.

ACHARIUS, E. Only 3 of his 4 major works are quoted. "Synopsis methodica lichenum" (1814) is an indispensable supplement and index to his "Lichenographia universalis" (1810). Very critical remarks to A.'s "Methodus" (1803) were published by F. WEBER and D. H. M. MOHR (Archiv Syst. Naturgeschichte, Leipzig 1804) together with A.'s "Vertheidigung" und "Nachträge". A.'s main lichen collections are at Helsinki, but a very valuable set of duplicates was given to the Linnean Society in 1803. In several cases this set (now transferred to the British Museum) contains the only type material preserved. Many isotypes from A. are also at Kew and Uppsala.

AGARDH, C. A. A detailed account (in Swedish) of A.'s collection of phanerogams, which was given to the High School of Karlstad (now partly destroyed; the ramainder transferred to Lund) was published by F. HÅRD AV SEGERSTAD: "C. A. Agardhs Fanerogamherbarium" (in Meddel. Värmlands naturhist. för. no. 1. Karlstad 1928). This paper also gives samples of the handwritings of C. A. AGARDH and other collectors.

AGARDH, J. G. Only one (small) phycological paper is quoted. The standard biography by JAKOB ERIKSSON (in Lefnadsteckn. Kungl. Svenska Vetensk. Akad. Ledam. Bd. 5, No. 89, Stockholm 1916, not quoted) lists 88 papers.

BONPLAND, AIMÉ has consistently got a female form (-ée) of his Christian name.

ENGLER & PRANTL, Die natürlichen Pflanzenfamilien ed. 1 (1887—1915) is listed in detail as to the date of publication of each fascicle. The ed. 2, unfortunately incomplete (1924—1940, some fascicles and reprints published after World War II), is not mentioned. Though wellknown to any taxonomist of some experience, it may not be so to a beginner.

LINNAEUS, C. Stafleu has spent much time in recalculating the dates of publication of L.'s works, especially many dissertations under his presidium, from the Julian calendar (old style) to the Gregorian calendar (new style). Similar alternative dates are also given under some other Swedish botanists from the last half of the 18th century, e.g. A. J. RETZIUS and C. P. THUNBERG. Under THUNBERG (p. 468), STAFLEU states that Sweden adopted the new style in 1823. This is not correct. In fact, this change took place in 1753, when 11 days at the end of February were excluded. Thus the dates on the title-pages of, e.g., the dissertations of LINNAEUS' and THUNBERG's pupils, refer to the new style.

RETZIUS, A. J. Main herbarium at Lund. Type material of several species lacking at Lund is sometimes at Copenhagen.

SWARTZ, O. P. Main herbarium at Stockholm (S or S—PA). The RETZIUS herbarium at Lund contains many SWARTZ types, sometimes of species not represented at Stockholm.

It is needless to state that STAFLEU's work is indispensable to any serious taxonomic botanist. Among to its merits should also be mentioned two Indexes, one to personal names and another to titles of botanical publications. Another index recording the generic and family names (or higher groups) of plants mentioned in the text would have made these repertoria still more valuable.

The reviewer would object to STAFLEU's opinion concerning the numerous taxa described in GANDOGER, Flora Europae (27 vols, 1883—1891). GANDOGER is rightly characterized as "one of the greatest splitters ever". GANDOGER's work is described as "a manuscript pseudomechanically reproduced by lithography and as such effectively published. All generally known species of the time are cited in the usual way but also (mostly) subdivided in numerous microspecies. These microspecies are designated by binomials. GANDOGER accepted therefore two categories of species. The category for which he used the conventional names can be chosen by us as GANDOGER's category of species as understood by the Code. The second category is then infraspecific; the binomials denoting those taxa are not validly published and can be disregarded".

This is definitely to make a complicated problem too simple. In his Préface of vol. I of Flora Europae (1883 pp. 1—12) GANDOGER discussed in detail the difference between the collective species ("espèces des types linnéens") recognized by "l'ècole synthétique" represented by, i.a. DE CANDOLLE and NYMAN, whose "Conspectus florae europaeae" (1878—1882) had just been published, and the "nouvelles espèces" described by "l'ècole analytique", i.e. JORDAN, GANDOGER et al. In his main work GANDOGER was firmly convinced of the stability of his new species representing a "monde inconnu", and he strongly defeated the ideas of botanists who might consider them as "variations parallèles d'un même type". In "Flora Europae" he never used words similar to "microspecies" or "subdivisions of species" for his "espèces nouvelles".

STAFLEU follows the opinion of W. ROTHMALER (Taxon 11, 1962, p. 156) who rejected GANDOGER's "Kleinarten" in a very superficial way. (He did not even spell G.'s main work correctly.) BOTHMALER states G.'s taxa to be "nomina seminuda", the descriptions being too short. Further G. was said to be "ein Fälscher", as he was supposed to have distributed plants from Spain or Morocco, which could not derive from these districts. These accusations may contain a certain amount of truth, but they are quite irrelevant according to the International Code of Botanical Nomenclature. Using the same arguments we could disqualify the taxa of several botanists of more or less good repute.

To the reviewer it is evident that H. P. FUCHS (Bull. Soc. Bot. France 107, 1960, p. 108) has tackled the problem in a more correct way. FUCHS rightly states that, unfortunately, G.'s taxa were both effectively and validly published. This is deplorable as, in many cases, they predate homonyms of more or less wellknown species described later by other authors. FUCHS also drew attention to the fact that in some respects G. was a modern taxonomist using the type method. "Quant aux espèces que je propose ici, toutes, sans aucune exception, ont été décrites sur des échantillons de mon herbier et s'y trouvent encore". As curator of a herbarium, the reviewer would emphasize that the Lyon Herbarium, which includes the GANDOGER herbarium (estimated by ROTHMALER and STAFLEU to contain some 800 000 specimens), has always been very generous in lending material to elucidate his taxonomy. FUCHS also records the discussions which took place during the Botanical Congresses at Amsterdam (1935) and Stockholm (1950) concerning blacklisting G.'s "Flora Europae". These discussions led to no decision.

As stated by FUCHS, GANDOGER later changed his opinion from the "Flora Europae". In "Novus conspectus florae Europae" (1910) he developed quite other ideas concerning the species concept. In this work he states: "Les espèces précédées d'un numéro sont celles que je considère comme types primordeaux" (i.e. his former "espèces linnéennes"). "A leur suite viennent les sousespèces, races ou formes, disposèes par ordre d'affinité ou alphabétique, selon le cas". The meaning of this is that his former "espèces nouvelles" should be regarded as subspecific taxa, a radically changed opinion.

ROTHMALER and STAFLEU have noticed these changed ideas, but they have applied them also to GANDOGER's main work. In the reviewer's opinion, this is a dangerous way from a nomenclatural point of view. It is puzzling that the Rapporteur-général of the section of nomenclature of the 11th International Botanical Congress urges a principle of retroaction in botanical nomenclature. There is no support in the Code for such a procedure.

The reviewer is in no way a friend af GANDOGER's negligent taxonomy. There is no reason to reckon with 41 species replacing *Drosera rotundifolia* or 61 species instead of *Parnassia palustris* as GANDOGER did.

But when his many superfluous taxa shall be excluded, it must be according to a decision of a Botanical Congress (cf. proposal no. 128 by W. GREUTER and no. 136 by A. CRONQUIST and H. A. GLEASON, both in Taxon 17 (4), 1968) or under a paragraph in the Code and not according to considerations which obviously violate the Code.

OVE ALMBORN

Publications on the South African Genus Aspalathus L. (Genisteae, Leguminosae)

The "Revision of the genus Aspalathus" is now completed. It comprises Opera Botanica 4, 6(2), 8(1), 10(1), 11(1), 21, and 22, and Botaniska Notiser 121: 165—208, and has been published between 1960 and 1968. A general treatment of the genus, "Studies in Aspalathus and some related genera in South Africa", is published in Opera Bot. 9(1), with a complementary phytogeographical account in Bot. Notiser 116: 431—472.

Some additional articles on the genus have also been published in Bot. Notiser, among them about the inclusion of the genus *Borbonia* L. into *Aspalathus,* in Bot. Notiser 116: 185—192; about the correct Latin name of the Rooibos-tea plant, in Bot. Notiser 117: 188—196; about some new and rediscovered species, in Bot. Notiser 120: 26—40; and about the distribution of *Aspalathus* species put in relation to the substrate, in Bot. Notiser 121: 505—534. The main cytological investigation remains to be presented, but some information on chromosome numbers in *Aspalathus* and related genera is given in Bot. Notiser 120: 149—160.

Aspalathus is apparently the largest genus of plants endemic in South Africa. It contains 257 known valid species distributed among 6 subgenera and a great number of "groups". The species are described, illustrated, and mapped in the revision, where the nomenclature, which is sometimes complicated, is also clarified, the variation outlined, and the studied collections enumerated. The revisional work was started with a period of field work in South Africa 1956—57, but the main revisional work has been carried out at the Institute of systematic botany, Lund. The field studies were later complemented considerably in 1965—66, when about half of the revision had already been published. The necessary complements to the first parts are published in Bot. Notiser 120: 26—40 and 121: 505—534. A comprehensive index to all the species, their descriptions, illustrations, and maps, is given at the end of the last part of the revision, in Opera Bot. 22.

The genus is composed of shrubs of variable size, from prostrate to some metres tall, the great majority with subterete and needle-like, often spine-tipped, ternate leaflets, but many with flat, rigid or weak leaflets. A reduction of the three leaflets to a single one, i.e. to a "simple leaf", has occurred in some groups of species: in the species of the former genus *Borbonia,* in some other species with flat leaflets (*A. sericea, altissima* and *caledonensis*), in *A. nudiflora* (representing subgenus *Rafnioides*), and in *A. linearis* and *pendula* (composing subgenus *Nortieria*). Therefore, the often cited generic character of the trifoliolate, petioleless leaves is not quite valid.

The diverse types of spines and thorns in the genus, apparently an adaptive differentiation as protection against grazing animals are noteworthy. Thus projecting leaf bases, leaflets, lateral branchlets, and terminal branch ends (inflorescence tips), in different groups, may all have the shape of spines, exhibiting a parallel development of unique kind. As might be expected, this is more pronounced in the lowland species than in the montane ones, which are more protected in their habitats.

The development of lateral branchlets as brachyblasts is also typical. When these are floriferous the flowers in each brachyblast are usually solitary, often resulting in spikelike zones of floriferous brachyblasts distributed along the branch ends.

The floral bracts and bracteoles contribute characters of some taxonomic value in being sometimes trifoliolate but more often simple, and they vary much in shape and size. The petals are usually yellow, but often with violet, orange, or purplish shades. Only in a few species they are exclusively white or violet. The flower size is highly variable, like the shape and pubescence of calyx lobes and petals. Of great interest is the rich differentiation of the legumes, which develop from a 2—multi-ovular ovary. The legume is generally relatively short and triangularly ovate or lanceolate, occasionally indehiscent, but in some cases it is long and linear. The variation in this respect is sometimes considerable even in groups with very similar flowers and vegetative features, as in the *A. pinea* group.

The background of the great differentiation in the case of *Aspalathus* seems to be a combination of conditions: the general flexibility of the genus, the highly complex topography and diversity of soils of the Cape region, and the fluctuating climate in the past, which has caused oscillating movements of the populations without causing prevailingly extinction. In consequence, most species, which are concentrated to the mountains and hills, are split up into populations with a limited number of individuals, where genetic drift has been acting strongly.

The *Aspalathus* species, mostly for the sake of convenience, have been divided among groups, which have been kept as "natural" as possible (judging from the morphological variation). As many species are rather isolated morphologically and lack apparent close affinity to others, many groups comprise a single species. The groups are therefore admittedly too many for a convenient survey. Some groups, and some species, are extremely variable. They consist of many populations each with more or less characteristic features and different from each other to a variable extent. Other species are restricted in distribution ("narrow endemics") and have little variation. Allogamy as well as autogamy occur in the genus.

The different groups of species have different geographic concentrations, some being strictly southwestern, others southern or even southeastern. A few groups are rather widely distributed. Many cases of geographic vicarism of related species can be pointed out, the most conspicuous geographic-ecological example being, perhaps, the species pair *A. callosa - tylodes* (Bot. Notiser 116: 464). The variation centre of the genus, as estimated from the concentration of species, is in the mountains of the Caledon—Paarl Divisions, with great variation also in the mountains north and east of these, towards the Cedarberg and Langeberg Mountains respectively, and on the Cape Peninsula.

It is demonstrated, in Bot. Notiser 121: 505—534, that the distribution area of each species generally falls mainly or entirely within the area of a particular soil type, usually formed by a particular geological formation, although there are a number of generally highly variable species which are quite eurytope.

It is interesting to note that the great differentiation in the genus — as far as has been able to prove — has occurred exclusively within the diploid level, although the somatic chromosome number varies between 16 and 20 (Bot. Notiser 120: 149—160).

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