Drawings of Scandinavian Plants 83–85

Chenopodium L.

By Lennart Engstrand and Mats Gustafsson[1]

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

Sect. **Pseudoblitum** HOOK. FIL. em. AELLEN

Glabrous or farinose, annual species, with inflorescences composed of branched, axillary and terminal panicles. Flowers 3-, 4- or 5-merous with perianth lobes free to a length of one half or more. Stamens 0—5. Seeds horizontal or vertical. Embryo annular. Four or five species distributed all over the world. The species are of little economic importance, but according to ILJIN 1936 *Chenopodium rubrum* has been used as a vegetable and in the preparation of a borsch-like soup. Previously used for treatment of contusions and wounds.

83. **Chenopodium glaucum** L. 1753

Annual, usually 1—5 dm high, erect to procumbent, much-branched. Lower branches mostly long, ascending or decumbent. Stem angular, striated. Leaves alternate, the lower ones at least tapering gradually to a long petiole, elliptical, lanceolate or ovate, obtuse, usually 1—7 cm long, length usually greater than breadth, green, glabrous and with a prominent, light midvein above, blue-green to greyish, conspicuously farinose beneath. Margins sinuate, dentate, rarely subentire, teeth unevenly distributed, somewhat rounded, obtuse to acute and pointing forwards. Inflorescences situated both axillary and terminally. The terminal ones branched, composed of small, rounded or oblong cymes, each consisting of a varying number of more or less clustered flowers. The cymes form rather long, narrow, often lax panicles or spikes. Axillary inflorescences unbranched and flowers arranged in relatively small, oblong cymes. Flowers of two kinds, either perfect with 3- to 5-lobed perianth, 1 to 5 stamens and horizontal seeds, or with vertical seeds pistillate or perfect with 3- to 4-lobed perianth and 1 stamen. Perianth glabrous or almost so, generally free to the base, lobes elliptic to oblanceolate, obtuse, somewhat rounded or keeled and greenish in the centre, thin and membraneous in the outer parts. At maturity the perianth lobes only partly cover the seed. Pistil short and thick, with two small stigmas, papillate to the base. Seeds orbicular to ovoid, 0.5—0.8 mm in diameter, rather narrow but rounded margins, dark brown to black. Pericarp thin, more or less greenish, loosely attached to the seed. Testa lustrous, smooth or minutely pitted, sometimes inconspicuously reticulate. Radicula short, thick and usually pointing obliquely outwards. Embryo annular.

Flowering time: July to September.

Chromosome number: $2n=18$.

Variation: *Ch. glaucum* is rather polymorphic and a number of different forms have been described. However, these are usually difficult to distinguish, as most vegetative characters are very variable. One of the easiest to recognize is f. *humile* (PETERM.) AELLEN, characterized by a low, decumbent, more or less branched

---

[1] ENGSTRAND is responsible for the drawings and GUSTAFSSON for the text.

Bot. Notiser, vol. 126, 1973

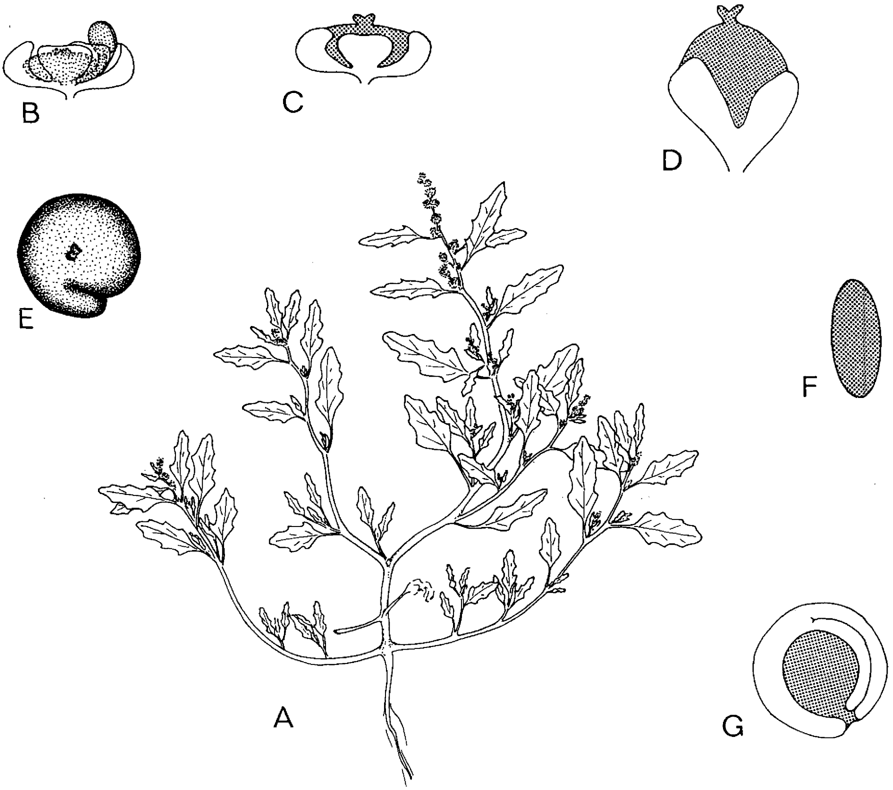


Fig. 83. *Chenopodium glaucum* L. — A: Habit. — B: Hermaphrodite flower. — C: Horizontal fruit, enclosed in the perianth. — D: Vertical fruit, enclosed in the perianth. — E: Fruit. — F: Seed in transection. — G: Section through a seed showing the embryo. — A: ×0.5. — B—G: ×20.

habit and by elliptic to spatulate leaves scarcely 1 cm long. It occurs in various wet habitats, especially sandy or saline.

Habitat and distribution: It grows preferably in eutrophic habitats rich in nitrogen, more or less occasional as a weed and usually close to human settlements, e. g. in gardens, on roadsides and manure heaps. It also occurs as a halophyte on eutrophic seashores and in other saline habitats.

Ch. glaucum is distributed throughout most parts of Europe except the westernmost regions of the British Isles and the southernmost parts of the Mediterranean area, further in the central parts of Asia to Japan and Kamchatka. Other closely related species or deviating subspecies are distributed in South Africa, in Australia and in North America.

In Scandinavia all the material belongs to ssp. *glaucum.* It is frequently distributed in the eastern parts of Denmark, more rare in the province of Jylland, in Sweden northwards to Stockholm, less common further north, and in Norway preferably around Oslo. In Finland scattered localities mostly in the southern parts.

84. **Chenopodium rubrum** L. 1753

Annual, up to 8 dm high, but usually less, habit erect to ascending, rarely de-

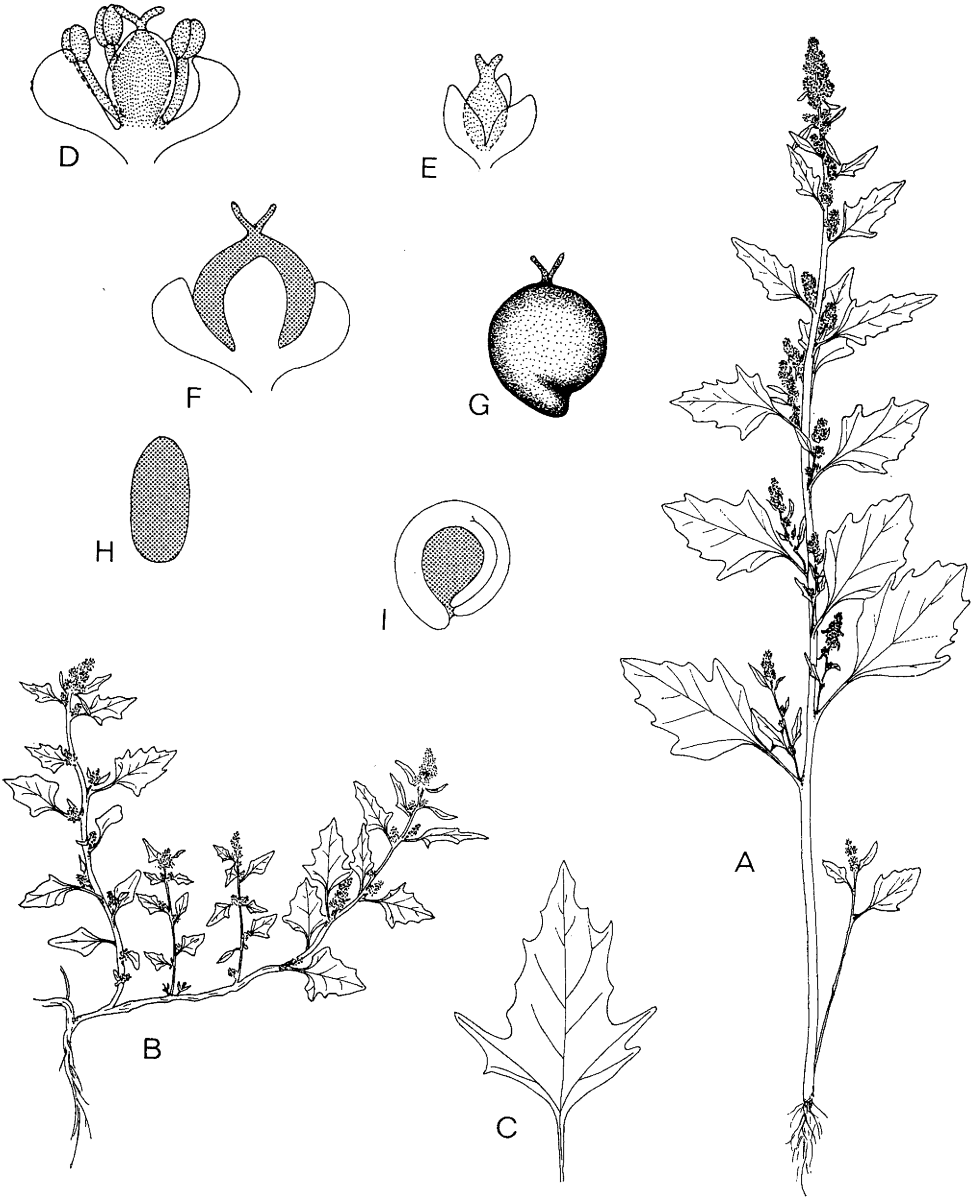


Fig. 84. *Chenopodium rubrum* L. — A—B: Habit of different forms. — C: Shape of a lower leaf. — D: Hermaphrodite flower. — E: Pistillate flower. — F: Vertical fruit, enclosed in the perianth. — G: Fruit. — H: Seed in transection. — I: Section through a seed showing the embryo. — A—C: ×0.5. — D—I: ×20.

cumbent, much-branched. Stem angular, green striated. Foliage fleshy, reddish and glabrous, sometimes somewhat farinose when young. Leaves alternate, the lower ones long-petiolate, rhomboid to triangular, usually cuneate at base, 1—9 cm long, length greater than or equal to the breadth, more or less red-coloured both above and beneath, at apex acute. Margins sinuate to irregularly dentate, the lowest teeth largest, sometimes lobe-like, pointing forwards, acute. Upper leaves petiolate, deltoid to lanceolate, entire to sharply dentate. Inflorescences composed of many-flowered, compact, oblong cymes forming dense panicles or spikes, situated both in axils and terminally. Flowers glabrous and of two kinds, terminal ones with 4- to 5-merous perianth, 3—5 stamens and horizontal seeds, the others pistillate or perfect, generally with 3-merous perianth and vertical seeds. Perianth lobes usually only united below, lanceolate to elliptic, rarely ovate, obtuse to acute, in the middle part often fleshy, rounded or somewhat keeled, greenish. Pistil with two rather short, papillate stigmas. Seeds orbicular to ovoid, 0.5—1.1 mm in diameter, rounded in transection, reddish-brown to dark brown. Pericarp greenish, loosely attached to the seed. Testa lustrous, closely pitted, sometimes with small furrows. Radicula situated laterally or opposite the vestiges of the style, apex attached to the seed or pointing outwards. Embryo annular.

Flowering time: July to September.

Chromosome number: 2n=36.

Variation: Like many other *Chenopodium* species it is very variable in all vegetative characters and a number of more or less deviating forms have been distinguished (cf. AELLEN 1960).

Habitat and distribution: *Ch. rubrum* occurs on most waste ground such as on manure heaps, on different kinds of cultivated ground, more rarely on seashores and in saline habitats. Distributed throughout most of Europe but less common in the Mediterranean region, in the Middle East, in large parts of Asia to Pamir and Mongolia and in North America. In Scandinavia frequently occurring in Denmark, except in the westernmost part of Jylland, and in Sweden northwards to the provinces of Uppland—Bohuslän. Less common and occasional further north in Sweden, and in the southern provinces of Norway and Finland.

Comments: Certain forms of *Ch. rubrum* (see Fig. 84 B) have frequently been confused with *Ch. botryodes* SM. Morphologically they are distinguished on the different features of the perianth. The perianth lobes of *Ch. rubrum* are free to at least one half, those of *Ch. botryodes* usually united almost to the apex and forming a sac investing the seed. In addition they also have different chromosome numbers, *Ch. rubrum* being tetraploid and *Ch. botryodes* diploid, and different ecological preferences. *Ch. botryodes* is almost exclusively a halophyte, while *Ch. rubrum* mostly occurs as a weed.

Sect. **Degenia** AELLEN

Annuals. Perianth of some terminal flowers 5-merous, segments free to the base, seeds horizontal, the others pistillate or perfect with perianth segments entirely united, forming a sac enclosing the vertical seed. Embryo annular. Sect. *Degenia* comprises three species, two of them native to North and South America, *Ch. macrospermum* HOOK. FIL. and *Ch. frigidum* PHIL.

85. **Chenopodium botryodes** SMITH 1811

(Syn.? *Ch. chenopodioides* (L.) AELLEN 1933. At least in Scandinavia this taxon has been called *Ch. chenopodioides,* but according to BRENAN 1964 the typification seems to be uncertain.)

Annual, 10—50 cm high, rarely more, stem angular, erect or ascending, branched or unbranched. Foliage green, mostly fleshy, glabrous or in young stages somewhat farinose. Leaves alternate, the lower ones triangular, broadest at the base,

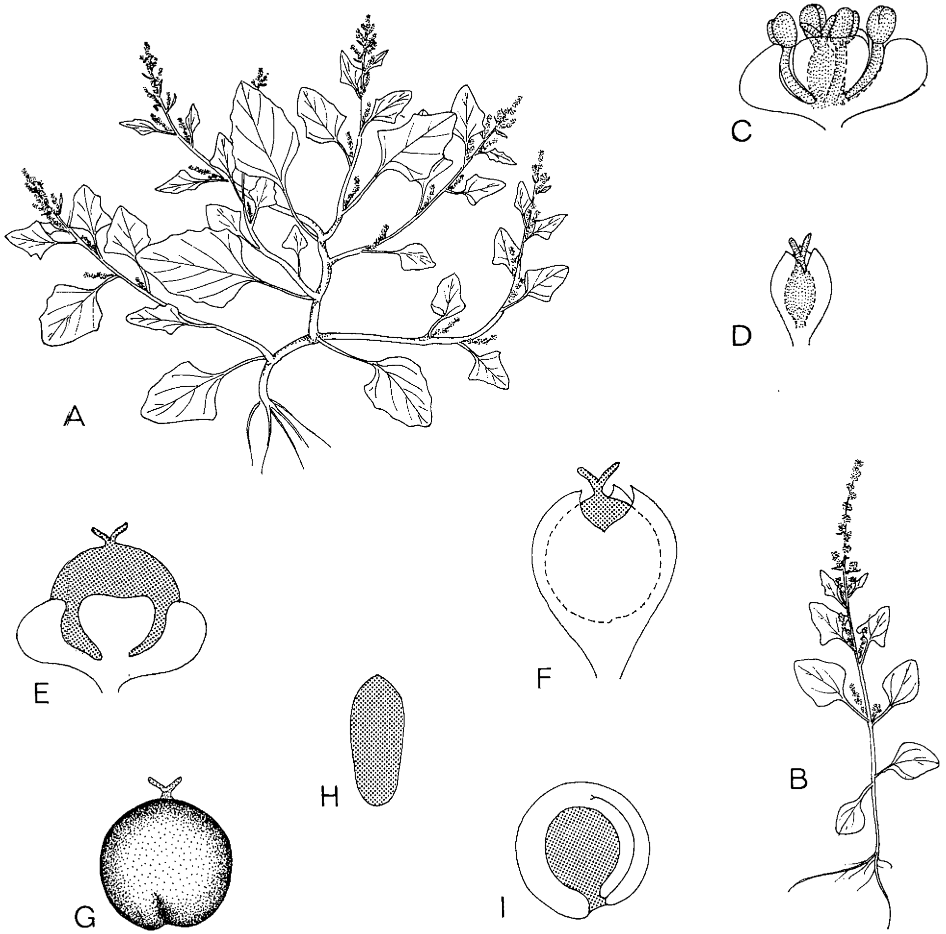


Fig. 85. *Chenopodium botryodes* Sm. — A—B: Habit of different forms. — C: Hermaphrodite flower. — D: Pistillate flower. — E: Terminal flower, with vertical fruit. — F: Vertical fruit, entirely enclosed within the perianth. — G: Fruit. — H: Seed in transection. — I: Section through a seed showing the embryo. — A—B: ×0.5. — C—I: ×20.

gradually tapering towards the petiole, which is at least 1/3 of the lamina, up to 9 cm long, 1—1.5 times longer than broad, apex obtuse to acute. Margins entire to dentate, the basal teeth largest, sometimes lobe-like, pointing outwards. Upper leaves triangular to rhomboid, rarely lanceolate, entire or dentate. The terminal inflorescences consisting of many-flowered cymes, forming much-branched, dense, more or less pyramidal, sparsely leafy panicles, the axillary ones more lax and few-branched. Flowers glabrous, some terminal ones 5-merous, with perianth lobes only united below, horizontal or vertical seeds, the others with vertical seeds, either pistillate or perfect with 1—2 stamens, and with the perianth segments usually entirely united, forming a sac completely enclosing the seed. Perianth narrowed at base, conspicuously thin and membraneous, except for green-coloured keels, particularly obvious above. Pistil with two short, rather thick, papillate stigmas. Seeds globular to ovoid, often narrowing towards the radicula, small, usually 0.3—0.5 mm in diameter, dark brown, with or without a small, narrow ridge. Pericarp greenish, loosely attached to the seed. Testa lustrous, minutely pitted and small-furrowed or somewhat reticulate. Radicula situated opposite the vestiges of the style, short and thick, usually bent inwards and attached to the seed. Embryo annular.

Flowering time: July to September.

Chromosome number: $2n = 18$.

Habitat and distribution: *Ch. botryodes* grows almost exclusively on seashores and in saline habitats together with other halophytes, such as *Triglochin maritimum, Juncus gerardii, Spergularia* species, *Glaux maritima* and *Aster tripolium,* but also in habitats dominated by *Suaeda maritima* and *Salicornia* species. In Europe it is distributed along the coasts of the Mediterranean and Atlantic regions northwards to Denmark and in the southwestern part of Great Britain, in addition in saline habitats in Germany, Czechoslovakia, Austria, Hungary and Romania. Native also in Asia, Africa and North America. In Scandinavia *Ch. botryodes* is confined to Denmark, mainly to an area between the western coast of Sjælland and the southeastern part of Jylland.

LITERATURE CITED

AELLEN, P. 1960. Chenopodium. — In HEGI, Illustrierte Flora von Mitteleuropa, 2. Aufl., III (2). — München.

BRENAN, J. P. M. 1964. Chenopodium. — In 'Flora Europaea' I. — Cambridge.

ILJIN, M. M. 1936. Chenopodium. — In KOMAROV, Flora SSSR VI. — Leningrad.

Male Meiosis in Some Amphimictic and Apomictic Hierochloë (Gramineae)

By Gunnar Weimarck

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

ABSTRACT

Weimarck, G. 1973. Male meiosis in some amphimictic and apomictic Hierochloë (Gramineae). — Bot. Notiser 126: 7—36.

Male meiosis in 25 *Hierochloë* collections is described. They represent *H. australis, H. repens, H. odorata* ssp. *odorata* and ssp. *baltica, H. hirta* ssp. *hirta* and ssp. *arctica,* and *H. alpina* ssp. *alpina* and ssp. *orthantha.* Special attention has been paid to the study of abortion, chiasma frequency, characteristics of chromosome pairing, occurrence of laggards, bridges and fragments, and of micronuclei, and the percentage of stainable pollen.

The aberrations found are discussed in relation to level of polyploidy, growth habit and balance between amphimixis and apomixis. Segmental allopolyploidy and autoallopolyploidy are discussed as regards the origin of the polyploids on the basis of meiotic behaviour, morphology and other data available.

INTRODUCTION

The present paper deals with male meiosis in some taxa of *Hierochloë* (see Table 1). The paper forms part of an investigation of the genus in the Northern Hemisphere. Other parts that have been published are Weimarck 1963, 1967 a, b, 1970 a, b, c, and 1971 a and b. The nomenclature used in the papers of 1963, 1967 and 1970 was provisional. The correct nomenclature was given in Weimarck 1971 a p. 130. Some results of the study of male meiosis were briefly anticipated in Weimarck 1971 a.

The taxa studied have the basic chromosome number of x=7. Chromosome numbers, mode of reproduction, germinating capacity of caryopses and growth habit are given in Table 1. Reproduction in *Hierochloë odorata* ssp. *odorata* 2n=42 and in the more or less aberrant cytotypes *H. hirta* ssp. *arctica* 2n=70 and 84, *H. alpina* ssp. *alpina* 2n=72, 75, 76 and 77, and *H. alpina* ssp. *orthantha* 2n=58 has not been studied. The figures given for germinating capacity are based on a small amount of material only. The data are compiled from Weimarck 1967—71 and unpubl.

AIMS

The aims of the present investigation were:

(1) to describe male meiosis in plants chosen to represent the taxa investigated,

(2) to compare the taxa with respect to the types of meiotic irregularities occurring and their frequencies,

(3) to set these irregularities in relation to the level of polyploidy, to the balance between amphimixis and apomixis and to the growth habit of each taxon concerned, and

(4) to discuss possible structural heterozygosity and the degree of auto- or

allopolyploidy on the basis of chromosome configurations observed in different taxa.

MATERIAL

Spikelets were initially fixed from a rather large number of collections. Those dealt with in this paper were chosen to be as representative as possible from a geographical point of view within the limits of material available. Male meiosis was usually studied within one plant only per collection.

Most of the specimens studied were cultivated in the open in the Botanical Gardens, Lund. *Hierochloë alpina* ssp. *alpina* and ssp. *orthantha* were cultivated in the Arktisk Hus at the Botanical Gardens in Copenhagen. All specimens with the exception of the *H. hirta* ssp. *arctica* collection A K K and the *H. repens* collection B E S were grown from rhizomes collected in the field. The *H. hirta* ssp. *hirta* collection B H P was studied on the original site. Each locality is designated with three capital letters. Voucher specimens are deposited at the Botanical Museum, Lund (LD).

Data on the collections are given in an appendix on p. 35.

METHODS

Spikelets were fixed in absolute alcohol, glacial acetic acid and chloroform (6:3:1). The spikelets were stored in 70 % alcohol in a deep-freeze for a short time, or in some cases up to about five years. They were stained overnight in hydrochloric carmine (SNOW 1963) at 60°C, and then put back into 70 % alcohol to remove excess stain. They could then be stored anew in a deep-freeze, but if storage after staining extended over months or years the cytoplasm tended to become too heavily stained. The anthers were dissected out and crushed in a drop of 45 % acetic acid on a slide. A droplet of Hoyer's medium (BEEKS 1955) was added and mixed with the acetic acid while being gently heated. The tissue was squashed under an ordinary coverslip.

Sections of anthers were studied for certain complementary purposes. Slides originally made for embryological investigations were used. They had been stained in iron haematoxylin and light green (WEIMARCK 1967 a p. 210).

Pollen diameter and the stainability of pollen were determined from cotton blue preparations. The pollen was taken from dried specimens. Two hundred pollen grains were studied in all determinations of stainability and 100 in the pollen diameter measurements.

The calculation of chiasma frequency was usually possible only in the diploid and the tetraploids. The number of laggards at anaphase I is expressed in terms of lagging chromatids, as at anaphase II.

The results that are possible to express graphically or numerically are presented in Figs. 1—7 and in Tables 2—4.

The photomicrographs (Figs. 8—12) were made with a Nikon Microflex camera on a Leitz Ortholux microscope. The objective was a Pl Apo Oel 100/1.32.

Slides studied are deposited at the Department of Plant Taxonomy, Lund.

RESULTS

General Observations

Male meiosis usually took place about at the time when the young panicle penetrated the uppermost culm leaf sheath. Its top was then about 5—12 cm above the ground in *Hierochloë australis* and *H. alpina* ssp. *alpina,* 8—25 cm in the other taxa studied. Some variation in stage of development amounting to a few days was found between separate spikelets in a panicle and between different florets in the same spikelet and even between anthers in the same floret.

The number of nucleoli per PMC at diakinesis was usually 1, but 2 or even 3 nucleoli occurred in some taxa.

All chromosomes were approximately metacentric. They were of about equal size being medium-sized except for the small B-chromosomes of one *H. repens* collection. Satellites were only rarely discernable.

The number of chiasmata at diakinesis and metaphase I did not exceed one per chromosome arm as far as could be observed at these stages (cf., however, p. 25).

Pollen formation was successive, a cell wall dividing the PMC at the dyad stage.

Pollen grains were shed at the 3-nucleate stage. They were 1-ulcerate, spheroidal, and smooth. Malformed grains could deviate from this general description.

Table 1. Chromosome number, mode of reproduction, germinating capacity of caryopses, and growth habit in taxa studied of *Hierochloë*.

Taxon	2n	Mode of reproduction	Germinating capacity of caryopses %	Growth habit
H. australis (SCHRADER) ROEMER & SCHULTES	14	facultative apomict	0—3	tufted
H. repens (HOST) SIMONKAI	28 (28+2B)	amphimict	—	rhizomatous
H. odorata (L.) WAHLENB. ssp. *odorata*	28 (42)	amphimict	6—36	rhizomatous
ssp. *baltica* G. WEIM.	42	apomict	3	rhizomatous
H. hirta (SCHRANK) BORBÁS ssp. *hirta*	56	apomict	1	rhizomatous
ssp. *arctica* (PRESL) G. WEIM.	56 (70, 84)	(facultative?) apomict	9	rhizomatous
H. alpina (WILLD.) ROEMER & SCHULTES ssp. *alpina*	56 (66, 72, 75, 76, 77)	(facultative) apomict	—	tufted
ssp. *orthantha* (SØRENSEN) G. WEIM.	63 (58)	apomict	—	moderately tufted

Hierochloë australis 2n=14

PACHYTENE. Only normally paired chromosomes were found in the PMCs studied with the exception of some cases of abortion.

DIAKINESIS. Chiasma formation was localized almost completely to the ends of the chromosomes. Ring bivalents were most frequent (Fig. 8 A), but there were a number of arms with no chiasma. In this way rod bivalents and, infrequently, univalents were formed. The mean number of chiasmata per chromosome arm was thus less than one (Table 2).

METAPHASE I. The frequencies of ring bivalents, rod bivalents and univalents also indicate at this stage that the number of chiasmata was somewhat lower than the somatic chromosome number (Figs. 1 A and 8 B, C; Table 2). Abortion in the form of despiralization was found infrequently in A H T (Fig. 8 D).

ANAPHASE I. Most PMCs behaved normally. No lagging chromatids were found (Fig. 2 A). Two cases of bridge and fragment formation occurred (Fig. 6 A). The fragments were very small as was to be expected from the location of the chiasmata. Bridge formation without a visible fragment in A H T was obviously caused by stickiness. All PMCs where the segregation of chromosomes could be studied had the regular distribution 7:7 with one exception in B B C which contained a bridge and fragment (Table 3).

DYAD. No dyad contained any micronuclei (Fig. 3 A).

ANAPHASE II. Most PMCs behaved normally. One case of lagging chromatids occurred in A H T (Fig. 4 A). Two bridges, apparently formed due to stickiness, were also found in A H T (Fig. 7 A).

UNINUCLEATE POLLEN. No micronuclei were detected (Fig. 5 A).

MATURE POLLEN. Pollen stainability was high compared to that in other *Hierochloë* studied (Table 4).

Hierochloë repens 2n=28, 28+2B

The behaviour of the B-chromosomes in the B C D collection is not dealt with in detail here but will be reported on in a

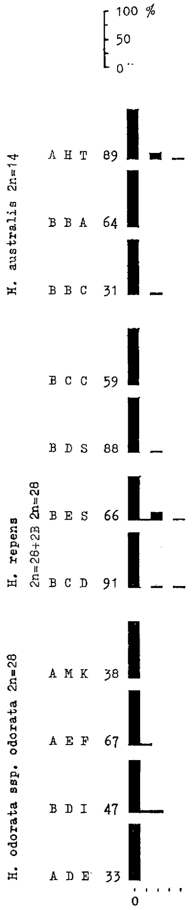


Fig. 1 A.

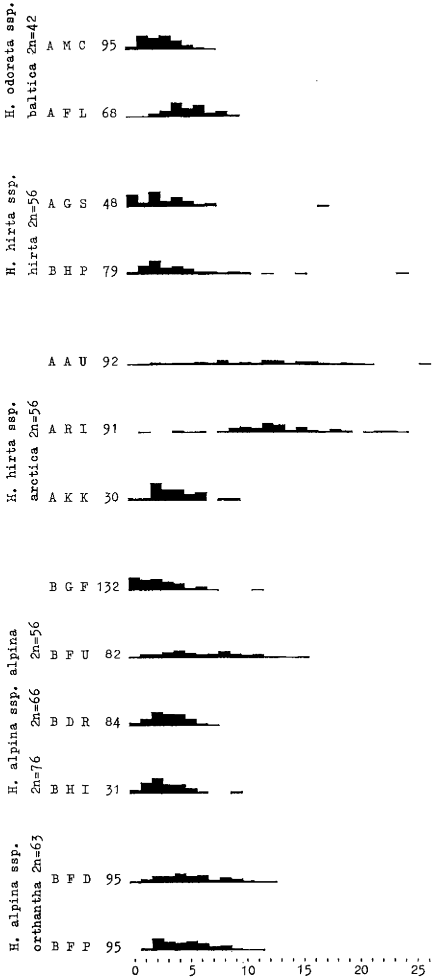


Fig. 1 B.

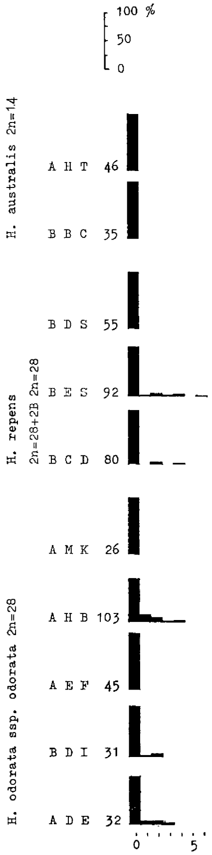


Fig. 2 A.

Fig. 1. Number of univalents per PMC at metaphase I in *Hierochloë*. — In Figs. 1—5 the number is given on the horizontal axis, the percentages of PMCs on the vertical. The number of PMCs studied is given for each collection in connection with the collection code. — A: diploid and tetraploid, amphimictic and facultatively apomictic taxa. — B: apomictic taxa at hexaploid and higher levels of polyploidy.

Fig. 2. Number of lagging chromatids per PMC at anaphase I in *Hierochloë*.

later paper. The B-chromosomes are not accounted for in the tables.

Anaphase I and II and the dyad and uninucleate pollen stages were not studied in B C C.

PACHYTENE. Normal pairing usually took place. Unpaired parts of chromosomes could, however, be found. In some cells of B C C some of the chromosomes were broken up into shorter fragments (Fig. 8 E).

DIAKINESIS. Chiasma formation was

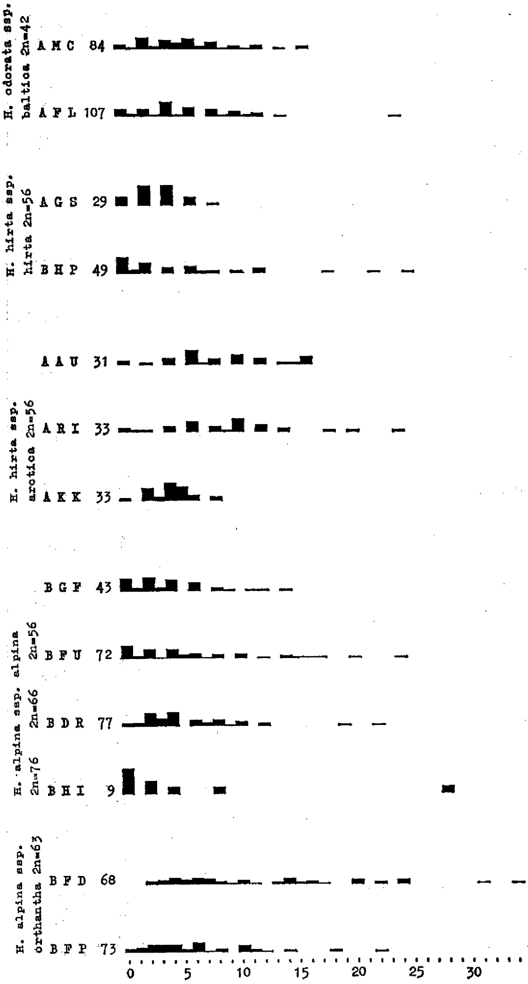


Fig. 2 B.

not localized to the ends of the chromosomes in this taxon, nor in the following ones. Only bivalents were found in B C C and B E S (Fig. 8 F; Table 2). One single cell with $1_{IV}+12_{II}$ was found in B D S. The B-chromosomes in B C D generally formed univalents (Fig. 8 G). Univalent A-chromosomes were found in one cell only. The number of chiasmata per cell was lower in B D S, B E S and B C D than in *Hierochloë odorata* at the same level of polyploidy. No signs of abortion were seen.

METAPHASE I. Only bivalents occurred in B C C (Fig. 1 A; Table 2). A few cells containing $13_{II}+2_{I}$ or $1_{IV}+12_{II}$ were found in B D S. About one-fourth of the cells of B E S contained $13_{II}+2_{I}$, and the configurations $12_{II}+4_{I}$, $1_{III}+12_{II}+1_{I}$ and $1_{IV}+12_{II}$ were found in one cell each. Apart from the B-chromosomes, which almost always formed univalents, bivalent formation was fairly regular in B C D (Fig. 8 H). The number of chiasmata per chromosome arm in all four collections was significantly lower than at the corresponding diakinesis stages (Table 2). No signs of abortion were seen.

ANAPHASE I. Only in B E S and B C D were a few PMCs found containing up to six lagging chromatids (Fig. 2 A). A few cells in B D S and B E S contained a bridge and fragment (Fig. 6 A). Bridges without fragments occurred rarely in all collections represented and had a sticky appearance. All analysable cells in B D S showed regular chromosome segregation except those containing a bridge (Table 3). Uneven segregation occurred rarely in B E S and B C D (Fig. 8 I). No other signs of aberration were observed.

DYAD. A few PMCs of B E S contained one to four micronuclei. About one-third of the B C D cells contained one, or in one case two (Fig. 3 A). In these cells the micronuclei probably represent eliminated B-chromosomes. No otherwise abnormal cells were observed.

ANAPHASE II. A small number of PMCs contained one or two lagging A-chromatids (Fig. 4 A). One B-chromatid lagged behind in 22 of the 64 PMCs studied in B C D, and in 4 cells two B-chromatids lagged behind. Bridge and fragment formation was rarely found in B D S and B E S (Fig. 7 A).

UNINUCLEATE POLLEN. A fairly large proportion of the tetrads contained up to four micronuclei (Fig. 5 A).

MATURE POLLEN. The percentage of stainable pollen was high in B C C and

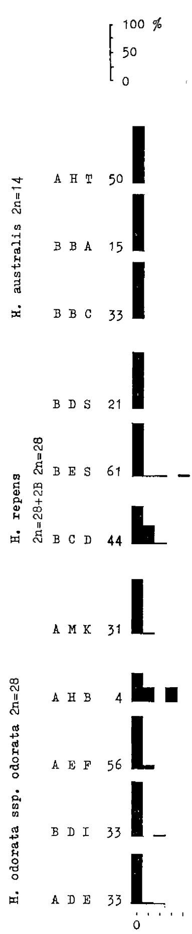


Fig. 3 A.

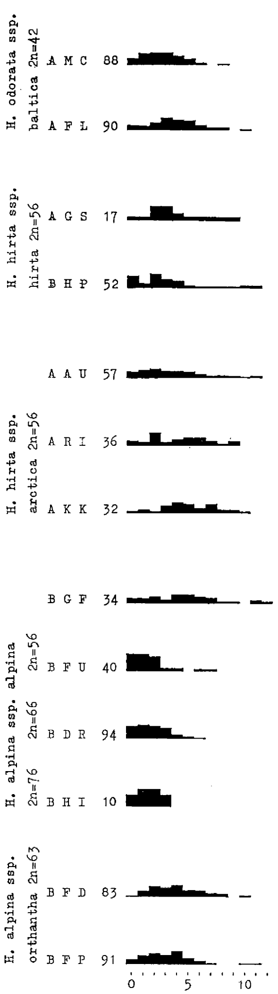


Fig. 3 B.

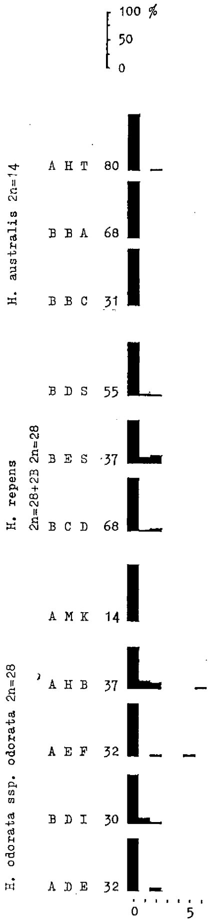


Fig. 4 A.

Fig. 3. Number of micronuclei per PMC at the dyad stage in *Hierochloë*.

Fig. 4. Number of lagging chromatids per PMC at anaphase II in *Hierochloë*.

Fig. 5. Number of micronuclei per PMC at the stage of uninucleate pollen in *Hierochloë*.

B D S, lower in B E S and B C D (Table 4). Single malformed grains were found in B C D.

Hierochloë odorata ssp. **odorata** 2n=28

PACHYTENE. Pairing was normally regular, but in some PMCs some unpaired chromosomes could be seen.

DIAKINESIS. The mean number of chiasmata per chromosome arm was usually less than one (Table 2). Univalents were rarely found. The configuration $1_{IV}+12_{II}$ was fairly frequent in A E F (Fig. 8 J). No trivalents occurred. The diakinesis of A H B was abnormal-looking due to despiralization and stickiness, and its pairing properties could not be analysed.

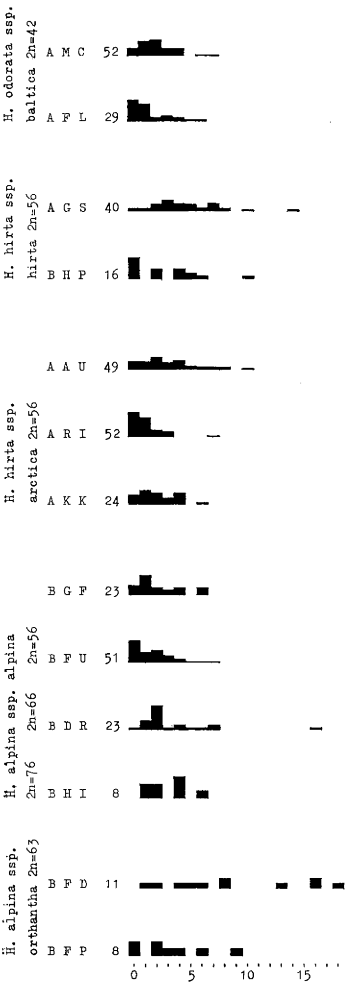


Fig. 4 B.

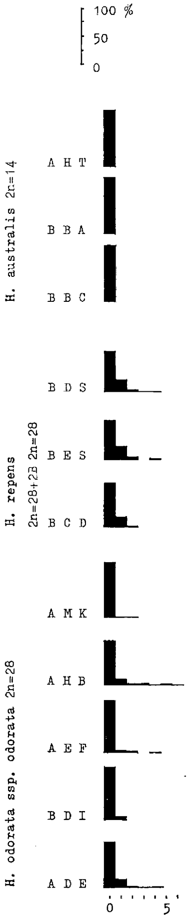


Fig. 5 A.

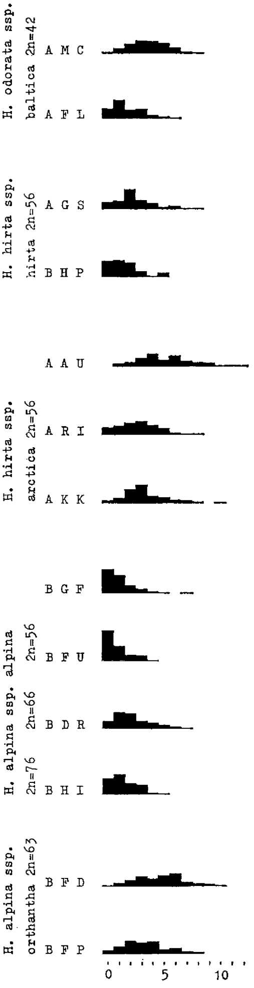


Fig. 5 B.

METAPHASE I. It was not possible to interpret the chromosome configurations of A H B with certainty, due to stickiness and also partly to despiralization and degeneration. Univalents were visible in some cells. In the other plants the PMCs were mainly normal. The estimated number of chiasmata per chromosome arm was significantly less than at diakinesis in A M K and B D I (Table 2). The configuration $1_{IV}+12_{II}$ was fairly frequent in A E F (Fig. 8 K), and in the same plant a few PMCs had $1_{III}+12_{II}+1_{I}$. A few PMCs with one or two univalents but apparently no trivalents were found in B D I (Fig. 1 A).

ANAPHASE I. Lagging chromatids were present in about one-fourth of the PMCs of A H B, and less frequently in B D I and A D E (Fig. 2 A). One or two bridges and fragments were found in a few cases. Most of the PMCs of A H B had up to six bridges without a fragment and with a characteristic sticky appearance (Figs.

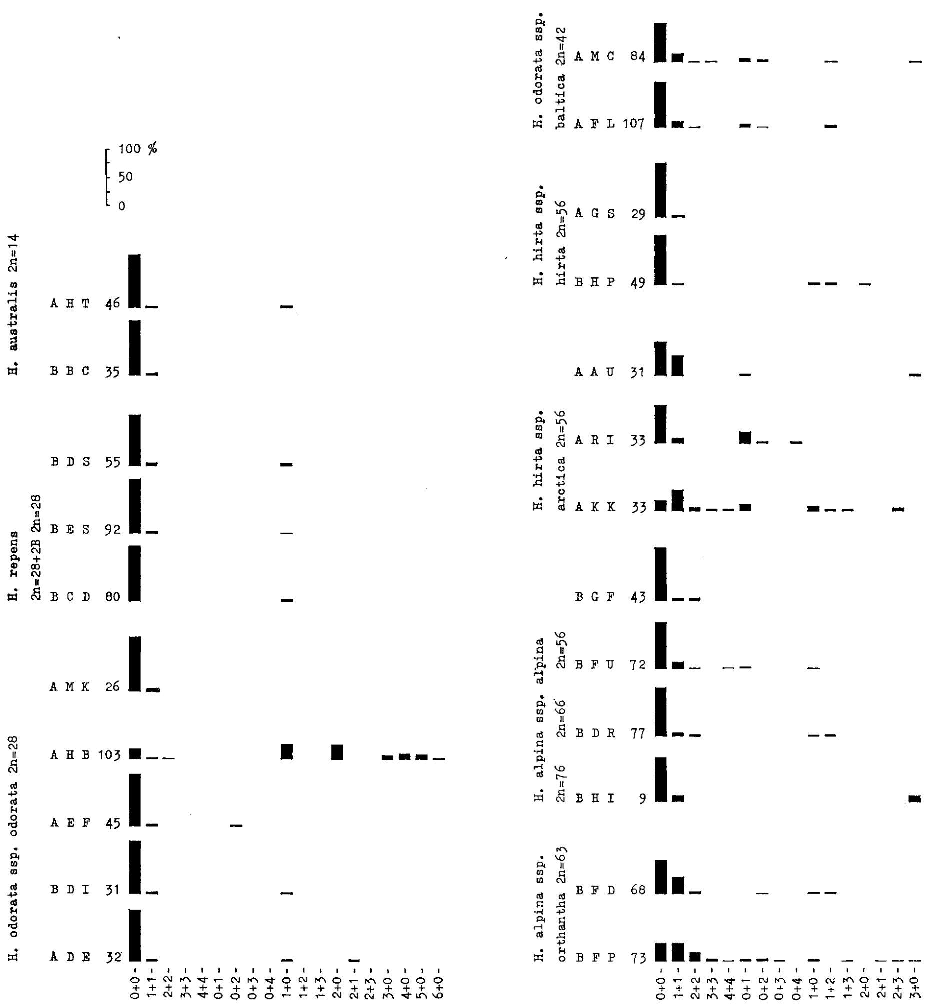


Fig. 6 A. Fig. 6 B.

Fig. 6. Combinations of bridges and fragments in PMCs at anaphase I in *Hierochloë*. — In Figs. 6 and 7 the number of bridges+the corresponding number of fragments is given on the horizontal axis. As to the rest, the arrangement conforms with that in Figs. 1—5.

6 A and 8 L, M). The segregation of chromosomes was usually regular (Table 3).

DYAD. One or a few micronuclei were found in all plants (Fig. 3 A). The frequency could not be estimated in A H B because of the rareness of the stage in the preparations. It was low in the other plants.

ANAPHASE II. Lagging chromatids were observed in all collections but A M K. A H B had the highest numbers and frequencies (Fig. 4 A). A H B had also up to three bridges and fragments per cell and

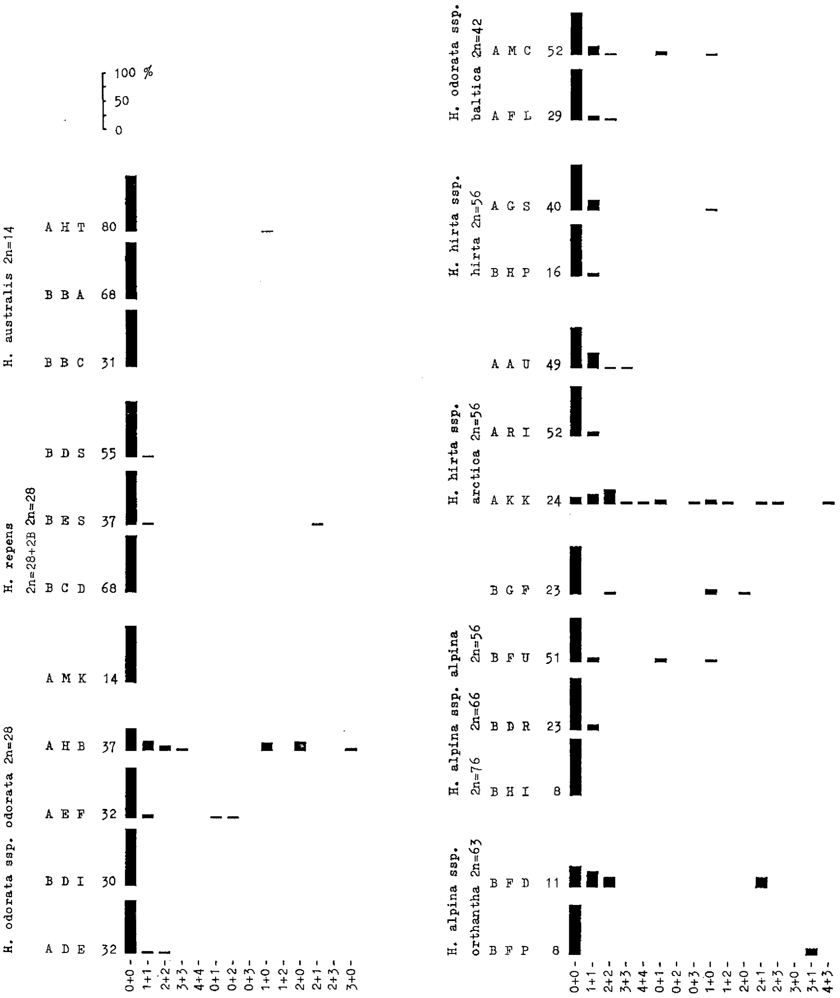


Fig. 7 A. Fig. 7 B.

Fig. 7. Combinations of bridges and fragments in PMCs at anaphase II in *Hierochloë*.

sticky bridges. Most PMCs in the other plants behaved normally (Fig. 7 A).

UNINUCLEATE POLLEN. A H B had the highest numbers and frequencies of micronuclei per PMC, A D E coming next. In the other plants micronuclei were fairly rare (Fig. 5 A). A H B formed a few giant pollen grains and dyad pollen grains.

MATURE POLLEN. Pollen stainability varied a great deal between plants (Table 4).

Hierochloë odorata ssp. **baltica** 2n=42

PACHYTENE. Unpaired chromosomes were frequently observed (Fig. 9 B). Pairing between more than two chromosomes was also observed. PMCs with two nucleoli (Fig. 9 B) and abortive PMCs occurred rather frequently.

DIAKINESIS. Most PMCs were not analysable. Two PMCs of A F L showed partial desynapsis in the sense of Li et al. (1945 p. 94). Some homologues were perhaps not held together by chiasmata but formed only loose associations due to affinity. The number of chiasmata given in Table 2 may be too high for this reason. Some univalents also seemed to associate in a non-random way. In one of the cells (Fig. 9 C) six satellite chromosomes were visible, one pair of which being attached to the nucleolus. In the other cell a univalent was attached to the nucleolus. Complete lack of synapsis was found in one cell (Fig. 9 A; not in Table 2) of a specimen of the collection A F A not further dealt with in this paper (Sweden, Västergötland, Hällstad).

METAPHASE I. Almost all PMCs contained univalents, up to nine in number (Figs. 1 B and 9 D). No complete analysis of configurations was made due to a strong tendency of the chromosomes to clump together. Rod-bivalents and cross-bivalents were frequent. Straight tri- and quadrivalents occurred. The number of chiasmata was in all likelihood not very high.

ANAPHASE I. Most PMCs contained lagging chromatids, up to 24 (Figs. 2 B and 9 E, F). Bridge formation with or without fragment formation was found in many cases (Figs. 6 B and 9 E). Fragments without bridges also occurred (Fig. 9 F). A case of incomplete misdivision of a univalent was found in A M C. One chromatid arm went to one pole, the three other chromatid arms lagged or went to the other pole. Most countable PMCs had an irregular segregation of chromosomes (Table 3).

DYAD. Most dyads contained micronuclei, up to 10 per PMC (Fig. 3 B). Irregularities such as tri- or quadripolar divisions and abortion were also observed.

ANAPHASE II. Lagging chromatids were frequent (Fig. 4 B). Some bridge and fragment formation was also found (Fig. 7 B). The irregular distribution of chromatids at anaphase I was also reflected at anaphase II. For example, of two PMCs analysed in A F L, one had the distribution 20: 18+23: 22: 1 lagging chromatid, the other 19: 19+23: 23.

UNINUCLEATE POLLEN. Up to eight micronuclei per PMC could be found, A M C having almost no tetrads without micronuclei (Fig. 5 B). Some giant pollen grains occurred.

MATURE POLLEN. Pollen stainability was very different in the two plants studied (Table 4). Malformed, 8-shaped grains occurred.

Hierochloë hirta ssp. **hirta** 2n=56

PACHYTENE. Unpaired chromosomes or chromosome parts were visible. Some PMCs had two nucleoli (Fig. 10 A). One case of loop formation was found, involving at least three chromosomes.

DIAKINESIS. The cells were usually difficult to interpret. Univalents and multivalents occurred. Cells showing almost no synapsis (not in Table 2) were observed.

METAPHASE I. Most PMCs contained univalents, usually not more than 10 but up to 24 (Figs. 1 B and 10 B). Tri- and quadrivalents were observed. Only two cells were entirely analysed. They had less than one chiasma per chromosome arm (Table 2). PMCs with despiralized chromosomes occurred.

ANAPHASE I. Up to eight lagging chromatids were present in most cells of A G S, up to 25 but usually less than 12 in B H P (Fig. 2 B). Tetrapolar divisions and abortive PMCs occurred. Only few cells with bridge and/or fragment were observed (Fig. 6 B). Only one of the analysable cells showed regular segregation of chromosomes (Table 3).

DYAD. Most dyads contained micronuclei, up to 11 (Figs. 3 B and 10 C). No other abnormalities were observed.

ANAPHASE II. Almost all cells contained lagging chromatids, up to 14 in number (Fig. 4 B). Some cells with bridge and fragment also occurred (Figs. 7 B and 10 D).

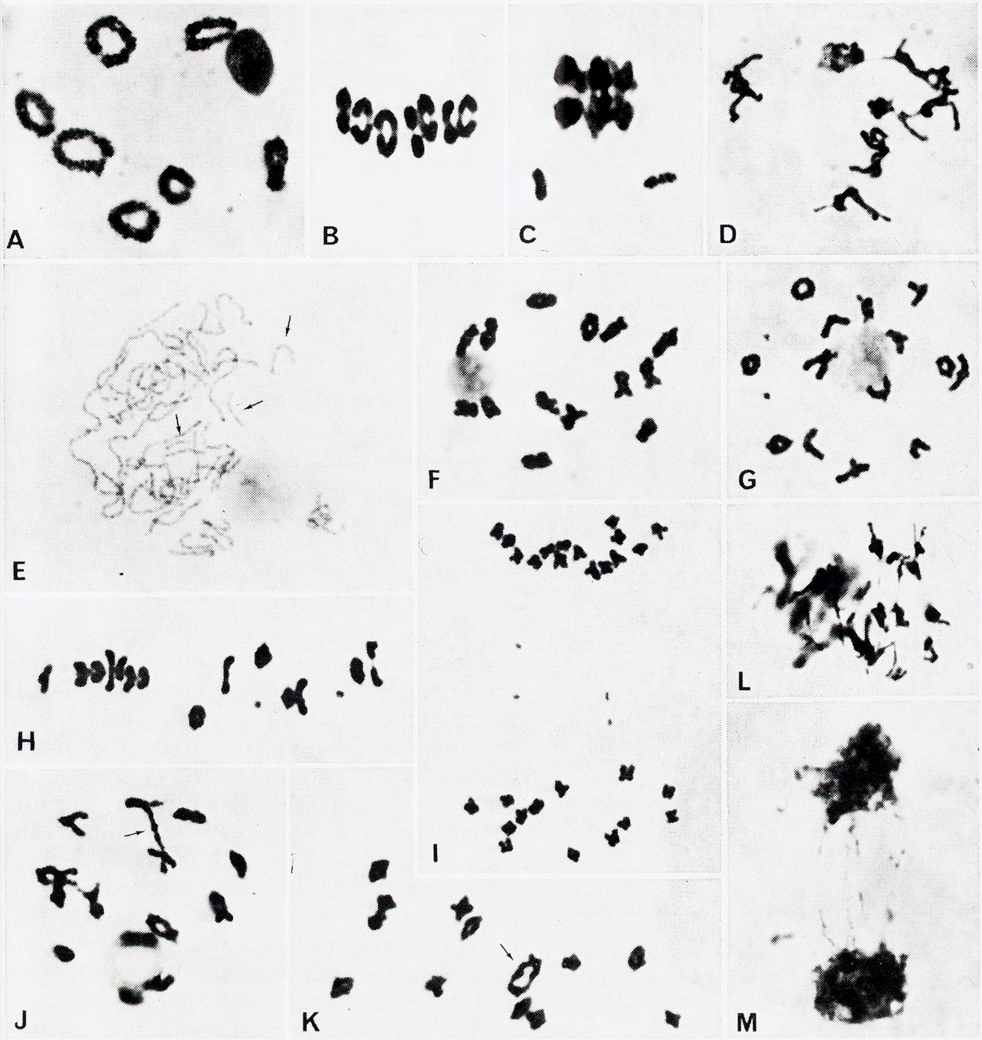


Fig. 8. Pollen mother cells of *Hierochloë*. — A: *H. australis,* B B A. — B—D: *H. australis,* A H T. — E, F: *H. repens,* B C C. — G—I: *H. repens,* B C D. — J, K: *H. odorata* ssp. *odorata,* A E F. — L, M: *H. odorata* ssp. *odorata,* A H B. — A: Diakinesis; 7_{II}. — B: Metaphase I; 7_{II}. — C: Metaphase I; $6_{II}+2_{I}$. — D: Metaphase I?, abortive. — E: Pachytene; some chromosomes fragmented (arrows). — F: Diakinesis; 14_{II}. — G: Diakinesis; $14_{II}+2B_{I}$. — H: Metaphase I—beginning anaphase I; $14_{II}+2B_{I}$. — I: Anaphase I; 4 lagging B-chromatids; chromosome distribution 15: 13. — J: Diakinesis; 1_{IV} (arrow) $+12_{II}$. — K: Metaphase I; 1_{IV} (arrow)$+12_{II}$. — L: Early anaphase I, sticky. — M: Late anaphase I, sticky. — ×1000.

UNINUCLEATE POLLEN. Most tetrads contained micronuclei, the maximum number being eight (Fig. 5 B). Dyad pollen grains and misdivided tetrads were observed.

MATURE POLLEN. Pollen stainability was different in the two plants, being remarkably low in A G S (Table 4).

Hierochloë hirta ssp. **arctica** 2n=56

PACHYTENE. The pairing was frequently incomplete. Abnormal and degenerating PMCs occurred frequently.

DIAKINESIS. Univalents were very common. Some cells showed almost no synapsis (Fig. 10 E; not in Table 2). Associations up to hexavalents also occurred. Aborting PMCs were found frequently.

METAPHASE I. Practically all cells contained univalents, some cells of A A U and A R I having almost half their chromosome complement in the unpaired condition (Figs. 1 B and 10 F). Associations up to pentavalents were observed. The mean number of chiasmata per chromosome arm was less than 0.5 in cells where all configurations were analysable (Table 2).

ANAPHASE I. Almost all cells contained lagging chromatids, up to 24 in A A U but considerably fewer in the others, especially in A K K (Fig. 2 B). Cases of stickiness and tetrapolarity occurred (Fig. 10 G). Many cells (in A K K almost all) had bridges and/or fragments (Fig. 6 B). Chromosome segregation was unbalanced as far as studied (Table 3).

DYAD. Almost all dyads contained micronuclei, up to 11 per PMC (Fig. 3 B). Tripolar and tetrapolar divisions were observed.

ANAPHASE II. Most cells contained lagging chromatids, up to ten in number (Figs. 4 B and 10 H). Bridges and/or fragments were formed (Figs. 7 B and 10 I), being most frequent in A K K. A R I was least abnormal in both respects. Micronuclei persisting from the dyad stage occurred. Two chromatid distributions in A A U were 30: 29: 3 lagging chromatids + 22: 24: 4 lagging chromatids, and 26: 26: 4 lagging chromatids + 26: 24: 6 lagging chromatids. The first case implies an uneven distribution at anaphase I as well.

UNINUCLEATE POLLEN. Of the tetrads studied, most of them in A R I and A K K and all in A A U contained up to 12 micronuclei (Fig. 5 B).

MATURE POLLEN. Pollen stainability was low (Table 4).

Hierochloë alpina ssp. **alpina** 2n=56, 66, 76

PACHYTENE. Univalents, multivalents and fragmented chromosomes were seen. Two and even three nucleoli occurred in some cells (Fig. 11 A). Abortive PMCs occurred.

DIAKINESIS. Moderate numbers of univalents were usually discernable. Multivalents also occurred. The stage was not well represented in the preparations and no cells could be completely analysed. Two nucleoli sometimes occurred.

METAPHASE I. Univalents, up to 15 in number, were found in almost all cells of B F U, B D R, and B H I. They were somewhat less frequent in B G F (Fig. 1 B). Bi-, tri- and quadrivalents were also observed. Chiasmata were impossible to analyse. Some degenerating PMCs were found in B F U.

ANAPHASE I. Most PMCs contained lagging chromatids, up to 28 but usually far fewer (Fig. 2 B). A few cells showing stickiness, tripolarity, tetrapolarity and total degeneration occurred (Fig. 11 C, E). Up to four bridges and fragments in the same cell were found in B F U, while most cells in the other collections contained no bridges and fragments at all (Fig. 6 B). The chromosome segregation was uneven in most cases (Table 3). Fig. 11 B shows regular segregation. Two cells with an approximately double chromosome number were observed in B G F.

DYAD. Most dyads contained micronuclei, 12 in number in one case in B G F, but usually fewer (Fig. 3 B). Some few tripolar, tetrapolar, asymmetric, degenerating or otherwise abnormal dyads were found. In one cell some chromosome material was still at a pachytene-like stage (Fig. 11 D).

ANAPHASE II. Most PMCs contained lagging chromatids, usually up to seven but up to 16 in B D R (Fig. 4 B). Bridges and/or fragments occurred in some cases (Fig. 7 B). Micronuclei persisting from the dyad stage occurred in some cells.

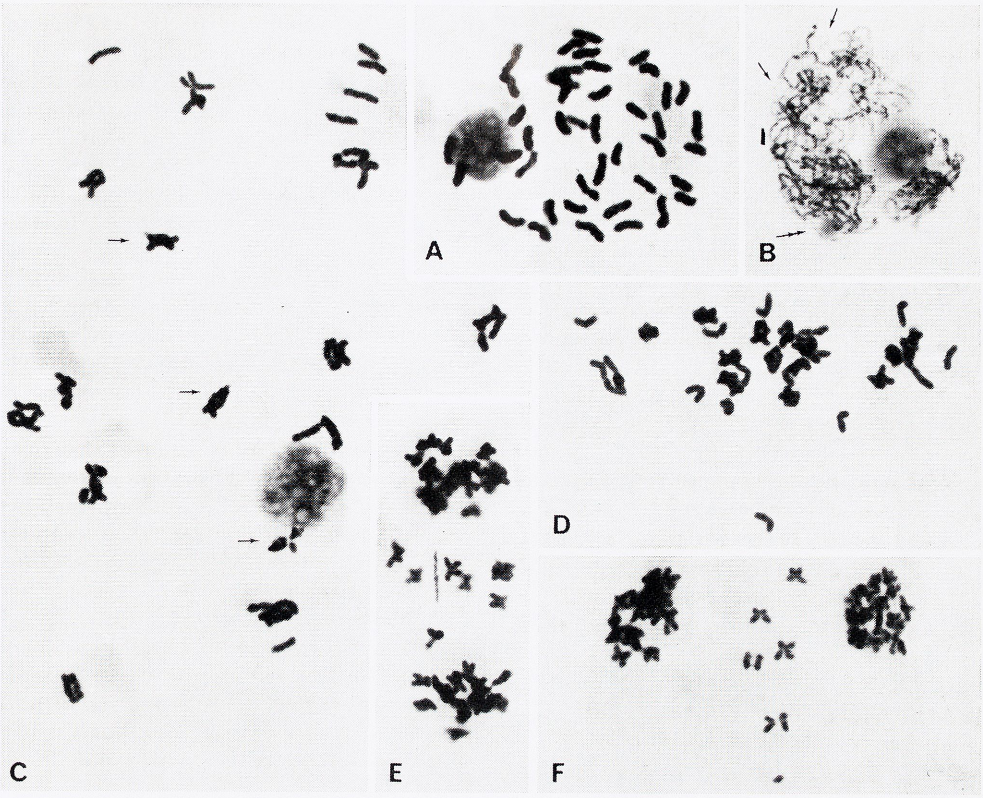


Fig. 9. Pollen mother cells of *Hierochloë*. — A: *H. odorata* ssp. *baltica,* A F A. — B—F: *H. odorata* ssp. *baltica,* A F L. — A: Diakinesis; 42_{I}. — B: Pachytene; 1 big and 1 small (double arrow) nucleolus; unpaired segments visible (arrows). — C: Diakinesis; probably $1_{\text{IV}}+6_{\text{III}}+7_{\text{II}}+6_{\text{I}}$; 3 satellite chromosome pairs visible (arrows); 4 univalents placed together in a non-random way? (top right). — D: Metaphase I; at least $1_{\text{III}}+8_{\text{I}}$. — E: Anaphase I; 14 lagging chromatids (4 of them on top of one another); bridge of sticky appearance, without fragment. — F: Anaphase I; 10 lagging chromatids; fragment without bridge. — ×1000.

UNINUCLEATE POLLEN. Many tetrads contained up to seven micronuclei (Fig. 5 B). B D R had the highest number of tetrads containing micronuclei, B F U the lowest. Dyad pollen grains were found in B G F, giant grains in B D R.

MATURE POLLEN. The percentage of stainable pollen was about the same in all the plants studied except for in B H I, which had a low value (Table 4).

Embryo sacs were found in anthers of B G F and B H I (see p. 29 for references).

Hierochloë alpina ssp. **orthantha** 2n=63

PACHYTENE. Poor synapsis occurred. Many PMCs were abortive.

DIAKINESIS. No cells permitted of an analysis of configurations.

METAPHASE I. All or practically all PMCs contained univalents, up to 12 in number (Fig. 1 B). Trivalents, quadrivalents and even higher associations were frequently seen. No cell could be completely analysed to estimate the number of chiasmata. Cells containing approximately double the number of chromosomes occurred (Fig. 12 A).

ANAPHASE I. All or practically all PMCs contained a varying number of lagging chromatids, up to 34 but usually not more than 24 (Fig. 2 B). A rather frequent occurrence of lagging chromatid arms (Fig. 12 B) was probably caused by stickiness. One tetrapolar division was observed. A large number of cells contained one or up to four bridges and/or fragments (Fig. 6 B). Chromosome segregation was unbalanced in the two cells studied (Table 3).

DYAD. Most PMCs contained micronuclei, up to 11 in number (Fig. 3 B). One tetrapolar and a number of tripolar and abortive dyads were observed.

ANAPHASE II. Practically all PMCs contained lagging chromatids, up to 18 (Fig. 4 B). One pentad was found. One to three bridges and fragments per PMC occurred (Fig. 7 B).

UNINUCLEATE POLLEN. Almost all tetrads contained up to 10 micronuclei (Fig. 5 B).

MATURE POLLEN. Pollen stainability was considerably lower in B F P than in B F D (Table 4).

DISCUSSION

The meiotic process is influenced by external factors. The effects of temperature and season of the year were shown for instance in *Potentilla verna* (Rutishauser 1943), *Medicago sativa* (Grun 1951), *Poa* spp. (Grun 1952), *Endymion non-scriptus* and *Hyacinthus orientalis* (Elliott 1955, 1958), *Tradescantia bracteata* and *Uvularia perfoliata* (Dowrick 1957), *Poa annua* (Hovin 1958), and *Picea abies* (Eriksson et al. 1970).

As can be seen from the list of collections studied, many of the *Hierochloë* plants studied were taken from far distant original sites. It can be presumed they were adapted to temperatures, humidity, day-length, etc., other than those prevailing in the open in Lund or in the Arktisk Hus in Copenhagen. Occasional low temperatures, heavy rainfall, etc., may also affect a plant at a critical stage of meiosis, though not plants at other stages. The modifying effect cannot, however, be estimated within this study.

It is also a well-known fact that meiosis in different specimens of the same taxon may vary considerably. This was shown for instance in *Poa* spp. (Grun 1952), *Endymion non-scriptus* and *Hyacinthus orientalis* (Elliott 1955, 1958), and *Phleum pratense* (Simonsen 1972).

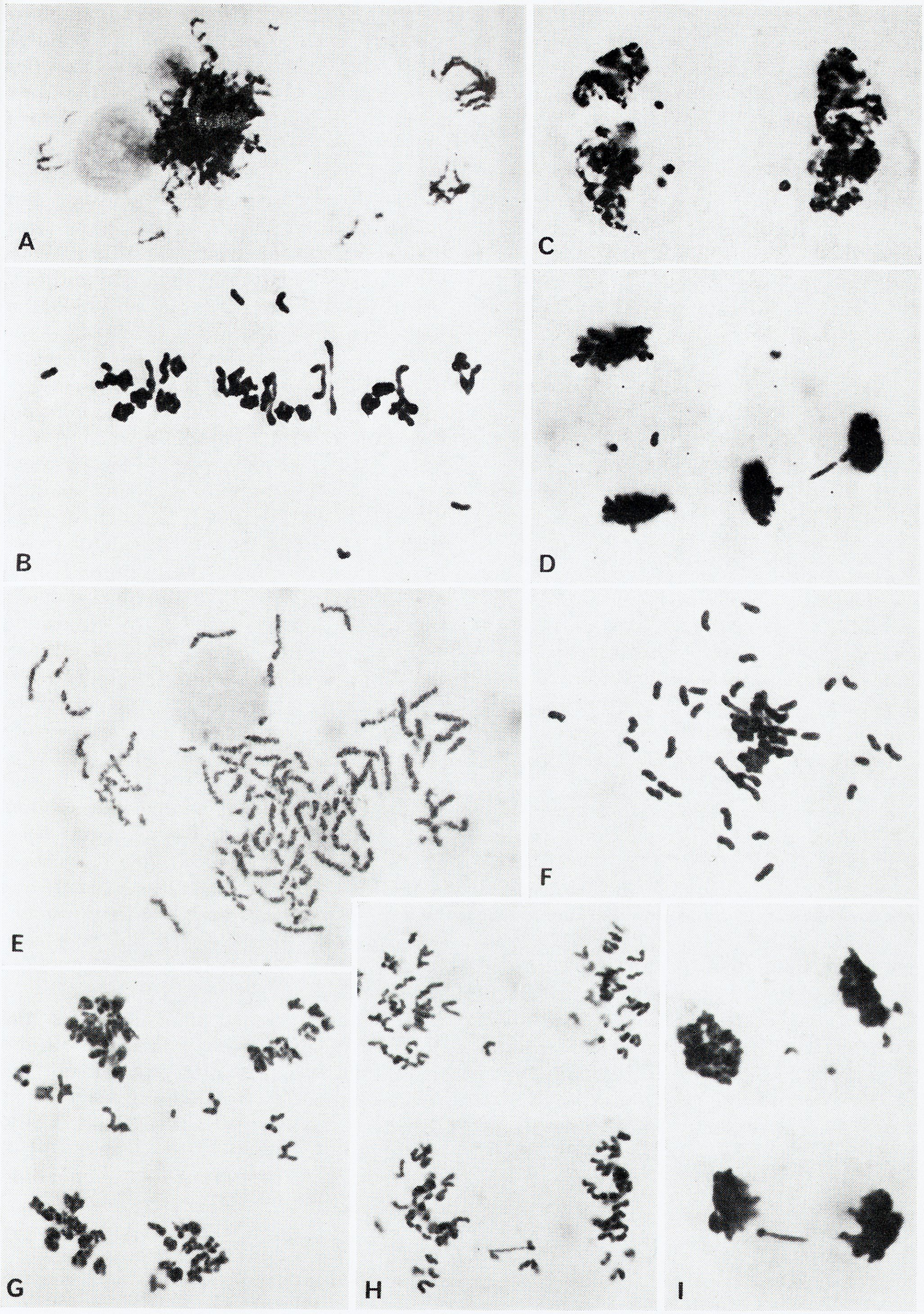
When a limited number of plants and collections per taxon are studied, as in the present paper, there is the risk of non-representative sampling. Too much generalization should therefore be avoided.

Types of Aberration Found

The few cases where an approximately double chromosome number in PMCs of *Hierochloë alpina* ssp. *alpina* and ssp. *orthantha* were found have probably been caused by endoduplication in some archesporial cells intermingled with normal ones.

Poor pairing was found in all taxa except *H. australis* and was more apparent at higher levels of polyploidy. Pairing between segments from more than two chro-

Fig. 10. Pollen mother cells of *Hierochloë*. — A—D: *H. hirta* ssp. *hirta,* A G S. — E—H: *H. hirta* ssp. *arctica,* A A U. — I: *H. hirta* ssp. *arctica,* A R I. — A: Pachytene, probably abortive; 1 big and 1 small nucleolus; some chromosomes fragmented. — B: Metaphase I; 5_{I}. — C: Dyad, possibly tripolar; 4 micronuclei. — D: Anaphase II, abnormal polarity; bridge and fragment in one cell, 2 lagging chromatids in the other. — E: Diakinesis, abortive; no synapsis; some chromosomes fragmented. — F: Metaphase I; 26_{I}. — G: Anaphase I, quadripolar; 15 lagging chromatids. — H: Anaphase II; 3 lagging chromatids, one of them misdividing. — I: Anaphase II; bridge in one cell, fragment and lagging chromatid in the other. — ×1000.


A
C
B
D
E
F
G
H
I

mosomes was visible at tetraploid and higher levels. In one cell of *H. alpina* ssp. *alpina* four chromosomes were found paired two and two in different combinations in adjacent segments.

A single case of loop formation at pachytene indicating inversion heterozygosity was found in the *H. hirta* ssp. *hirta* collection A G S. The frequency of loops may well be far higher than indicated by this single finding, because loops were difficult to distinguish with certainty.

Distal localization of the chiasmata was found in the PMCs of *H. australis*. Fragments found together with bridges were very small, as could be expected.

Distal localization is likely to strongly restrict the recombination of genetic material in the pollen, since the chromosomes are recombined in almost entire blocks. The biological effect of localization is impossible to determine so long as the formation of chiasmata is not known in female meiosis. Different localization of chiasmata in male and female meiosis are known in a number of cases, for example in *Allium pallens* (Ved Brat 1966 pp. 34, 35).

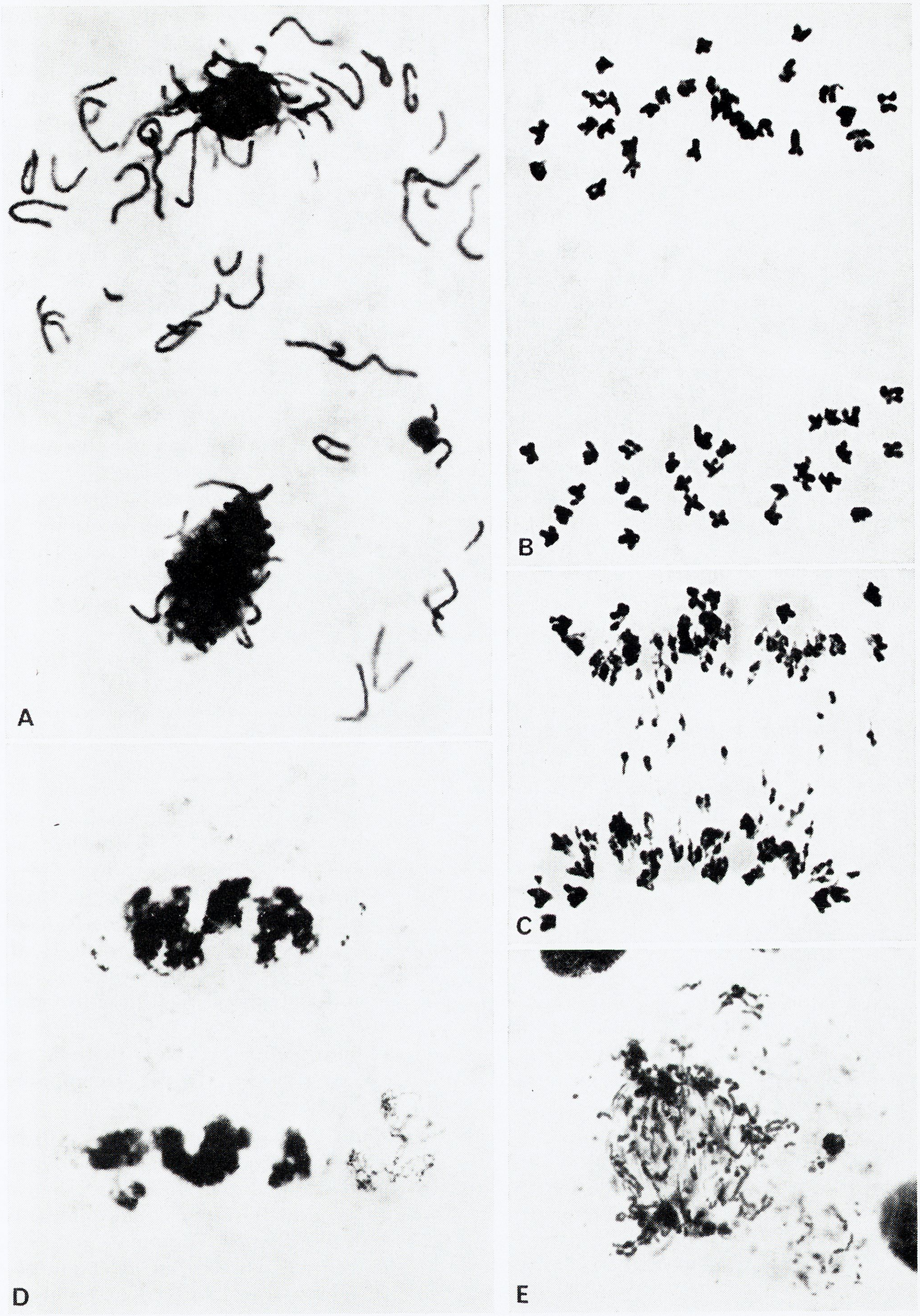
It cannot be completely excluded that more than one chiasma per chromosome arm is regularly formed and very early terminalised, thus giving the impression of there being at most one per arm. The frequent occurrence of interstitial chiasmata in all taxa but *H. australis* does not, however, support such a hypothesis, and I consider it unlikely. From Table 2 can be seen that terminalisation (in terms of the quotient rod/rod+cross bivalents) in *H. repens* and *H. odorata* ssp. *odorata* usually increases between diakinesis and metaphase I but was never found to be complete at the last-mentioned stage.

Univalents at diakinesis and metaphase I occurred in all taxa, in some of the high polyploids at high frequencies. The few univalents in *H. australis,* where the number of chiasmata is slightly less than 1 per chromosome arm, might well have originated if chiasma formation happened to fail in both arms of a chromosome pair simultaneously. The frequencies of ring bivalents, rod bivalents, and univalents found do not contradict such a hypothesis.

Univalents can occur in polyploids if homologous chromosomes or chromosome segments in, for example, a tetraploid individual form $1_{III}+1_{I}$. Such cases were found rarely in *H. odorata* ssp. *odorata,* collection A E F, and in *H. repens,* collection B E S. Homology between chromosomes or chromosome segments cannot, however, be the sole explanation of why such high numbers of univalents were found in my material at hexaploid level and higher. There is an obvious connection with the low number of chiasmata per chromosome arm which is already indicated at diploid and tetraploid level and accentuated at higher polyploid levels. A small number of PMCs in *H. odorata* ssp. *baltica, H. hirta* ssp. *hirta* and ssp. *arctica,* and *H. alpina* ssp. *alpina* showed no synapsis at all. One embryo sac mother cell of the at least almost obligately apomictic *H. hirta* ssp. *arctica* collection A N C (Weimarck 1967 a p. 227, as "octoploid *H. odorata*") showed practically no synapsis. Whether this is a case of asynapsis or desynapsis is impossible to determine.

In some of the plants studied the chiasma frequency was roughly the same at diakinesis and at metaphase I, but the frequency was significantly lower at metaphase I in B D S, B C D and A M K ($p < 0.001$) and in B C C and B E S ($0.001 < p < 0.01$) (Table 2). A possible

Fig. 11. Pollen mother cells of *Hierochloë*. — A—D: *H. alpina* ssp. *alpina,* B G F. — E: *H. alpina* ssp. *alpina,* B F U. — A: Pachytene; 1 big, 1 medium-sized and 1 small nucleolus; some chromosomes fragmented. — B: Anaphase I, regular; segregation of chromosomes 28: 28. — C: Anaphase I, sticky. — D: Dyad; abnormal nuclei; some chromosome material (bottom right) at pachytene-like stage. — E: Anaphase I, abortive. — ×1000.


A
B
C
D
E

explanation is that chiasmata were loosely formed and easily broke up precociously.

Some chromosome associations at diakinesis in the *H. odorata* ssp. *baltica* collection A F L (p. 16; Fig. 9 C; Table 2) showed striking similarities to associations found in cells of *Allium amplectens* (Levan 1940 p. 360; Fig. 3), where zygotene pairing was normal-looking, but no chiasmata were formed. The homologous chromosomes were still placed together showing residual pairing at diplotene and diakinesis due to their relational spiralization.

Li et al. (1945) found that desynapsis in their *Triticum* material had a simple Mendelian recessive character. Prakken (1943 pp. 487, 488) refers to a number of similar cases. All these are mutants of amphimictic taxa. In the present apomictic material the poor synapsis is likely to be of a more complex origin.

In the *H. hirta* ssp. *hirta* and ssp. *arctica* collections the numbers of chiasmata per cell given in Table 2 are not representative values but are merely examples of how low the values can be. The technical difficulties at these levels of polyploidy bias the values because only the PMCs with many univalents and thus a low number of chiasmata were possible to analyse. Cells with clustered chromosomes impossible to analyse are likely to have in general a greater number of chiasmata. The mean number is nevertheless certainly far below 1 per chromosome arm.

The values for the two diakinesis cells of *H. odorata* ssp. *baltica,* although likely to be non-representative for the same reason as mentioned above, may still not be low enough (cf. above).

The univalents seemed usually not to be attached to the spindle by their kinetochore at metaphase I. They tended to be distributed more or less "at random" (cf. Östergren & Vigfússon 1953) in the cytoplasm outside the metaphase plate. Most of them were found to lag behind during the anaphase movement, and those not already in a position adjacent to the spindle poles were not included in the daughter nuclei at telophase. That not all univalents were excluded can be seen from a comparison between Figs. 1 and 2. The uneven segregation of chromosomes (Table 3) which was common in the hexaploids and higher polyploids is most likely to be mainly due to "random" distribution of univalents. In some PMCs bivalents lagged behind too. Asymmetrically separating multivalents may also contribute to the uneven distribution.

The univalent B-chromosomes of the *H. repens* collection B C D divided frequently at anaphase I, and the chromatids could move to the poles (Fig. 8 I). This contrasts to the findings of Östergren (1947), who studied B-chromosomes in the related genus *Anthoxanthum.* The B-chromosomes of *A. aristatum* never divided into chromatids at anaphase I.

The formation of fragments at anaphase I can be explained in at least four ways: (1) as a result of crossing-over within the inversion of a heterozygote for a paracentric inversion; the fragment is accompanied by a bridge; (2) as a result of a U-type bridge implying chromatid breakage and false reunion; the fragment is accompanied by a bridge; (3) as a result of an E-type bridge implying crossing-over in a non-inverted segment translocated from one chromosome arm to the other; the fragment is accompanied by a bridge and is of the size of an entire chromosome; and (4) as a result of chromatid or sub-chromatid breakage without reunion; the fragment is not accompanied by a bridge.

I found it impossible to distinguish between the two first-mentioned possibilities. Due to the small size of the chromosomes it was unfortunately not possible to measure the exact length of the fragments and so get information on whether an inversion of a certain length was involved in each case (cf. Brandham 1969 a). If all bridges and

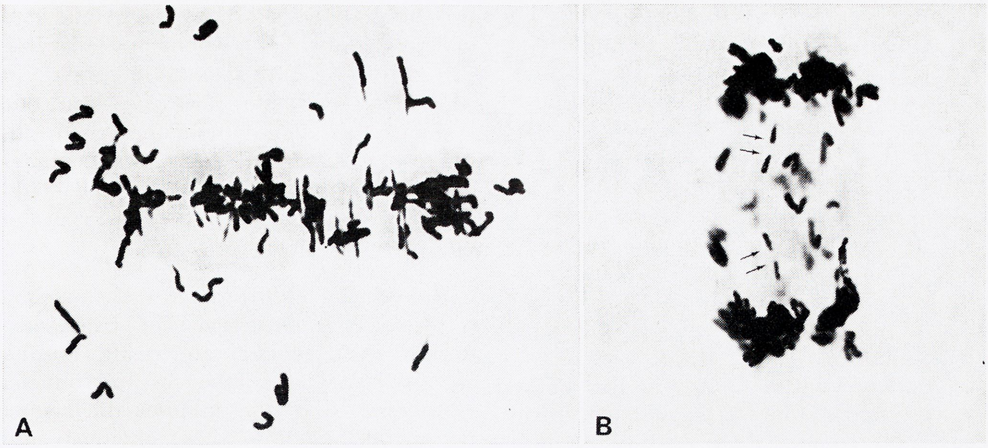


Fig. 12. Pollen mother cells of *Hierochloë alpina* ssp. *orthantha,* B F D. — A: Metaphase I—early anaphase I; approximately the double chromosome number. — B: Anaphase I; lagging chromatid arms (arrows) presumably due to stickiness. — ×1000.

fragments in, for example, *H. odorata* ssp. *baltica, H. hirta* ssp. *arctica* and *H. alpina* ssp. *orthantha* were postulated to be caused by crossing-over in structurally heterozygous plants, the heterozygosity would be very pronounced. The number of chiasmata was so relatively restricted that one would not otherwise expect such high frequencies of bridge and fragment formation (Fig. 6). It is most likely that some of the observed bridges and fragments were caused by breakage and reunion. This mechanism was observed in *Secale* by Rees and Thompson (1955). Its importance was especially stressed by John and Lewis (1965 pp. 27—32).

One PMC of the *H. odorata* ssp. *baltica* collection AFL contained two bridges and fragments. The bridges were attached to both chromatids of the same arm of two homologues. The fragments seemed to be of equal size. The occurrence of a double breakage and the reunion of four chromatids may be less plausible than two chiasmata in an inverted segment (cf. Brandham 1969 a p. 278). This contrasts, however, with the general impression that at most one chiasma is formed per arm.

The E-type bridge explanation of the formation of bridge and fragment seems less plausible in this material. Fragments in *Hierochloë* are usually fairly small. The E-type bridge was originally described (Brandham 1969 b) from acrocentric chromosomes of the Aloïneae (Liliaceae).

Some cases of a fragment without a bridge at late anaphase I may have had a bridge which had been broken and drawn into the anaphase groups. Fragmentation without reunion is, however, likely to be responsible for most fragments without bridges at early and mid-anaphase. Some PMCs at pachytene showing the chromosomes broken up into short pieces point to an apparent tendency to spontaneous breakage. Such cells were often found in *H. alpina* ssp. *alpina* and ssp. *orthantha* but were also found in other taxa.

The genus *Hierochloë* contains coumarin, probably in a glucoside form (Hegnauer 1963 pp. 165, 478). Coumarin is known to cause chromosome breakage under experimental conditions. It should be checked whether coumarin occurring as a natural component of the plant could have any such effect.

The occurrence of a bridge without a

fragment can be explained as being the result of (1) the formation of a bridge and such a small fragment that it has escaped detection; (2) sub-chromatid breakage and reunion, giving a side-arm bridge (see HENEEN 1972 for discussion and references); and (3) stickiness.

Typical sticky bridges at anaphase I were frequent in the *Hierochloë odorata* ssp. *odorata* collection A H B. They also occurred but were rare in all other taxa. Most of them also showed sticky bridges at anaphase II. In *H. alpina* ssp. *alpina* and ssp. *orthantha* especially the sticky association could be so strong that acentric aggregates composed of ruptured homologous chromosome arms lagged between the anaphase groups.

A bridge with two side arms at anaphase I in the *Hierochloë alpina* ssp. *orthantha* collection B F P may be due to stickiness but can also be the result of a sub-chromatid breakage and reunion. A third possibility is that it represents an E-type bridge. The corresponding fragment could, however, not be identified with certainty.

To sum up, there is some evidence indicating both structural heterozygosity and breakage and reunion at the chromatid and sub-chromatid level in the material. BRANDHAM (1970), who studied chromatid and sub-chromatid aberrations in the Aloïneae (Liliaceae), suggested that both types of aberration are produced by four-strand sub-chromatid breakage at a chiasma.

The occurrence of tri- and quadripolar anaphases I and dyads in *Hierochloë odorata* ssp. *baltica, H. hirta* ssp. *hirta* and *H. alpina* ssp. *alpina* and ssp. *orthantha* may be caused by the presence of genomes from different parent species and which form separate spindles.

One dyad cell of the *Hierochloë alpina* ssp. *alpina* collection B G F contained some prophase chromosome material (Fig. 11 D). This asynchrony may be connected with the tendency in the plant to have two nucleoli per PMC at pachytene and diakinesis. Such a phenomenon was observed by A. WEIMARCK (in press) in octoploid, synthetic *Triticale*. In one strain of this allopolyploid the synchronisation of the *Triticum* and *Secale* genomes operating in one and the same cell could be upset in the presence of one rye and one wheat nucleolus.

Micronuclei at the dyad stage are the result of the occurrence of fragments, torn-off bridges and, above all, lagging chromatids. The number of micronuclei is far less than the number of lagging chromatids. Each of these obviously did not form a separate micronucleus but clustered together. It is also possible, but not very likely, that some chromatids classified as lagging at anaphase I would have eventually been incorporated in the dyad nuclei.

Some of the lagging chromatids at anaphase II probably represent univalents that divided precociously at anaphase I. However, it may also be possible that chromosomes more or less randomly incorporated in the daughter nuclei after the first division do not function normally in the second division when they do not occur in even genomes.

A few cases of misdivision at anaphase II were seen (Fig. 10 H).

Bridge and fragment formation at anaphase II can follow loop formation at anaphase I (LEWIS & JOHN 1963 p. 63, BRANDHAM 1969 a pp. 276, 277, 281). The case of a bridge occurring in one of the two anaphase cells and a fragment in the other (Fig. 10 I) may be explained as being the result of either a two-chromatid inversion bridge at anaphase I showing stickiness or false reunion at anaphase II, or sister strand union at anaphase I. In both alternatives the bridge would have been incorporated in one dyad cell and the fragment in the other. They may in such a case also be of independent origin.

Table 2. Configuration, chiasma frequency, and terminalization observed at diakinesis (Diak.) and metaphase I (M I).

Taxon	Collection	Stage	Number of PMCs	% of all configurations				Number of chiasmata per PMC		Number of chiasmata per chromosome arm	p-value of difference between Diak. and M I	Quotient rod/rod+cross bivalents
				IV	III	II	I	Range	Mean			
H. australis 2n=14	A H T	Diak.	28	.	.	100.0	.	12—14	13.6	0.97	$0.1 < p < 0.2$	1.00
		M I	89	.	.	96.5	3.5	10—14	13.4	0.96		1.00
	B B A	Diak.	40	.	.	99.3	0.7	12—14	13.8	0.99	$0.9 < p$	1.00
		M I	64	.	.	100.0	.	12—14	13.8	0.99		1.00
	B B C	Diak.	3	.	.	100.0	.	12—14	13.3	0.95	$0.9 \cong p$	1.00
		M I	31	.	.	99.1	0.9	12—14	13.4	0.96		1.00
H. repens 2n=28	B C C	Diak.	32	.	.	100.0	.	23—28	26.6	0.95	$0.001 < p < 0.01$	0.09
		M I	15	.	.	100.0	.	21—28	24.8	0.89		0.10
	B D S	Diak.	8	0.9	.	99.1	.	20—24	21.6	0.77	$p < 0.001$	0.32
		M I	53	0.2	.	99.1	0.8	14—20	17.2	0.61		0.63
	B E S	Diak.	10	.	.	100.0	.	18—26	21.0	0.75	$0.001 < p < 0.01$	0.36
		M I	30	0.2	0.2	95.3	4.4	14—21	17.8	0.64		0.43
H. repens 2n=28+2B	B C D	Diak.	51	.	.	99.7	0.3	15—24	19.1	0.68	$p < 0.001$	0.32
		M I	63	.	.	99.0	1.0	14—21	17.8	0.64		0.56
H. odorata ssp. *odorata* 2n=28	A M K	Diak.	20	.	.	100.0	.	21—27	23.4	0.84	$p < 0.001$	0.15
		M I	11	.	.	100.0	.	17—24	20.3	0.73		0.13
	A E F	Diak.	28	4.2	.	95.2	0.5	22—27	24.6	0.88	$0.8 < p < 0.9$	0.40
		M I	52	4.0	0.3	95.4	0.3	19—28	24.6	0.88		0.66
	B D I	Diak.	14	.	.	100.0	.	21—26	22.9	0.82	$0.02 < p < 0.05$	0.24
		M I	6	.	.	97.6	2.4	18—23	20.5	0.73		0.40
	A D E	Diak.	3	.	.	100.0	.	28	28.0	1.00	—	—
		M I	3	.	.	100.0	.	23—25	24.0	0.86		0.25
H. odorata ssp. *baltica* 2n=42	A F L	Diak.	2	5.7	48.6	25.7	20.0	31—41	36.0	0.86	—	0.33
H. hirta ssp. *hirta* 2n=56	A G S	M I	1	31.8	4.5	50.0	13.6	45	45.0	0.80	—	0.43
	B H P	M I	1	12.0	8.0	72.0	8.0	43	43.0	0.77	—	0.25
H. hirta ssp. *arctica* 2n=56	A R I	M I	9	1.0	7.0	43.0	49.0	19—30	24.9	0.44	—	0.72

Table 3. Segregation of chromosomes at anaphase I. B-chromosomes of the *H. repens* collection B C D are not taken into account.

Taxon	Collection	Number of PMCs studied	Number of PMCs	One anaphase group	Other anaphase group	Lagging chromosomes	Bridges
Hierochloë australis 2n=14	A H T	20	20	7	7	.	.
	B B C	21	20	7	7	.	.
			1	6	6	.	1
H. repens 2n=28	B D S	32	26	14	14	.	.
			6	13	13	.	1
	B E S	10	8	14	14	.	.
			1	15	13	.	.
			1	13	13	.	1
H. repens 2n=28+2B	B C D	79	72	14	14	.	.
			1	15	13	.	.
			3	14	13	1	.
			1	13	13	2	.
			2	13	13	.	1
H. odorata ssp. *odorata* 2n=28	A M K	1	1	14	14	.	.
	A E F	17	16	14	14	.	.
			1	13	13	.	1
	B D I	4	4	14	14	.	.
	A D E	3	3	14	14	.	.
H. odorata ssp. *baltica* 2n=42	A M C	8	1	21	21	.	.
			1	21	20	1	.
			1	20	19	3	.
			1	20	18	4	.
			1	21	17	4	.
			1	17	17	8	.
			1	19	18	3	1
			1	17	17	6	1
	A F L	9	2	21	21	.	.
			1	22	20	.	.
			1	23	19	.	.
			2	26	16	.	.
			1	21	20	1	.
			1	20	20	2	.
			1	20	19	3	.
H. hirta ssp. *hirta* 2n=56	A G S	1	1	28	27	1	.
	B H P	4	1	28	28	.	.
			1	30	26	.	.
			1	24	21	11	.
			1	26	23	3	2
H. hirta ssp. *arctica* 2n=56	A R I	5	2	28	27	1	.
			2	27	27	2	.
			1	29	24	3	.

Taxon	Collection	Number of PMCs studied	Number of PMCs	One anaphase group	Other anaphase group	Lagging chromosomes	Bridges
H. alpina ssp. *alpina* 2n=56	B G F	7	1	28	28	.	.
			1	28	27	1	.
			1	29	27	.	.
			1	29	26	1	.
			1	27	27	2	.
			1	30	25	1	.
			1	31	25	.	.
	B F U	12	2	28	28	.	.
			1	28	26	2	.
			1	28	25.5	2.5	.
			1	29	27	.	.
			1	29	24	1	1
			1	27	27	2	.
			1	27	25	.	2
			1	26	25	5	.
			3	30	26	.	.
H. alpina ssp. *alpina* 2n=66	B D R	1	1	29	27	6	2
H. alpina ssp. *alpina* 2n=76	B H I	4	1	39	37	.	.
			1	39	36	1	.
			1	38	36	2	.
			1	37	35	4	.
H. alpina ssp. *orthantha* 2n=63	B F D	1	1	24	23.5	15.5	.
	B F P	1	1	30	26	7	.

Micronuclei in tetrads result from laggards, parts of bridges, fragments and other eliminated material such as persisting micronuclei since the dyad stage. Supernumerary chromosome material in one tetrad cell or uninucleate pollen grain can be expected to be missing in one of the other three. Thus the presence of one micronucleus in a tetrad indicates that two pollen grains out of four are likely to be aberrant. The other two grains may be unaffected unless other aberrations have affected their genetic constitution. This should be borne in mind when comparing the sometimes high numbers of micronuclei in tetrads with the percentages of stainable pollen. It is also possible that pollen from high polyploid plants is fairly tolerant towards at least minor deviations in the content of genetic material. Further, determination of pollen stainability by the cotton blue method is usually held to give values that are too high when used as an estimate of "pollen fertility".

The diameter of pollen grains generally increases with level of polyploidy (Table 4). The standard deviation found is mostly 2.5 or lower in amphimictic taxa, mostly 2.5 or higher in apomictic ones.

Embryo sacs in anthers of *Hierochloë* were reported on earlier by WEIMARCK (1967 a p. 227, 1967 b p. 450, 1970 c pp. 498, 500).

Male meiosis could be even more disturbed than is immediately clear from

Table 4. Percentage of stainable mature pollen. Pollen diameter in μ; mean and standard deviation.

Taxon	Collection	% stainable pollen											Pollen diameter	
		0	10	20	30	40	50	60	70	80	90	100	Mean	S. D.
H. australis 2n=14	A H T	.	.	.	.	.	.	.	.	×	.		26.4	1.9
	B B A	.	.	.	.	.	.	.	.	×	.		28.0	1.9
	B B C	.	.	.	.	.	.	.	.	×	.		26.5	2.0
H. repens 2n=28	B C C	.	.	.	.	.	.	.	.	×	.		28.7	2.0
	B D S	.	.	.	.	.	.	.	.	.	×		27.9	2.5
	B E S	.	.	.	.	.	.	.	×	.	.		27.0	2.0
H. repens 2n=28+2B	B C D	.	.	.	.	.	.	.	×	.	.		26.1	2.2
H. odorata ssp. *odorata* 2n=28	A M K	.	.	.	.	.	.	.	×	.	.		28.4	2.0
	A H B	.	.	.	.	.	×	.	.	.	.		30.0	2.3
	A E F	.	.	.	.	.	.	×	.	.	.		30.2	2.5
	B D I	.	.	.	×	.	.	.	.	.	.		30.2	3.1
	A D E	.	.	.	.	.	.	.	.	×	.		34.1	2.0
H. odorata ssp. *baltica* 2n=42	A M C	.	.	.	.	.	.	.	×	.	.		34.6	3.0
	A F L	×	.	.	.	.	.	.	.	.	.		33.0	2.5
H. hirta ssp. *hirta* 2n=56	A G S	.	.	.	.	×	.	.	.	.	.		36.8	2.8
	B H P	.	.	.	.	.	.	.	×	.	.		33.3	2.4
H. hirta ssp. *arctica* 2n=56	A A U	.	.	.	.	.	×	.	.	.	.		30.4	3.2
	A R I	×	.	.	.	.	.	.	.	.	.		—	
	A K K	.	.	.	.	.	.	×	.	.	.		38.1	3.4
H. alpina ssp. *alpina* 2n=56	B G F	.	.	.	.	.	.	.	.	×	.		34.8	3.1
	B F U	.	.	.	.	.	.	.	×	.	.		33.7	2.4
H. alpina ssp. *alpina* 2n=66	B D R	.	.	.	.	.	.	.	×	.	.		35.3	2.5
H. alpina ssp. *alpina* 2n=76	B H I	.	.	.	×	.	.	.	.	.	.		42.2	3.3
H. alpina ssp. *orthantha* 2n=63	B F D	.	.	.	.	.	.	.	×	.	.		36.3	2.8
	B F P	.	.	.	.	×	.	.	.	.	.		35.6	3.8

the diagrams and from Tables 2—4. Degeneration of the archesporium or abortion of PMCs during meiosis could not be studied with accuracy in the squash preparations. The data on abortion were therefore completed for each taxon using sectioned florets from slides originally made for embryological purposes.

Comparisons Between Taxa

Male meiosis in the diploid, facultatively apomictic *Hierochloë australis* was only slightly aberrant. Abortion, univalent formation, stickiness and the formation of bridges and fragments occurred but were infrequent. Female meiosis could be regular, irregular or failing (WEIMARCK 1967 a pp. 212, 214).

The tetraploid, amphimictic *H. repens* displays almost regular male meiosis. Female meiosis was apparently regular (WEIMARCK 1971 a p. 155, and unpubl.).

The plants of the tetraploid, amphimictic *H. odorata* ssp. *odorata* studied were markedly different from each other as to meiotic behaviour. The A H B collection from Bohuslän displayed badly disturbed meiosis, the A M K collection from Jämtland was almost regular. A H B was also found to have irregular female meiosis and irregular development of the embryo sac (WEIMARCK 1967 a p. 220). Male meiosis of the A D E collection from Quebec should be compared with that of the Connecticut plants described by NORSTOG (1963 p. 819). He found his material of tetraploid *H. odorata* to be regular.

The hexaploid *H. odorata* ssp. *baltica* and the octoploid *H. hirta* ssp. *hirta* are obligate or almost obligate apomicts. With regard to male meiosis they are fairly similar and show a high degree of aberrations of all types. Female meiosis of ssp. *baltica* was rare or abnormal (WEIMARCK 1967 a pp. 221, 224).

The octoploid *H. hirta* ssp. *arctica,* which is also apomictic, had very high rates of aberrations. The A K K collection from Minnesota should be compared with NORSTOG's Michigan material (1963 p. 815). He also found severe aberrations at male meiosis. Female meiosis was rare in my material and could be aberrant (WEIMARCK 1967 a pp. 226, 227).

Male meiosis in the octoploid and aneuploid, apomictic *H. alpina* ssp. *alpina* collections and in the enneaploid, likewise apomictic ssp. *orthantha* collections was disturbed to a high degree. As a whole the octoploid ssp. *alpina* and the enneaploid ssp. *orthantha* plants had a greater range of the numbers of aberrations than the aneuploid ssp. *alpina* plants, a fact which seems remarkable. The octoploid ssp. *alpina* plants had, however, greater numbers of unaffected PMCs than the ssp. *orthantha* plants. SØRENSEN (1954 pp. 6—8) reported that *H. alpina* (ssp. *alpina*) in Greenland studied by him produced regular pollen but *H. orthantha* (*H. alpina* ssp. *orthantha*) produced irregular pollen or none at all. JØRGENSEN et al. (1958 p. 12) mention only some irregularity in pollen formation of *H. alpina* (ssp. *alpina).* In my material the difference in pollen quality is not so marked, the octoploid *H. alpina* ssp. *alpina* plants from Greenland being only somewhat less irregular than the ssp. *orthantha* plants.

The 2n=66 collection B D R from Northern Finland was suspected to be not obligately apomictic (WEIMARCK 1970 b p. 263, 1970 c p. 502). A more thorough study of aneuploid *H. alpina* ssp. *alpina* from Northern Scandinavia is being carried out.

Growth Habit, Amphimixis, Apomixis, and Polyploidy

Apomixis often seems to be directly connected with hybridism and allopolyploidy. Relationships between meiotic aberrations, apomixis, and polyploidy are complex. Meiotic aberrations in a polyploid apomict can be mere segregational difficulties due to the number of genomes present, or they may reflect more of the specifically apomictic nature of the plant concerned. Growth habit should also be considered in connection with the mode of reproduction.

Several of the aberrations found in *Hierochloë* seem to be associated with the occurrence of apomixis. Abortion, low chiasma frequency with univalent formation, and stickiness occurred although at low frequencies even in the diploid, facultative apomict *H. australis.* They were most frequent in taxa held to be obligate apomicts. Selection against genes for abnormal meiosis is weaker in an apomict than in an amphimict. Mechanisms that upset female meiosis in favour of unreduced initials may easily have effects on male meiosis also. These effects are normally more pronounced in diplosporous plants than in aposporous ones and more in autonomous than in pseudogamous plants (see, for example, RUTISHAUSER 1967 pp. 63—121 for a survey). Apomixis in *Hierochloë* was claimed to be of the aposporous type although diplospory was suspected in some cases (WEIMARCK 1967 a pp. 214, 227, 228; 1967 b p. 449; 1970 c p. 502).

Hierochloë odorata ssp. *odorata,* although amphimictic, was claimed to be comparable to a facultative apomict (WEIMARCK 1967 a p. 230; 1970 b p. 263). This was based upon its vigorous clonal propagation and a low capacity for setting germinable seed. It is, as are all members of the *odorata* complex, a rhizomatous perennial. Selection against meiotic aberrations can be supposed to be almost as weak as in an apomict. The same is presumably true of *H. repens.*

H. alpina ssp. *alpina* is, as well as *H. australis,* a tufted perennial with a fairly limited length of life. It has somewhat lower rates of aberration than the apomictic members of the rhizomatous *odorata* group. *H. alpina* ssp. *orthantha,* which is a loosely tufted or shortly creeping perennial, has somewhat higher rates of aberration than ssp. *alpina.* It may be possible that the differences in meiotic behaviour reflect differences in growth habit, provided meiosis is of any selective importance for reproduction by caryopses.

NORSTOG (1963) found *H. hirta* ssp. *arctica* in the U.S.A. to be pseudogamous. However, both pollination experiments and chromosome counts of endosperm nuclei have failed to provide adequate information on the occurrence of autonomous or pseudogamous development in my material. Such aberrating male meiosis as found in the present apomictic, polyploid *Hierochloë* can presumably be well tolerated by pseudogamous plants.

The present *Hierochloë* material shows similarities to some of the apomictic groups studied by other authors but differs from other groups. The connection between apomixis and at least some of the aberrations occurring at male meiosis makes it different from, for example, *Sorbus, Rubus* and *Ranunculus.* According to LILJEFORS (1955) amphimictic polyploids and aposporous, pseudogamous polyploids show the same types of aberrations in *Sorbus.* It is therefore probable that the aberrations displayed in *Sorbus* are connected with polyploidy and hybridism. The diplosporous *Rubus caesius* and the facultatively aposporous, pseudogamous *Rubus* group *Moriferi veri* also show meiotic aberrations referable to polyploidy and hybridism (GUSTAFSSON 1942, 1943). The same is true of some taxa within the aposporous, pseudogamous *Ranunculus auricomus* (ROUSI 1956 p. 52). In addition these have still lower chiasma frequencies than *Hierochloë* (ROUSI 1956 p. 23).

The apomictic *Hierochloë* material studied differs from the aposporous, pseudogamous *Poa pratensis* ssp. *alpigena* in forming more uni- and multivalents at a comparable level of polyploidy (NYGREN 1950 pp. 31, 32). However, the high numbers of multivalents found by KIELLANDER (1935 pp. 92—94) in a tetraploid, diplosporous *Poa serotina* (*P. palustris*) are not met with in tetraploid *Hierochloë.*

I have not found such pronounced male sterility in my material as that described in *Poa arctica* ssp. *caespitans* (NYGREN 1950 pp. 16—18) or in diplosporous, autonomous *Calamagrostis* species (NYGREN 1946 pp. 147—169).

Many of the aberration types in apomictic *Calamagrostis* described by NYGREN (1946) were, however, found also in apomictic *Hierochloë.* Male meiosis in the amphimictic, tetraploid *Hierochloë* taxa are also reminiscent of that in amphimictic *Calamagrostis* species studied by NYGREN (1946 pp. 135—145). The representatives of both genera have about the same chiasma frequency and show roughly the same types of configurations at the tetraploid level. *Calamagrostis epigeios* forms, however, more quadrivalents.

Concerning the numbers of univalents and multivalents, male meiosis in the present *Hierochloë* material seems rather similar to that occurring in amphimictic and diplosporous, pseudogamous *Poa alpina* (MÜNTZING 1940 pp. 123—125, 136, 137). MÜNTZING does not, however, report on other types of aberration such as stickiness, abortion and fragmentation.

A very remarkable fact is that I have never found aneuploidy in my material of the *Hierochloë odorata* complex. Aneuploidy was found in *H. alpina* ssp. *alpina* from Northern Fennoscandia (WEIMARCK 1970 a, 1971 a p. 160, this paper and unpubl.). In ssp. *orthantha* one aneuploid collection was found (WEIMARCK 1971 a p. 163).

Structural Heterozygosity, Auto- and Allopolyploidy

The great number of multivalents observed in plants at hexaploid and higher levels of polyploidy indicates a high degree of homology, or at least homoeology between genomes or chromosome segments, provided that non-homologous associations do not occur. Homologous chromosome segments in different pairs causing multivalent formation can be due to translocations. Those bridges and fragments believed to be due to inversions indicate structural heterozygosity in the plants studied. Those which may be due to breakage and fusion indicate structural lability.

The prevailing formation of bivalents in the tetraploid taxa suggests they are not autopolyploid. The cases of tri- and quadrivalents indicate that their allopolyploidy may be segmental in the sense of STEBBINS (1947 p. 419). The frequent occurrence of only one quadrivalent in the *Hierochloë odorata* ssp. *odorata* collection A E F is notable. It may indicate a certain homologous segment of a considerable size in two chromosome pairs of an otherwise allopolyploid plant, perhaps as a result of a translocation. It is necessary to display caution when interpreting this, however. Genes prohibiting and controlling pairing between homoeologous chromosomes in a polyploid are known in several cases, for example in *Triticum aestivum* (SEARS & OKAMOTO 1958, RILEY & CHAPMAN 1958, DRISCOLL 1972).

H. odorata ssp. *baltica* was presumed to be a derivative from ssp. *odorata* evolved recently in geological terms and having acquired apomictic reproduction (WEIMARCK 1971 a p. 146). If the concept of ssp. *odorata* as a segmental allotetraploid is true, ssp. *baltica* should be an autoallohexaploid. This fits in well with the facts known. The occurrence of multivalents and the great similarity to ssp. *odorata* in external morphology (WEIMARCK 1971 a pp. 141—146) and chromatographic pattern (WEIMARCK 1970 b p. 264) point to autopolyploidy. The occurrence of two nucleoli in some PMCs and of multipolar spindles suggest, on the other hand, the presence of genomes not cooperating in a balanced way.

The two *H. hirta* subspecies may likewise be autoallopolyploids combining characters partly from different ancestors. The assumption is also here based upon pairing conditions and the appearance of nucleoli and spindles as well as on morphological and other evidence. A tentative hypothesis is that *H. australis, H. hirta* ssp. *hirta,* and *H. stepporum* (a taxon closely affined to *H. repens;* see WEIMARCK 1971 a p. 156) might have some genome in common. The most striking similarity is that they share members of a characteristic spot group found by thin layer chromatography (WEIMARCK 1970 b p. 236, 1971 a pp. 149, 156). Some other characters, for example the somewhat similar type of bristle on the lemma of male florets and a preference for drier habitats compared with other members of the *odorata* group, do not speak against this hypothesis. It should be tested further by crossing experiments. The crosses attempted at the start of the present *Hierochloë* project were all unsuccessful due to technical difficulties, apomixis in most taxa and partial lack of plant material.

The two *H. alpina* subspecies may also be considered to be autoallopolyploids. The origin of the extra genome of ssp. *orthantha* in relation to octoploid ssp. *alpina* is unknown. On account of external morphology and choice of habitat the taxon might hypothetically have received it from some member of the *odorata* group. The extra chromosomes of aneuploid ssp. *alpina* are presumably homologous with those of some of the original genomes. They do not have the appearance of B-chromosomes. I have not found any external or internal character of the plants indicating a foreign source for these chromosomes.

ACKNOWLEDGEMENTS

The field work was made possible by grants from Lunds Universitet, Kungl. Vetenskapsakademiens Enanderfond, and Knut and Alice Wallenbergs Stiftelse. The Greenlandic material was collected with the aid of Grønlands Botaniske Undersøgelse and Grønlands Geologiske Undersøgelse. Thanks are also due to those who have collected material for me in the field. Cultivation facilities were put at my disposal in the Botanical Gardens, Lund, and in the Arktisk Hus, Copenhagen. The laboratory work was financed by Kungl. Fysiografiska Sällskapet, Lund, and was carried out by Mrs. I. Larsson, Miss E. Persson, and Miss I.-L. Svensson.

Mr. B. Bentzer, Mr. R. von Bothmer, Dr. P. Brandham, Dr. W. K. Heneen, Professor A. Levan, and Dr. J. Sjödin discussed the results and gave valuable criticism. Mrs. M. Greenwood-Petersson checked the manuscript.

LITERATURE CITED

Beeks, R. M. 1955. Improvements in the squash technique for plant chromosomes. — Aliso 3: 131—134.

Brandham, P. E. 1969 a. Inversion heterozygosity and sub-chromatid exchange in Agave stricta. — Chromosoma (Berlin) 26: 270—286.

— 1969 b. Chromosome behaviour in the Aloineae. I. The nature and significance of E-type bridges. — Ibid. 27: 201—215.

— 1970. Chromosome behaviour in the Aloineae. III. Correlations between spontaneous chromatid and sub-chromatid aberrations. — Ibid. 31: 1—17.

Dowrick, G. J. 1957. The influence of temperature on meiosis. — Heredity 11: 37—49.

Driscoll, C. J. 1972. Genetic suppression of homoeologous chromosome pairing in hexaploid wheat. — Can. Journ. Genet. Cytol. 14: 39—42.

Elliott, C. G. 1955. The effect of temperature on chiasma frequency. — Heredity 9: 385—398.

— 1958. Environmental effects on the distribution of chiasmata among nuclei and bivalents and correlation between bivalents. — Ibid. 12: 429—439.

Eriksson, G., Ekberg, I. & Jonsson, A. 1970: Meiotic investigations in pollen mother cells of Norway spruce cultivated in a plastic green house. — Hereditas 66: 1—20.

Grun, P. 1951. Variations in the meiosis of alfalfa. — Amer. Journ. Bot. 38: 475—482.

— 1952. Effect of environment upon chromosomeal pairing of some species and hybrids of Poa. — Ibid. 39: 318—323.

Gustafsson, Å. 1942. The origin and properties of the European blackberry flora. — Hereditas 28: 249—277.

— 1943. The genesis of the European blackberry flora. — Lunds Univ. Årsskr. N.F. Avd. 2, 39(6).

Hegnauer, R. 1963. Chemotaxonomie der Pflanzen. 2. Monocotyledoneae. — Basel und Stuttgart.

Heneen, W. K. 1972. Separation difficulties during anaphase I in Elymus (Agropyron) species. — Bot. Notiser 125: 430—438.

Hovin, A. W. 1958. Meiotic chromosome pairing in amphihaploid Poa annua L. — Amer. Journ. Bot. 45: 131—138.

John, B. & Lewis, K. R. 1965. The meiotic system. — Protoplasmatologia VI F 1. — Wien and New York.

Jørgensen, C. A., Sørensen, Th. & Westergaard, M. 1958. The flowering plants of Greenland. — Biol. Skr. 9(4).

Kiellander, C. L. 1935. Apomixis bei Poa serotina. — Bot. Notiser for 1935: 87—95.

Levan, A. 1940. The cytology of Allium amplectens and the occurrence in nature of its asynapsis. — Hereditas 26: 353—394.

Lewis, K. R. & John, B. 1963. Chromosome marker. — London.

Li, H. W., Pao, W. K. & Li, C. H. 1945. Desynapsis in the common wheat. — Amer. Journ. Bot. 32: 92—101.

Liljefors, A. 1955. Cytological studies in Sorbus. — Acta Horti Berg. 17(4): 47—113.

Müntzing, A. 1940. Further studies on apomixis and sexuality in Poa. — Hereditas 26: 115—190.

Norstog, K. 1963. Apomixis and polyembryony in Hierochloë odorata. — Amer. Journ. Bot. 50: 815—821.

Nygren, A. 1946. The genesis of some Scandinavian species of Calamagrostis. — Hereditas 32: 131—262.

— 1950. Cytological and embryological studies in arctic Poae. — Symb. Bot. Upsal. 10(4).

Östergren, G. 1947. Heterochromatic B-chromosomes in Anthoxanthum. — Hereditas 33: 261—296.

— & Vigfússon, E. 1953. On position correlations of univalents and quasi-bivalents formed by sticky univalents. — Hereditas 39: 33—50.

Prakken, R. 1943. Studies of asynapsis in rye. — Hereditas 29: 475—495.

Rees, H. & Thompson, J. B. 1955. Localisation of chromosome breakage at meiosis. — Heredity 9: 399—407.

Riley, R. & Chapman, V. 1958. Genetic control of the cytologically diploid behaviour of hexaploid wheat. — Nature 182: 713—715.

Rousi, A. 1956. Cytotaxonomy and reproduction in the apomictic Ranunculus auricomus group. — Ann. Bot. Soc. Zool. Bot. Fennica, 'Vanamo' 29: 2.

Rutishauser, A. 1943. Untersuchungen über die Fortpflanzung und Bastardbildung apomiktischer Potentillen. — Ber. Schw. Bot. Ges. 53: 5—83.

— 1967. Fortpflanzungsmodus und Meiose apomiktischer Blütenpflanzen. — Protoplasmatologia VI F 3. — Wien and New York.

Sears, E. R. & Okamoto, M. 1958. Intergenomic chromosome relationships in hexaploid wheat. — Proc. Xth Int. Congr. Genetics 2: 258—259.

Simonsen, Ø. 1972. Meiotic properties in populations of hexaploid Phleum pratense. — Hereditas 71: 301—312.

Snow, R. 1963. Alcoholic hydrochloric acid-carmine as a stain for chromosomes in squash preparations. — Stain Techn. 38: 9—13.

Sørensen, Th. 1954. New species of Hierochloë, Calamagrostis and Braya. — Meddr. Grønland 136(8).

Stebbins, G. L., Jr. 1947. Types of polyploids: their classification and significance. — Advances in genetics I: 403—429.

Ved Brat, S. 1966. Genetic systems in Allium. II. Sex differences in meiosis. — In Darlington, C. D. & Lewis, K. R. (eds.): Chromosomes today 1. — New York.

Weimarck, A. in press. Cytogenetic behaviour of 8x Triticale. I. Aneuploidy, meiosis and fertility. — Hereditas 74.

Weimarck, G. 1963. Kromosomtal hos Hierochloë odorata i Skandinavien. — Bot. Notiser 116: 172—176.

— 1967 a. Apomixis and sexuality in Hierochloë australis and in Swedish H. odorata on different polyploid levels. — Ibid. 120: 209—235.

— 1967 b. Apomixis in Hierochloë monticola (Gramineae). — Ibid. 120: 448—455.

— 1970 a. Hierochloë alpina (Gramineae) 2n=66 in Northern Finland. — Ibid. 123: 201—202.

— 1970 b. Spontaneous and induced variation in some chemical leaf constituents in Hierochloë (Gramineae). — Ibid. 123: 231—268.

— 1970 c. Apomixis and sexuality in Hierochloë alpina (Gramineae) from Finland and Greenland and in H. monticola from Greenland. — Ibid. 123: 495—504.

— 1971 a. Variation and taxonomy of Hierochloë (Gramineae) in the Northern hemisphere. — Ibid. 124: 129—175.

— 1971 b. Studies of Hierochloë (Gramineae) in the Northern hemisphere. — Diss. Lund.

APPENDIX

The following collections were studied (collections by the author unless otherwise stated):

Hierochloë australis 2n=14. Finland. Tavastia australis. Hollola, Hahmajärvi, Rautakorpi, southerly slope in dry forest (J. Puro): A H T. — Italy. Höhlensteintal. Landro, steep easterly slope, c. 1420 m s m: B B A. — Romania. Cluj. Aghires (K. Brunsberg): B B C.

Hierochloë repens 2n=28. Romania. Iaşi, Valea lui David. (C. Burduja): B C C. — Romania. Dobrudja. Babadag. Poiana "Calul Mort" (C. Burduja): B D S. — USSR. Minsk. (Bot. Gardens seed exchange): B E S.

Hierochloë repens 2n=28+2B. Czechoslovakia. Senica. Near Borský Mikuláš along road to Šaštín, in sand (J. Vicherek): B C D.

Hierochloë odorata ssp. **odorata** 2n=28. Sweden. Jämtland. Storlien. The station c. 800 m NNW, in open birch forest: A M K. — Sweden. Bohuslän. Stala. Tjuvekilen c. 800 m NNE, in scrub margin: A H B. — Sweden. Skåne. Kågeröd. Knutstorp castle c. 700 m ENE, fen: A E F. — Denmark. Møn. Damsholte. Askeby farm c. 1500 m NW, along ditch in margin of the former lake, Røddinge Sø: B D I. — Canada. Quebec. Kamouraska. Ste Anne-de-la-Pocatière, brackish tidal marsh; cult. in Ottawa (W. G. Dore et al. 17294): A D E.

Hierochloë odorata ssp. **baltica** 2n=42. Sweden. Jämtland. Frösö. Along brook to north part of the lake, Ändsjön, wet forest: A M C. — Sweden. Södermanland. Torö. Storudden, the church c. 1800 m NW, along ditch: A F L.

Hierochloë hirta ssp. **hirta** 2n=56. Sweden. Värmland. Övre Ullerud. The church c. 1000 m W, sandy hill near the river, Klarälven: A G S. — Sweden. Skåne. Bosjökloster. The former Youth Hostel c. 100 m N, open forest near the lake, Ringsjön: B H P.

Hierochloë hirta ssp. **arctica** 2n=56. Finland. Lapponia enontekensis. Enontekiö. Ala Saarikoski, close to River Könkämä, meadow in birch forest: A A U. — Norway. Sör-Tröndelag. Oppdal. Stölan station c. 300 m NE, among bushes in sandy island in River Driva: A R I. — USA. Minnesota. Kittson, Halma c. 5000 m N, wet meadow (J. W. MOORE): A K K.

Hierochloë alpina ssp. **alpina** 2n=56. Greenland. Godthåb. South-west slope of Mount Lille Malene, on rocks: B F U. — Greenland. Søndre Strømfjord. Ridge between · 520 and ⚠ 513: B G F.

Hierochloë alpina ssp. **alpina** 2n=66. Finland. Lapponia enontekensis. Enontekiö. Markkina, old cemetery c. 50 m E, near path: B D R.

Hierochloë alpina ssp. **alpina** 2n=76. Sweden. Torne Lappmark. Jukkasjärvi. Mountains S of Stordalen station, c. 750 m s m (G. SANDBERG): B H I.

Hierochloë alpina ssp. **orthantha** 2n=63. Greenland. Frederikshåb. Head of Nigerdleq fiord c. 4000 m SW, ridge near lake: B F D. — Greenland. Frederikshåb. Nerutussoq fiord, near Akugdleq fiord: B F P.

Frequency Mapping of Blackberry Species (Rubus L. Subgen. Rubus) in Sweden

I. Method and Preliminary Results

By Alf Oredsson

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

ABSTRACT

OREDSSON, A. 1973. Frequency mapping of blackberry species (Rubus L. subgen. Rubus) in Sweden. I. Method and preliminary results. — Bot. Notiser 126: 37—68.

The southern third of Sweden, the only part of the country in which blackberries occur, is divided into squares of 100 km², 1,499 in all. In each square a total stretch of road at least 20 km long has been investigated by means of observations made from a slow-moving car.

In all, nearly 24,000 occurrences were discovered during five summers of field work. For 18 species (the *Corylifolii* group is treated as one species), i.e. 4/5 of the total number known from Sweden, a given minimum frequency is exceeded. Maps show the primary frequency data in detail.

Except for some features common to all species such as preference for coastal habitats, the results are presented for each species individually. Various aspects of frequency are discussed. Co-variation between range, mean frequency and most abundant local occurrence is demonstrated.

INTRODUCTION

The investigation presents a method for assembling data on native bushes, which would serve as a basis for preparing frequency maps of large areas. The method used is a kind of linear investigation the main advantage of which is the saving of time, namely an investigation of roadsides by car. The area investigated is the southern third of Sweden.

STARTING POINT. During an excursion in northern Skåne in 1959, the author found *Rubus scissus,* a species then considered very rare in southern Sweden. As it was found 10 km from its nearest known occurrence, and in a habitat that had nothing remarkable about it, the author decided to investigate if the species really was so rare. This was the starting point of an investigation in which the frequencies of blackberry species in Sweden were mapped.

PREVIOUS KNOWLEDGE. In Europe *Rubus* subgenus *Rubus* is represented by the section *Rubus,* which is generally regarded as one of the taxonomically most difficult groups of phanerogams owing to apomixis. FOCKE (1914 p. 6) estimated the number of named European blackberries as 3,000.

In Sweden, HYLANDER (1955) recognized 42 species within *Rubus* subgenus *Rubus,* namely *caesius* (dewberry), 19 species belonging to the *Corylifolii* group, and 22 other wild blackberries.

During the two decades around the turn of the century a remarkable interest was shown in the blackberry flora of Sweden. Two Swedish floras from that time are outstanding as regards the genus *Rubus,* namely those by LINDMAN (1918, 1926) and NEUMAN (1901). All known taxa are treated in an exhaustive manner and the distribution records are detailed. Both authors regard the majority of blackberry species as rare in Sweden with the exception of 4 or 5 species only. According to the above floras wild blackberries occur in the southern third of Sweden only.

CIRCUMSTANCES FAVOURING THE METHOD

In a previous series of papers (OREDSSON 1969, 1970), the author has endeavoured to show that *Rubus* subgenus *Rubus* is represented in Sweden by distinct taxa, provided that the *Corylifolii* group is treated as a single unit. In fact, during the greater part of the vegetative period the majority of blackberry species can be determined at sight even at some distance, provided that the observer is well acquainted with the species and has been trained in the method of investigation presented here.

Blackberries are perennials with biennial shoots. The stem is 0.5—5 m long, erect, arched, or procumbent. The brambles are generally very conspicuous, often covering an area of several square metres and more. Together these facts make it possible to spot the majority of occurrences of blackberries along roads from a car travelling at slow speed, even in the winter if there is not too much snow.

The principal habitats of blackberries in Sweden are open woodland, meadows, and round the edges of cultivated fields. Some species grow mainly in wet habitats such as ditches, while others appear to prefer dry ground. Older roads generally run through open country, and roads in woodland tracts serve to open up the area they pass through. In addition ditches often run along the edges of roads, whereas in cultivated areas it is often the road itself that forms the borders of fields. Consequently, roads can be regarded as forming an optimum line of investigation for blackberries, even without taking the time-saving aspect into account.

AREA INVESTIGATED

The area investigated, the southern third of Sweden including the islands of Öland and Gotland, comprises a land area of about 150,000 km^2 (almost 40,000 squares miles). The area is bounded in the east, south and west by the sea, in the north-west by part of the Norwegian border, with a northern boundary running from Gävle in the east parallel with the river Dalälven south-westwards to Avesta where it turns due west, past Torsby in the province of Värmland, till it reaches the Norwegian border (Fig. 1).

MAPS USED. The only large-scale map of the whole area to be investigated that was available when the field work was carried out was "Generalstabens karta över Sverige" (Ordnance map) scale 1: 100,000, consisting of a series of maps. In the southernmost part of the area of investigation, a draft series of that map, scale 1 : 50,000 has also been used.

METHOD

The Grid

In order to facilitate the statistical treatment of the results the whole area of investigation was divided into 1,499 standard squares, the side of each square being 10 km (6.2 miles). The grid is defined by longitude 5° west Stockholm which is also the dividing line between two vertical rows of the series of maps, and by the dividing line between two horizontal rows namely those designated "8. Ängelholm" — "12. Ottenby", and "13. Halmstad" — "17. Kalmar" respectively.

The island of Gotland has a separate location on the grid, the northern and the western sides of the map designated "39. Visby" being the lines of definition.

The system of standard squares investigated is continuous on the mainland with the exception of the four great lakes Vänern,

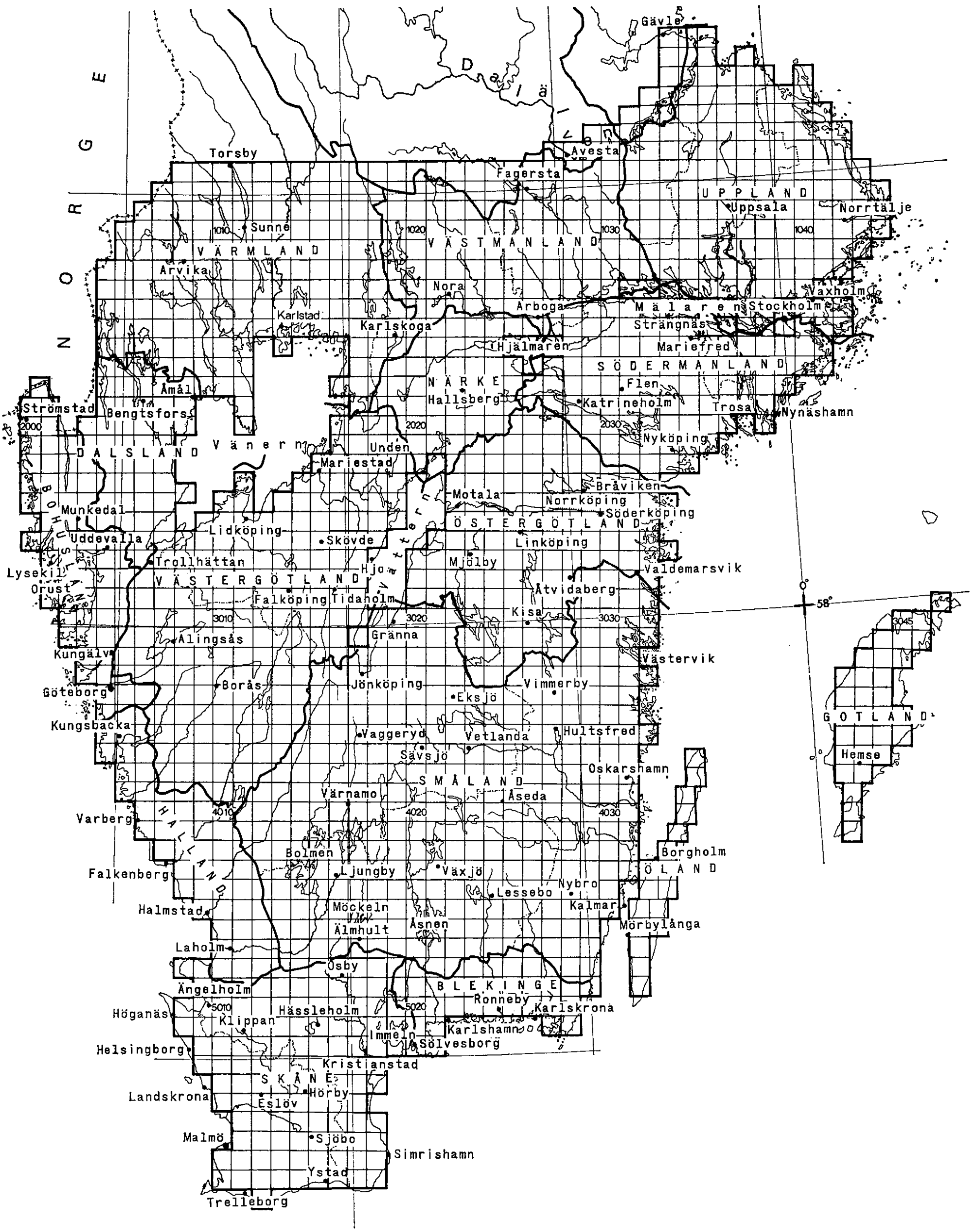


Fig. 1. The area investigated, divided into squares of 100 km². Provinces indicated by capitals and broad boundaries.

Vättern, Mälaren and Hjälmaren, and a populated area of 200 km^2 in the Stockholm area.

Along the coast, potential squares for investigation have as a rule not been investigated where the land area forms less than half a standard square. In a few cases squares have been moved 5 km, either horizontally or vertically in order to secure the required land area. In spite of this the outlying parts of some well-known *Rubus* districts have been cut out.

In the area north of the northern borderline, 27 additional squares shown in Fig. 3, have also been investigated. However, in some cases the stretches of road in the potential squares between the strips of squares investigated do not attain the stipulated minimum length of 20 km. Furthermore, no brambles have been found in these 27 squares. Hence, the author has decided neither to move the northern borderline further north, nor to include the 27 additional squares when dealing with the results.

Selection of Investigation Stretches

In each standard square a stretch of road of at least 20 km has been investigated. Because of differences in density of the road network in the area to be investigated, the minimum distance could not have been much longer if the size of the standard square was to be retained. A corresponding maximum stretch of road was not fixed.

In order to guarantee that the choice of roads was not influenced by the occurrence of blackberries the selection had to be made in advance. Keeping in mind the time-saving requirement, and without too much loss of representativeness, three rules were set up to be used as a guide in the selection of roads.

(1) Choose roads that pass through different parts of the square.

(2) Try to make the investigated stretch continuous, without too much exceeding the minimum distance.

(3) Try to find reasonably good roads, but avoid highways (the traffic being heavier and the upkeep of the roadsides more rigorous).

Streets, of course, were omitted.

Field Technique

Driving at a maximum speed of 40 km an hour (25 m.p.h.), or, when there was an exceptionally clear view, up to 60 km an hour, the author kept a lookout. When brambles were sighted the speed was reduced in order to facilitate the determination of the species. Where there was the slightest doubt the car was stopped for closer inspection.

When field work was carried out, 1959—63, you still drove to the left in Sweden. In the car used the driver's seat is on the left and consequently, the author sat near the left roadside, while the distance from the right side varied according to the width of the road.

Occasionally, where it was not possible to drive the author cycled or walked part of the way.

My map-readers (who succeeded each other about monthly) have made it possible to carry out the investigation. Their work was as follows:

(1) To instruct the author where to drive.

(2) To be able to plot the exact position the whole time.

(3) To mark on the map the occurrences of blackberry species as given by the author.

Locality Concept Used

The term locality denotes the occurrence of a given blackberry species on one or both sides of a road within a section measuring approximately 150 m, irrespective of whether it refers to an isolated plant or whether the brambles are abundant. The breadth of the locality is regulated by the free field of vision. Brambles occasionally sighted at a distance from the road are, however, omitted. The localities of two species sometimes overlap.

FREQUENCY

Data obtained by the above-mentioned method of investigation were standardized to give the average number of localities along 10 km of road for each species in each square as follows:

The number of localities for the species concerned was multiplied by ten, and divided by the total length (in kilometres) of road investigated in that particular square, measured on the map by means of a map-measurer. The result, a decimal fraction, was converted into a whole number as follows:

Decimal, maximum	0.270	1.499	2.499	
Whole number	0	1	2	etc.

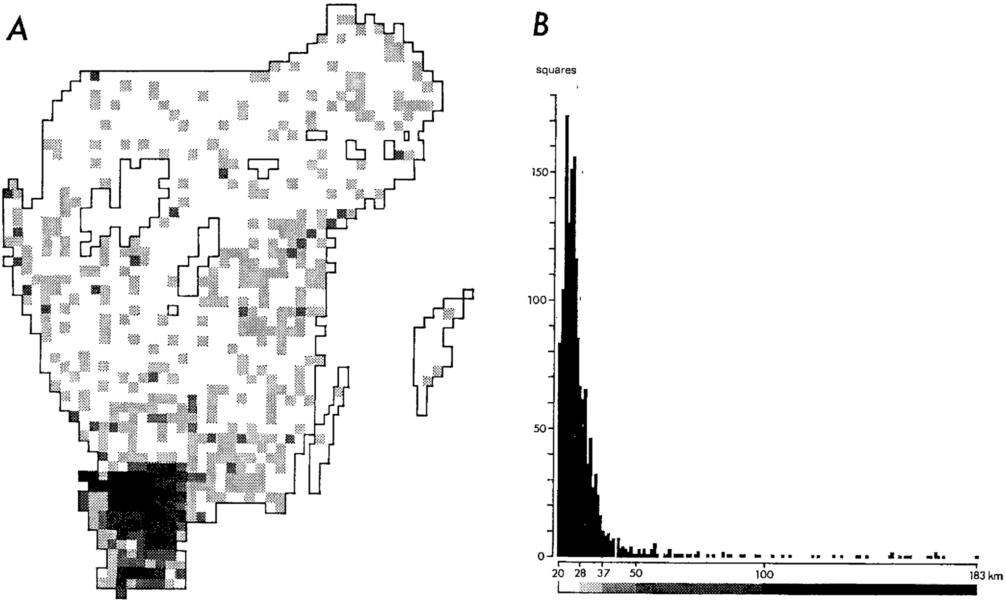


Fig. 2. A: Distribution map showing five categories of length of road investigated, as shown in B. — B: Number of Squares plotted against length of road investigated.

Whole numbers thus obtained, are henceforth referred to as frequencies.

Because of the low zero limit (0.270 instead of 0.499) a single locality has frequency 1 in all squares with an investigation stretch with a maximum length of 36 km (91 % of all squares). On the other hand, the limit is placed sufficiently high to eliminate most of the risk of giving bias to the frequency maps due to local over-representation of frequency 1 as compared with zero, in areas where the length of road investigated was exceptionally long (cf. Fig. 2).

Using the above concepts of locality and frequency the theoretical maximum frequency is 67 (10 km can be divided into 66 2/3 sections of 150 m).

THE COMPREHENSIVENESS OF THE INVESTIGATION

Length of Road Investigated

The total length of road investigated amounts to nearly 44,000 km (over 27,000 miles) and the number of localities registered is nearly 24,000.

Fig. 2 shows the distribution of the squares with respect to the length of road investigated. There are five categories of length as presented below:

Within the individual squares the length varies from 20 km (stipulated minimum) to 183 km. In squares where the length of road investigated is 37 km or longer, as is the case in 129 squares, occasional findings do not always result in a frequency above zero (cf. above). The chance of finding one locality, or two, rather than none, for a given species in a given square increases with the length of road investigated. The great number of squares that represent the interval between 20—36 km may have resulted in a disproportionately large number of squares having frequency 1, as compared with 0-squares, where the distances are long. By placing a dividing line at 28 km the error is reduced to a maximum of 1.35: 1.

Furthermore, variation of frequency

due to chance probably diminishes with an increase of the length of road investigated. If there is a gradual change of real frequency over areas larger than one standard square the prospects of observing the nature of the real change is then best in areas where the length of road investigated is exceptionally long. In order to indicate areas suitable for such studies, the squares where the length of road investigated is 37 km or longer have been divided into three categories, the two additional limits being 50 and 100 km respectively.

Area Investigated Year by Year

In 1959, the method was outlined and tested along a total length of road of nearly 1,700 km in northern Skåne (cf. Oredsson 1959, 1961). During the following four years intensive field work was carried out during the summer months, continuing into the autumn. By late 1963 the whole area of investigation had been covered.

Fig. 3 shows the areas covered during the different years of field work. The southern third of the area investigated, including the island of Öland, was completed as early as 1960, but in the province of Skåne the field work was continued in greater detail up to 1963. The vertical strips of connected squares that in 1961 were investigated up to the final northern borderline and in six cases beyond this, can be used to study the difference, if any, between results from that year and those obtained when filling in the space between the strips. This was done in two stages, in 1962 and in 1963.

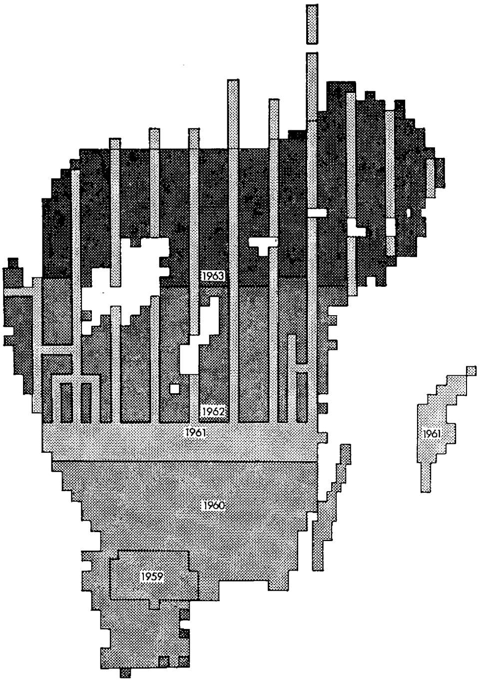


Fig. 3. Areas covered in the different years during the period of field work, 1959—63.

Time Budget

The total expenditure of time amounts to about five years, measured in terms of working days for one man. In Table 1 the total time has been divided into three kinds of work and three periods.

What is termed "preparatory work" consists of selecting roads to be investigated and marking them on the maps (2.5 months in all), and drawing the grid. During the period of field work about 3 weeks a year from 1960—63, were spent

Table 1. Time budget in months. Figures in brackets refer to map-readers.

Year	1959	1960—63	1964—72	Total
Preparatory work	0.5	2.5	.	3
Field work	2 (+2)	18 (+14)	.	20 (+16)
Treatment of data	0.5	4	18	22.5
Total	5	38.5	18	61.5

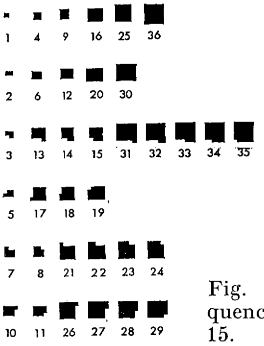


Fig. 4. Symbols of frequency used in Figs. 5—15.

on detailed investigation in Skåne, generally without a map-reader. Up to 1963 "treatment of data" implies measuring the investigation stretches and counting the number of localities for each separate species in each square. After 1963 it includes the calculation of frequencies, the drawing of frequency maps and making duplicates of the maps of the field work. The period after 1963 also includes six months for the writing of a thesis of which this is a part.

DATA BANK

The total distribution of blackberries in Sweden according to the present investigation is shown on maps, one for each of the 18 species with a total frequency above zero (Figs. 5—15). The frequency of each square is represented in the maps by a symbol proportionate in size to the frequency. A special technique for designing the symbols has been developed in order to facilitate identification (Fig. 4).

The frequency pattern, particularly as regards the more wide-spread species, presents such diversity of form that it would be difficult to describe it in words, primarily because of the intricate interplay between neighbouring squares. But then the maps represent a total sum of frequencies of 6,330 distributed among 741 standard squares.

As they are adapted for various kinds of comparison both inter- and intraspecifically the frequencies constitute the whole basis of the results to be discussed.

Reliability of Data

A glance at the frequency maps is enough to show that the distribution of frequencies is not due to chance alone. On the other hand most of the frequencies may well represent various deviations from the (unknown) real value. Nevertheless, it is generally only possible to speculate about the total effect. The author's own views will not be published until the final results of the treatment of data are to hand.

Apart from random variation, which tends to even itself out when frequencies are combined, there are some systematic errors that probably contribute to a lowering of reliability throughout.

GENERAL ERROR. The squares with frequency 1 tend to be over-represented at the expense of 0-squares because of the convertion practice applied (cf. p. 41).

ERRORS BETWEEN SQUARES. Firstly, the low average speed in squares with an abundance of brambles, as well as in squares where an exceptionally long stretch of road was investigated (including some almost impassable roads), probably increased the number of localities found, even though there are counteracting factors. Secondly, the extent to which brambles stand out from their background varies seasonally. Thirdly, differences in length of road investigated give rise to unequal random variation in the frequencies (cf. pp. 41—42).

ERRORS BETWEEN SPECIES. Differences in optimum habitat as well as variation in habit may favour certain species. The status in these respects is indicated in a previous series of papers (Oredsson 1969, 1970).

ERRORS OF INTERPRETATION. Generalization from roadsides to the whole

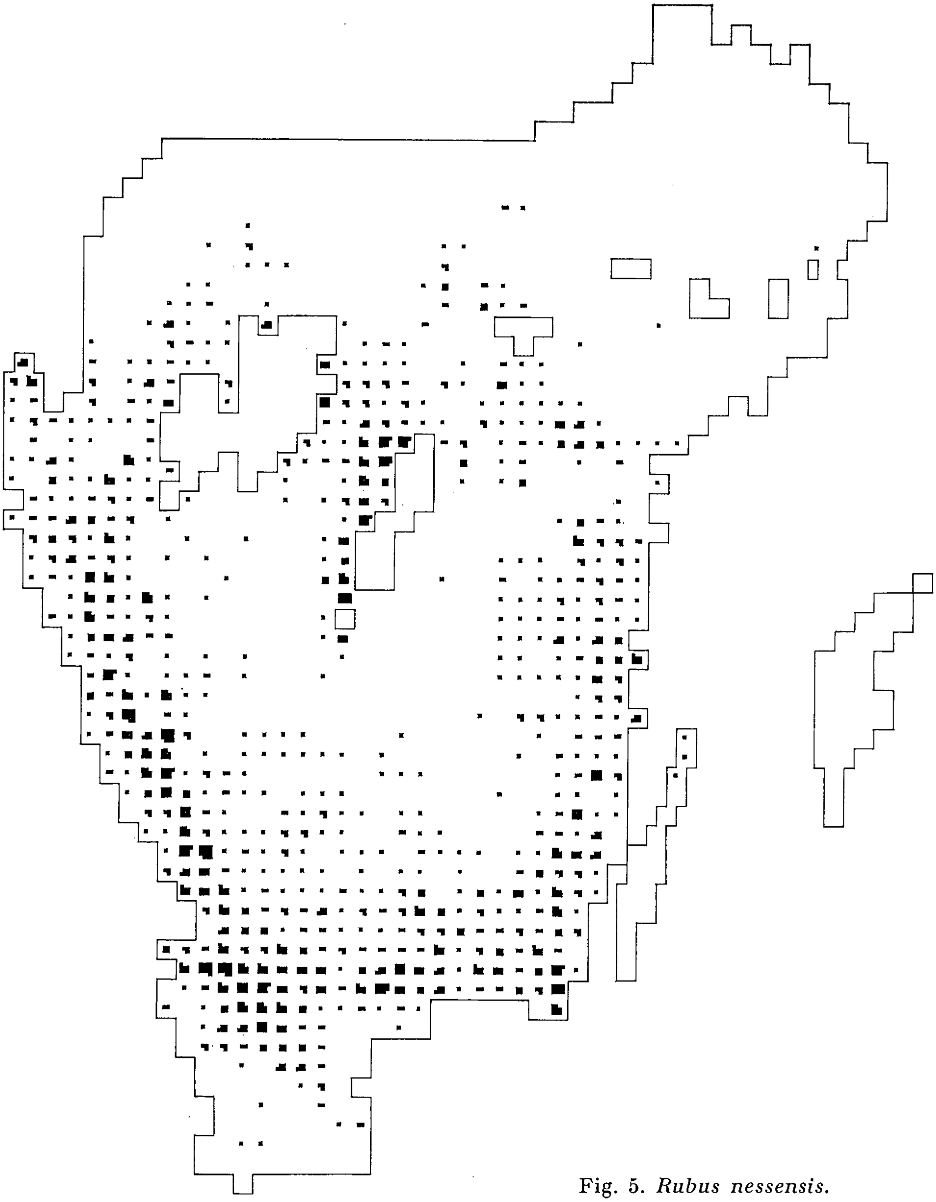


Fig. 5. *Rubus nessensis.*

Figs. 5—15. The frequency of each species within a standard square. Symbols as in Fig. 4.

area may lead to additional error. Firstly, roadsides can be regarded as one enormously over-represented habitat having the exceptional property of being disturbed ground close to transport, which favours ephemeral outpost occurrences, e.g. in connection with a widening of the range. Secondly, as all blackberry species found

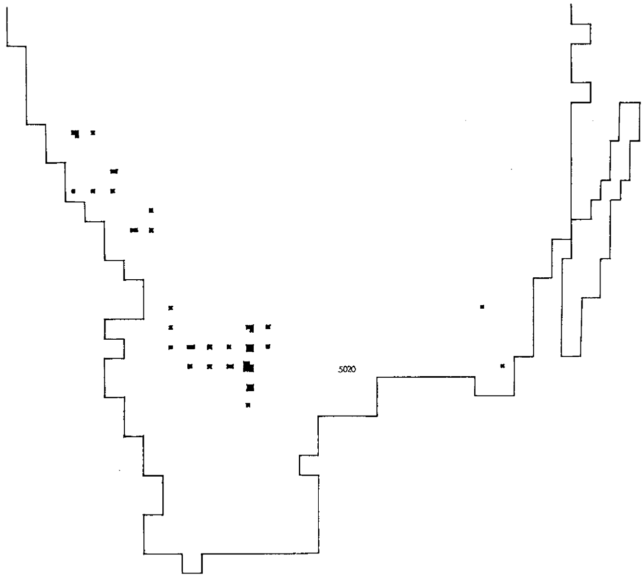


Fig. 6. *Rubus scissus.*

in Sweden have part of their northern limit within the area investigated they may change optimum habitat, as it is believed that many plants do at the margin of distribution as a result of the complicated interplay between factors regulating the absolute limit of occurrence.

Treatment of Data

As the amount of data is so extensive treatment cannot be completed within the scope of this paper. All interpretation of results will be published later.

The treatment of data begins with a discussion on various aspects of frequency without taking patterns of distribution into account.

As an obvious common trait, though more or less pronounced in individual species, coastal preference is studied on the basis of number of species. As it forms an exceptional area, the province of Skåne is then examined using the frequencies of the species occurring. A preliminary division of the area investigated follows, and the occurrence of the separate species in the six divisions is discussed. Finally, the species are divided into an eastern and a western group, according to their main distribution in one of the two vertical halves of the area investigated.

PROFILE OF FREQUENCY

The distribution of squares according to frequency, henceforth called Profile of Frequency, is shown for each species separately in Fig. 16 (p. 55).

COMMON TRAITS. Having noticed the difference in size between the frequency diagrams of the three species to the left and the remainder, three common traits come to the fore. Firstly, the predominance of frequency 1, higher frequencies being found in an equal number of squares in two cases only. Secondly, the rapid decrease in the number of squares with the following frequencies ending at number 6 (the three-species group), or earlier. Thirdly, the persistence of high frequencies, a tendency seen more or less clearly in all species having squares with a frequency above 3, pronounced in two of the dominating species, but only slight in the third.

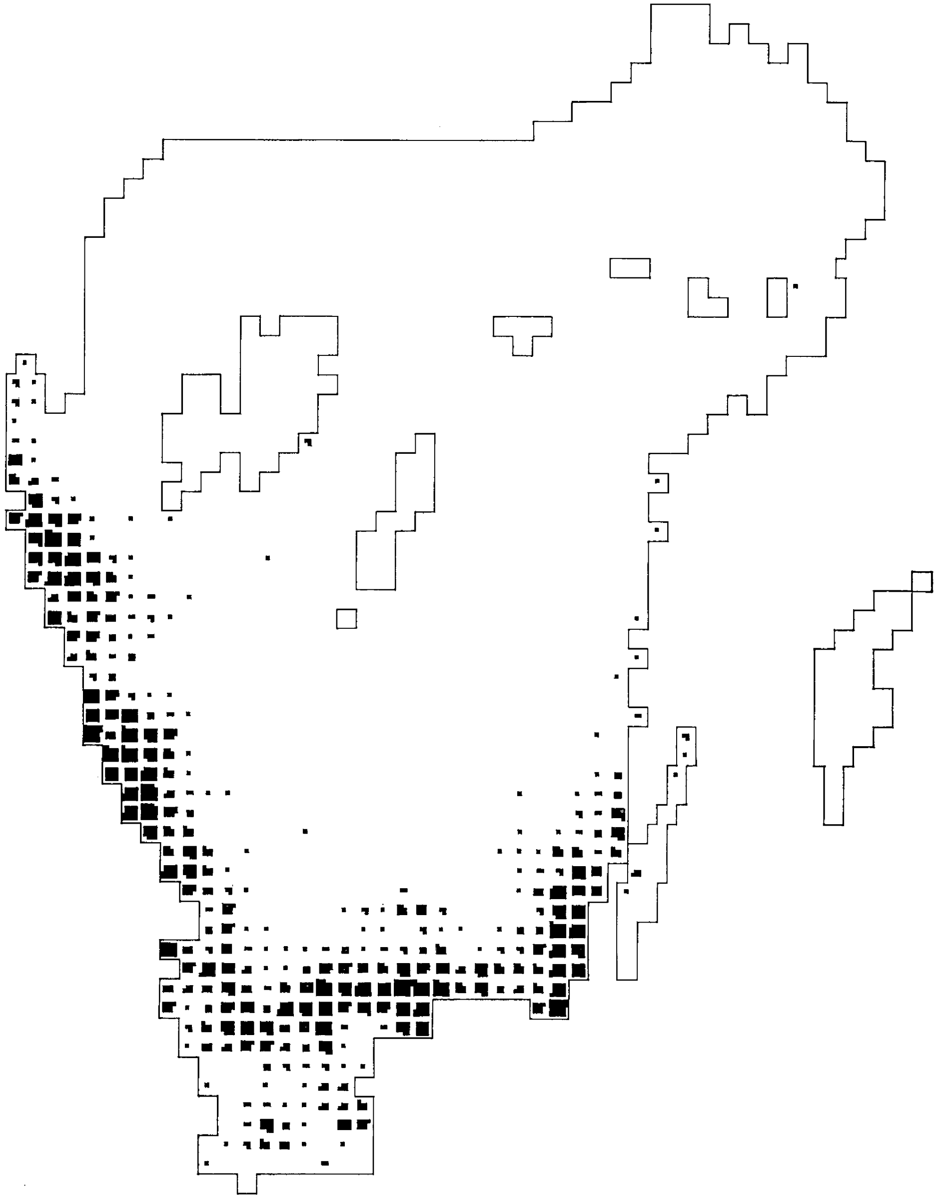


Fig. 7. *Rubus plicatus.*

RELATIVE FREQUENCY VALUES

In Table 2 the Profiles of Frequency have been divided into seven frequency classes in order to simplify the description of the profile of each species in terms of accumulated number of squares representing a certain proportion of the theoretical maximum frequency (67, cf. p. 41).

Rubus corylifolius is the only species with a frequency as high as 50 % of the

Table 2. Accumulated numbers of squares in seven classes of frequency, each *Rubus* species treated separately.

Lowest frequency	1	3	7	13	20	27	33
Lowest percentage of theoretical maximum	2	5	10	20	30	40	50
corylifolius agg.	273	155	93	54	**25**	**5**	**1**
plicatus	320	213	**143**	**74**	17	3	
nessensis	**648**	**237**	67	5			
thyrsanthus	56	11	3				
lindebergii	31	9	4				
radula	28	9	4				
scissus	27	5	1				
bellardii	10	5	2				
scheutzii	3	1					
sulcatus	19	1					
taeniarum	7	1					
insularis	7	1					
hartmanii	4	1					
sprengelii	2						
axillaris	6						
nitidus	1						
vestitus	1						
fuscus	2						

theoretical maximum, and this is in a single square only. The same species has the largest number of squares 30—50 % of the theoretical maximum, though *plicatus* is also represented at the 40 % level. The latter species takes the lead at 20 % and is in the fore also at the 10 % level, in both cases with *corylifolius* as number two. At 5 % of the theoretical maximum frequency, *plicatus* followed by *corylifolius* are both passed by *nessensis*, a species which comes into the picture at the 20 % level.

Five species are introduced at the 10 % level, namely *thyrsanthus, lindebergii, radula, scissus,* and *bellardii.* At the 5 % level those species have all increased their number of squares to at least five.

Another five species are added at the 5 % level, all with only one square each. The species are *scheutzii, sulcatus, taeniarum, insularis* and *hartmanii.*

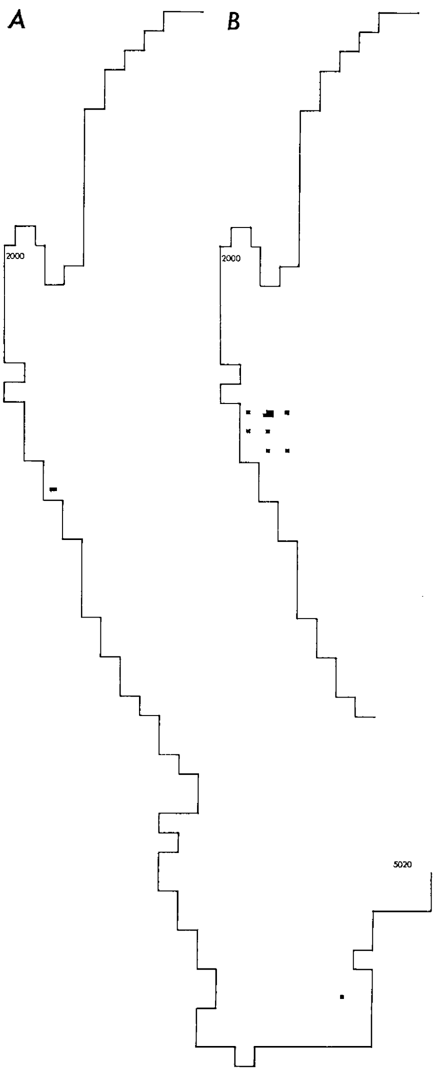


Fig. 8. A: *Rubus sprengelii.* — B: *R. taeniarum.*

None of the five remaining species has a frequency as high as 5 % of the theoretical maximum. Those species are *sprengelii, axillaris, nitidus, vestitus* and *fuscus.*

ASPECTS OF FREQUENCY

In order to test the usefulness of simplified frequency measures that need not

Table 3.

3 a. Four aspects of frequency. Theoretical maxima in brackets.

3 b. Three aspects of frequency as percentages of the theoretical maxima (cf. 3 a).

	3 a.				3 b.		
Rubus species	Total Frequency (100,433)	Number of Squares (1,499)	Mean Frequency (67)	Maximum Frequency (67)	Number of Squares	Mean Frequency	Maximum Frequency
corylifolius agg.	1,782	273	6.5	36	18	10	54
plicatus	2,359	320	7.4	27	21	11	40
nessensis	1,777	648	2.7	15	43	4	22
thyrsanthus	102	56	1.8	8	4	3	12
lindebergii	86	31	2.8	12	2	4	18
radula	77	28	2.8	12	2	4	18
scissus	48	27	1.8	8	2	3	12
bellardii	31	10	3.1	8	1	5	12
scheutzii	7	3	2.3	5	0	3	7
sulcatus	21	19	1.1	3	1	2	4
taeniarum	11	7	1.6	5	0	3	7
insularis	9	7	1.3	3	0	2	4
hartmanii	6	4	1.5	3	0	2	4
sprengelii	3	2	1.5	2	0	2	3
axillaris	7	6	1.2	2	0	2	3
nitidus	1	1	1	1	0	1	1
vestitus	1	1	1	1	0	1	1
fuscus	2	2	1	1	0	1	1

be based on a detailed knowledge of the entire frequency profile, four different aspects of frequency were chosen, viz.:

(1) Total Frequency, obtained by adding together all the frequencies.

(2) Number of Squares with a frequency above zero.

(3) Mean Frequency of the squares with a frequency exceeding zero.

(4) Maximum Frequency, i.e. highest frequency recorded.

Table 3 a gives the figures for each species with respect to these four aspects of frequency, and in Table 3 b the figures are transformed into relative values.

Total Frequency

Comparing the Total Frequency of individual species with the sum of frequency of all species, *plicatus, nessensis,* and *corylifolius* together make up 93 % of the sum of the frequencies, the first species with 37 % and the two others with 28 % each. Number four is *thyrsanthus,* with 2 %. Three species have 1 % each, viz. *scissus, lindebergii* and *radula.*

The remainder of the sum of frequencies, 2 %, is shared by 11 species. Of these *bellardii* has the highest Total Frequency, with *sulcatus* coming next. Then follows a group of five species, viz. *scheutzii, taeniarum, insularis, hartmanii* and *axillaris.* The four species, *sprengelii, nitidus, vestitus* and *fuscus* have the lowest Total Frequencies recorded.

Number of Squares

Again, comparing the individual species with the whole subgenus, as regards the number of squares with a frequency above zero, the dominating species is *nessensis,* with 87 % of the total number of squares. Number two is *plicatus* with 43 %, followed by *corylifolius* with 37 % and then *thyrsanthus,* which has 8 %. Then follow four species with 3—4 % of the

3 c. Separate ranking of the species according to the values from four aspects of frequency.

3 d. Three aspects of frequency as percentages of the totals of two groups, the minor one containing the first three species.

3 e. The percentages in 3 d added together. Ranking list according to the sums.

Total Frequency	Number of Squares	Mean Frequency	Maximum Frequency	Number of Squares	Mean Frequency	Maximum Frequency	Weighted Frequency	Rank number
2	3	2	1	22	39	46	107	1
1	2	1	2	26	45	35	106	2
3	1	6	3	52	16	19	87	3
4	4	8.5	7	27	7	11	45	4
5	5	4.5	4.5	15	11	16	42	5
6	6	4.5	4.5	14	11	16	41	6
7	7	8.5	7	13	7	11	31	7
8	9	3	7	5	12	11	28	8
12.5	14	7	9.5	2	9	7	18	9
9	8	15	12	9	4	4	17	10
10	10.5	10	9.5	3	6	7	16	11
11	10.5	13	12	3	5	4	12	12.5
14	13	11.5	12	2	6	4	12	12.5
15	15.5	11.5	14.5	1	6	3	10	14.5
12.5	12	14	14.5	3	4	3	10	14.5
17.5	17.5	17	17	1	4	1	6	17
17.5	17.5	17	17	1	4	1	6	17
16	15.5	17	17	1	4	1	6	17

squares in question, viz. *lindebergii, radula, scissus* and *sulcatus.*

None of the remaining 10 species have frequencies above zero in more than 1 % of squares with at least one blackberry species with a frequency above zero. Of these ten species *bellardii* comes first, followed by *taeniarum, insularis* and *axillaris* while the remaining six species, i.e. *scheutzii, hartmanii, sprengelii, nitidus, vestitus* and *fuscus* form a lower group.

Mean Frequency

With respect to the values of Mean Frequency (i.e. of squares having a frequency above zero), two species stand out, viz. *plicatus* (7.4) and *corylifolius* (6.5). Then come four species, *nessensis, lindebergii, radula* and *bellardii* (2.7—3.1). Number seven is *scheutzii* (2.3), followed by *thyrsanthus* and *scissus* (both 1.8), and then *taeniarum, hartmanii* and *sprengelii* (1.5—1.6). The remaining six species form a lower group (1.0—1.3) comprising *sulcatus, insularis, axillaris, nitidus, vestitus* and *fuscus.*

Maximum Frequency

The highest frequency recorded is for *corylifolius* i.e. 36 localities per 10 km though only in a single square. Species number two is *plicatus* with a Maximum Frequency of 27. Then there is another jump to *nessensis* with a maximum of 15. Then follow *lindebergii* and *radula,* both with 12, and three species with a frequency of 8 as maximum, viz. *scissus, thyrsanthus* and *bellardii.*

The remaining 10 species have a Maximum Frequency ranging from 1 to 5. In the following list the species in question are arranged in decreasing scale: *scheutzii, taeniarum* (5), *sulcatus, insularis, hartmanii* (3), *sprengelii, axillaris* (2), *nitidus, vestitus, fuscus* (1).

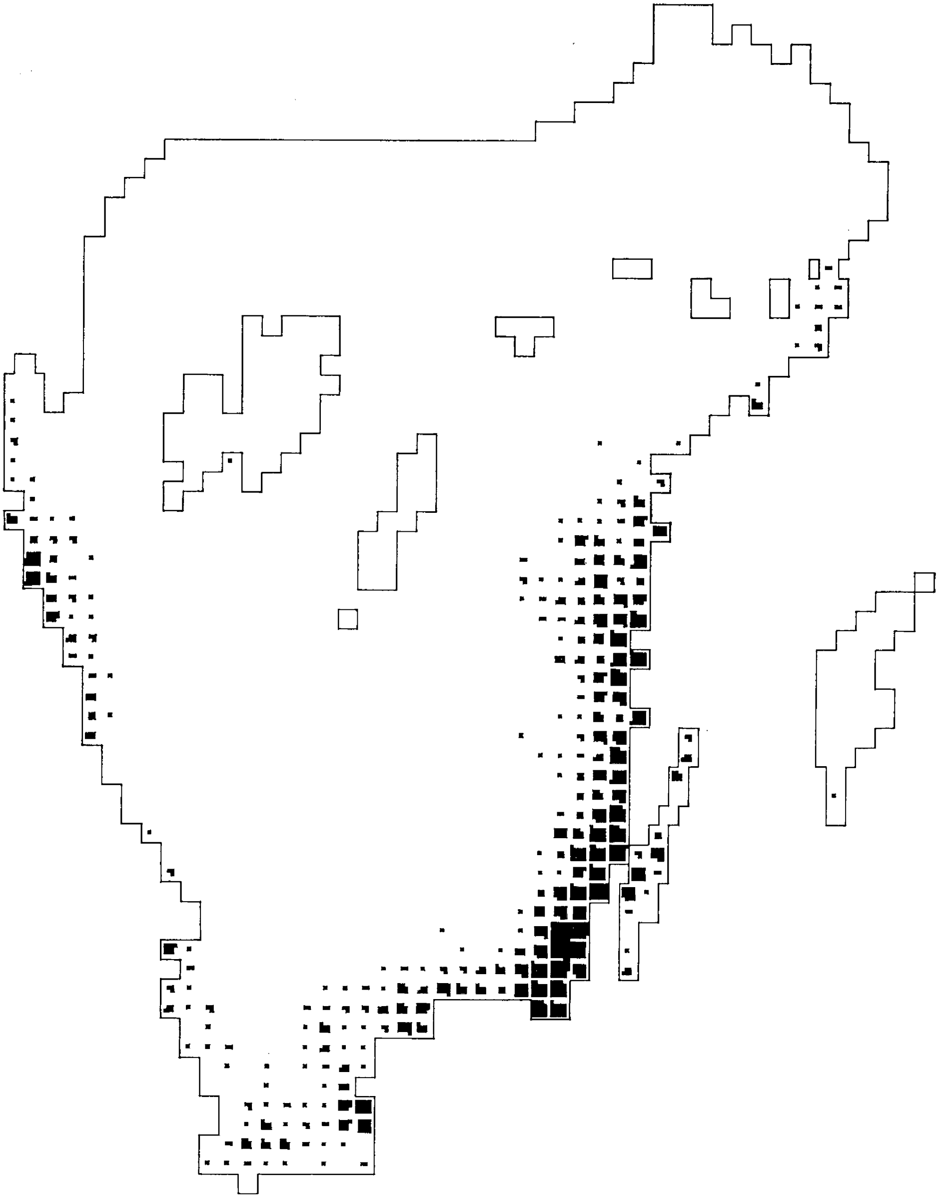


Fig. 9. *Rubus corylifolius* agg.

THREE ASPECTS OF FREQUENCY COMPARED

Three of the four aspects of frequency treated so far are suitable for comparison in that they are partly independent of one another, while the fourth aspect is the product of two of the three aspects referred to.

The values of Number of Squares (N) is independent of the values of the two

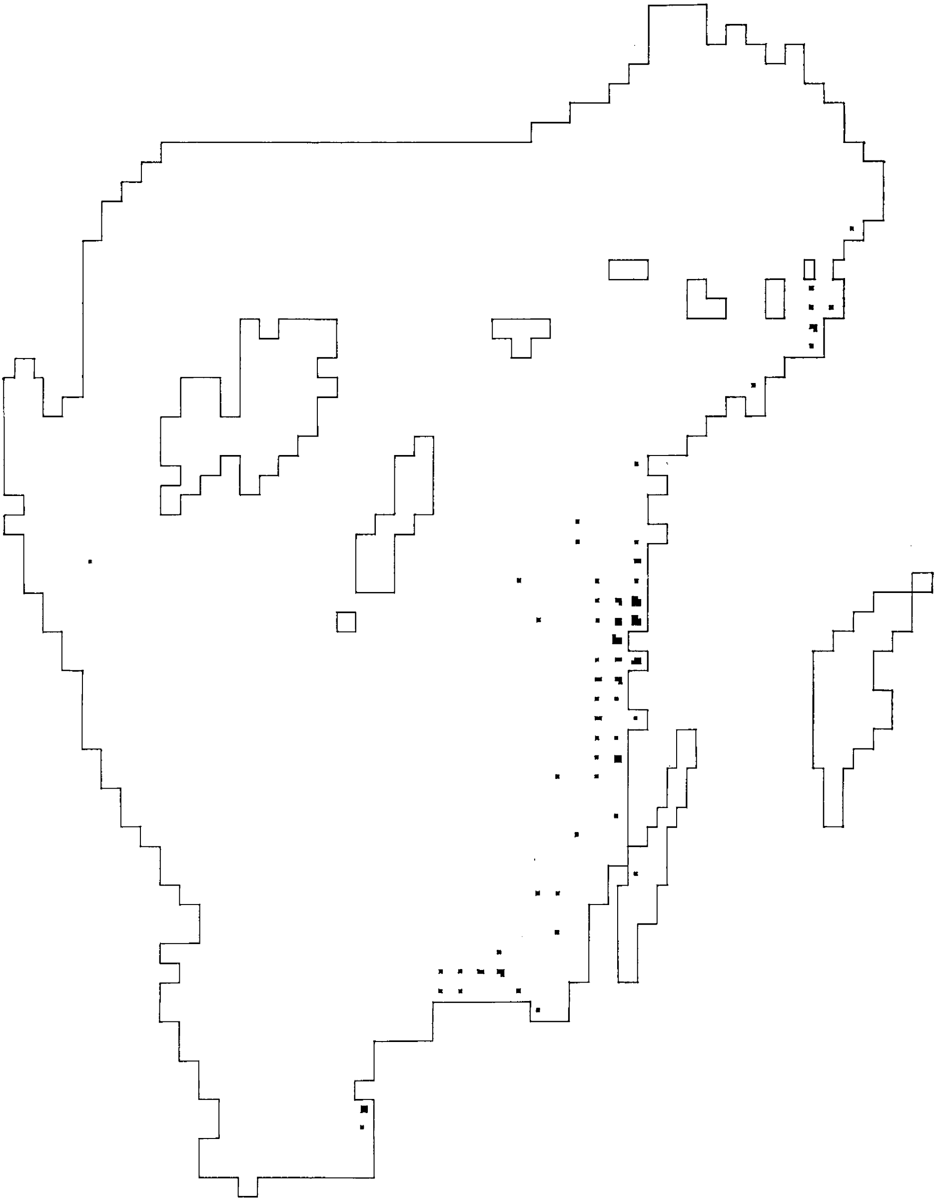


Fig. 10. *Rubus thyrsanthus.*

other aspects of frequency chosen for comparison, while Mean Frequency (M) is related to Maximum Frequency (H) as follows:

$$M_{min}=\frac{H+N-1}{N};\ M_{max}=H,$$ the left-hand formula implying that the minimum value of (M) is influenced by (H) only at low values of (N).

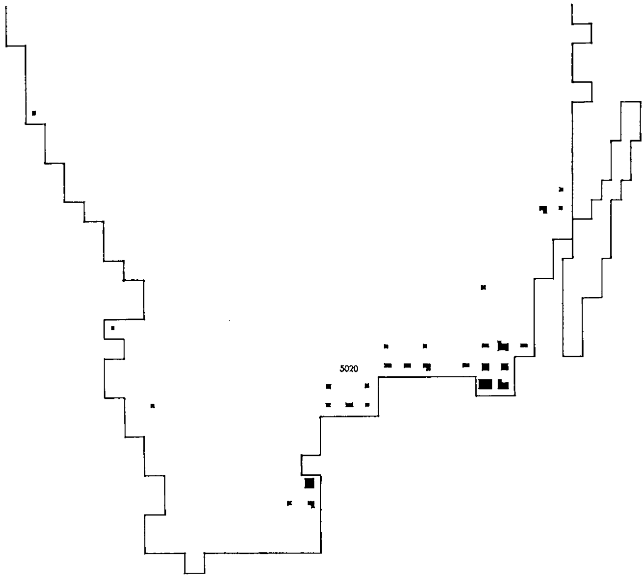


Fig. 11. *Rubus radula.*

The formula of Total Frequency (T) is: $T = N \times M$

The three aspects of frequency chosen for comparison also represent three different aspects of occurrence:

(1) Number of Squares corresponds to the extent of the area in which a plant is found.

(2) Mean Frequency is a measure of the proximity of a plant's localities that is an average for the whole area of distribution.

(3) Maximum Frequency shows the proximity of the localities in a minor part of the area of distribution where the species in question is most common.

It should be observed that the sole basis of the aspects of frequency hitherto discussed is the Profile of Frequency, and consequently breaks corresponding to 0-squares are not included in the concept of area of distribution used above.

Another weak point in the comparison is the fact that Maximum Frequency only represents one square, and therefore the random variation is greater than in the two other aspects chosen which take into account information from all squares having a frequency above zero.

Separate Ranking

According to the magnitude of their values from the three different aspects of frequency dealt with the species have been placed in three separate lists (Table 3 c).

Small discrepancies between the three ranking lists are prevalent, but on the whole the lists look similar with low figures at the top of the lists and high figures at the bottom.

In other words Number of Squares, Mean Frequency and Maximum Frequency are aspects of frequency which result in roughly the same ranking of the Swedish blackberry species.

Combined Ranking

Seeing that the ranking lists of the species are roughly the same irrespective of aspect of frequency, the author yielded

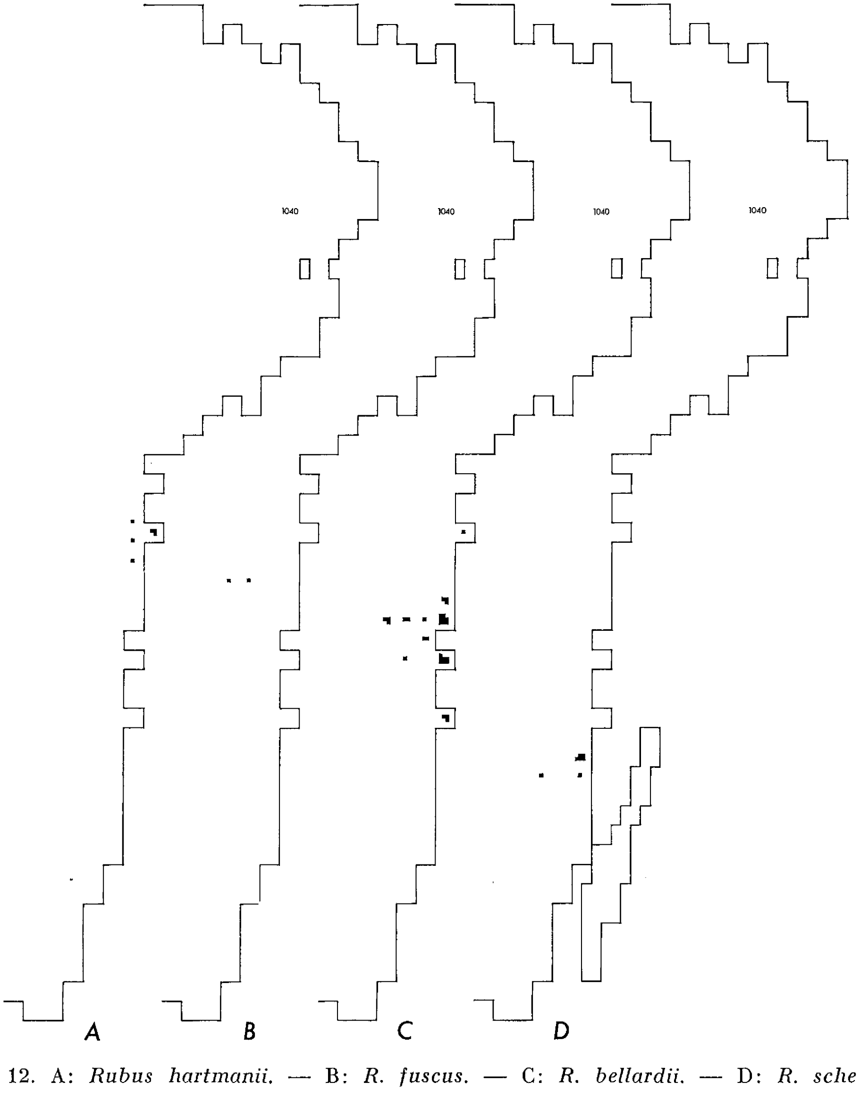


Fig. 12. A: *Rubus hartmanii.* — B: *R. fuscus.* — C: *R. bellardii.* — D: *R. scheutzii.*

to the temptation of combining the results from the three different aspects of frequency in order to get the conclusive frequency ranking of the 18 species. But had the ranking been of no other significance than to represent the species by ordinals it would of course have been of less interest.

However, the three aspects of frequency chosen do not represent any three different dimensions of the occurrence of plants (cf. p. 52), and together they may also be an indication of the chance of survival in the area in question should environmental conditions change.

(1) An extensive range means that the plant in question will be better able to stand up to reduction in area of distribu-

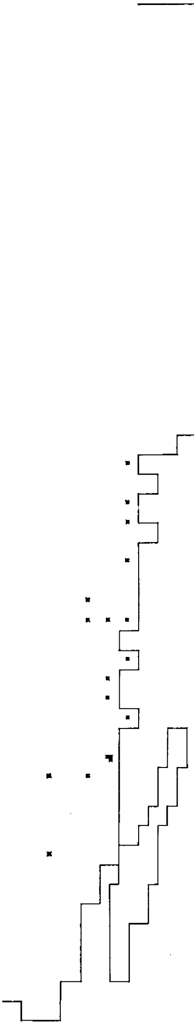


Fig. 13. *Rubus sulcatus.*

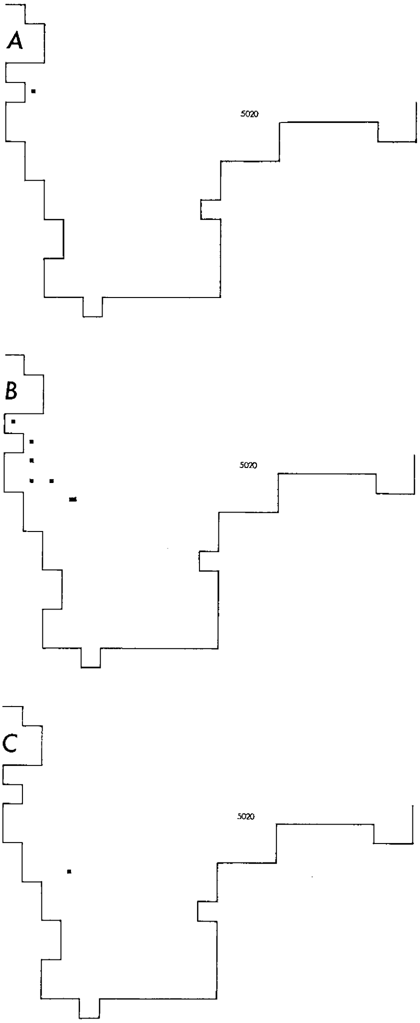


Fig. 14. A: *Rubus nitidus.* — B: *R. axillaris.* — C: *R. vestitus.*

tion, and will also have a greater chance of being represented in places where conditions may again turn more favourable.

(2) A higher Mean Frequency implies that over most of its area of distribution the plant may to a greater extent tolerate moderate changes, at least as regards some of the environmental factors, as the minimum requirements will still be well exceeded.

(3) A higher Maximum Frequency may signify that the plant has found a tract where conditions are closer to the optimum, and that consequently the chances are greater that the plant in question may resist even substantial changes for the worse, though in a limited area.

It has already been shown that the same species are always predominant, irrespective of aspect of frequency — Mean Fre-

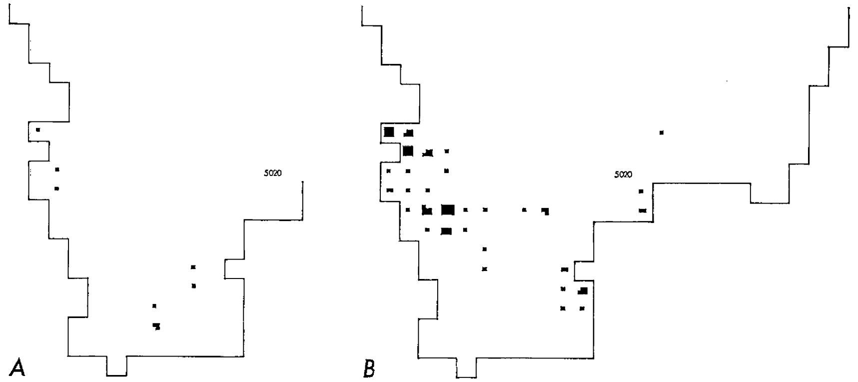


Fig. 15. A: *Rubus insularis.* — B: *R. lindebergii.*

quency of *nessensis* excepted — however not to the same extent when considered from all three aspects of frequency. The following table gives the values of the three dominating species together, with the remaining 15 species in another group, as percentages of the totals from each aspect of frequency (cf. Table 3 a):

Rank Numbers	Number of Squares	Mean Frequency	Maximum Frequency	Σ
1— 3	86	39	51	176
4—17	14	61	49	124

If all 18 species are weighted together the significance of the separate aspects of

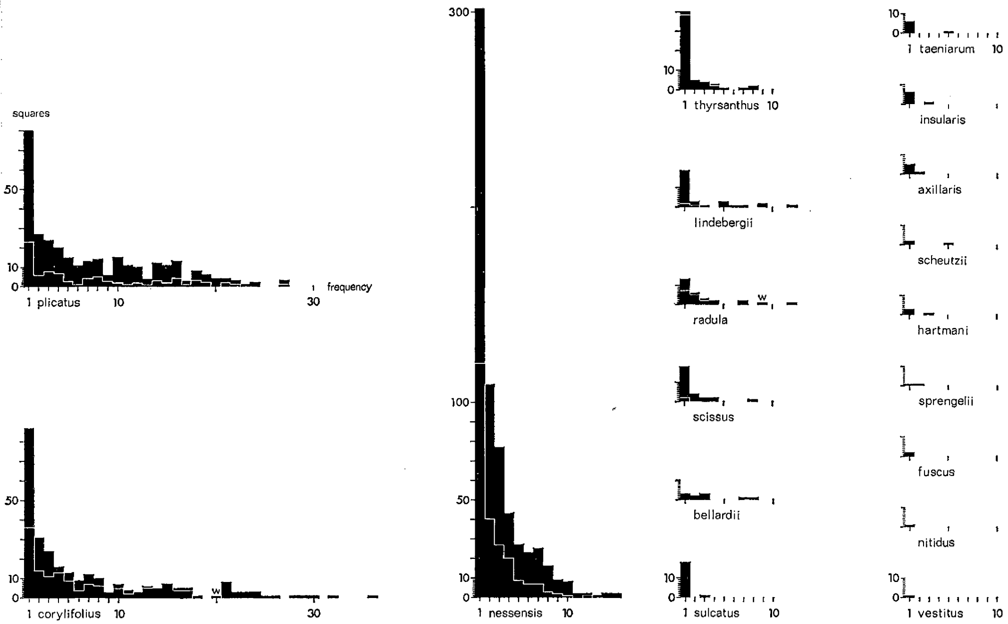


Fig. 16. Profiles of Frequency of 18 *Rubus* species, i.e. Number of Squares plotted against frequency. The white line separates eastern and western occurrences (cf. p. 66). Western occurrences above.

frequency would be considerably different for most of the species. This disadvantage has been avoided by making two independent weightings, one with the three dominating species, and another with the 15 remaining species. The difficulty that then arises when comparing two species from the different groups can be compensated for by multiplying the value of the species from the three-species group by a constant, say 1.42, which is the quotient of the horizontal totals in the table above.

Procedure of Weighting

Though weighted separately the two groups of species mentioned above have been treated identically with respect to Weighted Frequency, namely as follows:

(1) The values of each species have been transformed into percentage of the total of the relevant group, separately for the different aspects of frequency.

(2) The three figures obtained for each species are added together and the sum is called Weighted Frequency.

Example: *Rubus plicatus,* which belongs to the three-species group (cf. p. 55), has a value for Number of Squares of 320 (Table 3 a), or $\frac{320 \times 100}{(273+320+648)} = 26\ \%$ of the total of its group. The percentages of Mean Frequency and Maximum Frequency are calculated in the same way giving 45 % and 35 % respectively. Then the three percentages of *plicatus* are added together and the sum (106) is the value for the Weighted Frequency of that species.

The final ranking of the species has been done exclusively on the basis of the values of Weighted Frequency. Table 3 gives the separate percentages of each species (d), as well as the value of Weighted Frequency and respective Rank Number (e).

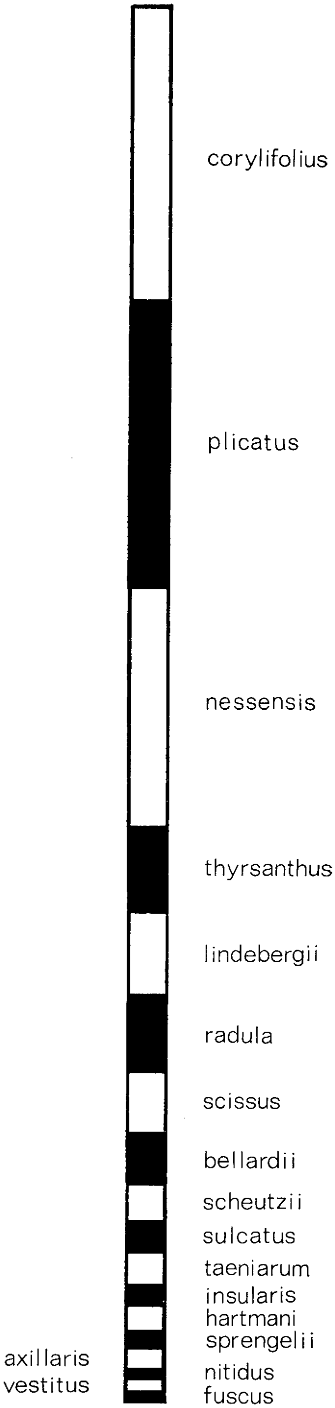


Fig. 17. The frequency relations between the *Rubus* species treated in terms of Weighted Frequency.

Frequency Grouping

In Fig. 17 all values of Weighted Frequency are shown in a graph, with the figures of the three dominating species compensated for as proposed (cf. p. 56).

The superiority of the three-species group is very obvious, with *corylifolius, plicatus* and *nessensis* together accounting for more than half of the total Weighted Frequency.

Among the other 15 species, arranged according to their gradually diminishing values of Weighted Frequency, two major groups are discernible. One of them comprises *thyrsanthus, lindebergii, radula, scissus* and *bellardii,* five species which together have almost two thirds of the remaining Weighted Frequency.

The third group consists of the remaining 10 species together with less than a sixth of the total Weighted Frequency, viz. *scheutzii, sulcatus, taeniarum, insularis* and *hartmanii, sprengelii* and *axillaris,* and finally, with a Weighted Frequency value equal to the minimum, *nitidus, vestitus* and *fuscus.* The last three species form a minor subgroup.

The above grouping is based solely on the values of Weighted Frequency. The outcome of an equivalent distribution of the species into frequency classes based on Total Frequency records would be strikingly similar. The superiority of the species in the three-species group would be still more accentuated; *sulcatus* might be moved to the second group, and to the minor subgroup of the third group might be added *sprengelii; fuscus* might be transferred to the major subgroup. Further alterations would hardly come into question (cf. Table 3 a and 3 c).

TOTAL AREA OF BLACKBERRIES

It has already been stated that the number of squares with a minimum of one species represented by a frequency exceeding zero is 741, or about half the total area investigated (1,499 squares). Fig. 18 shows the distribution of squares with respect to number of species with a frequency exceeding zero.

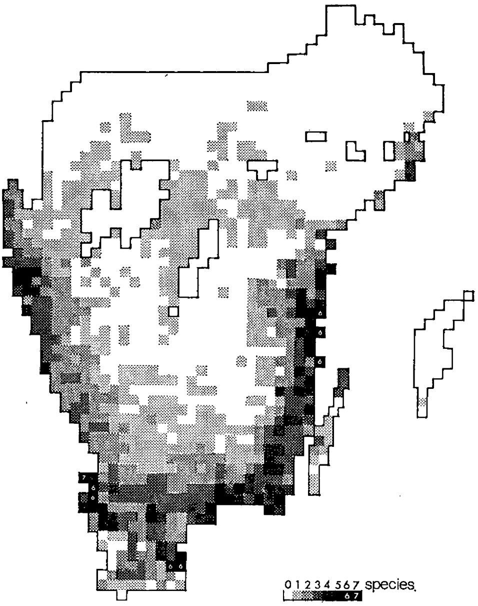


Fig. 18. Number of species having a frequency exceeding zero.

With the exception of the Stockholm archipelago, practically none of those squares are met with north of an east-west zigzag line connecting Nyköping—Katrineholm — Arboga — Fagersta — Karlskoga—Sunne—Bengtsfors. Blackberries seem to be almost equally rare on the island of Gotland, as well as in an inland area, enclosed by, from west clockwise, Trollhättan — Mariestad — Vaggeryd — Motala—Norrköping—Kisa—Hultsfred—Lessebo—Borås—Trollhättan.

Hence, the total distribution area of Swedish blackberries may be considered continuous on the mainland, with one large sparse zone in the middle. On the latitude of Stockholm there is a transitional zone, with a width of about 100 km, in which the number of squares with a frequency exceeding zero gradually decreases until the final northern limit is reached. The island of Öland is associated with the adjacent mainland coast, while blackberries are almost lacking on the isolated island of Gotland.

COASTAL PREFERENCE

Survey

For the purpose of quantifying the strong coastal preference of Swedish blackberries (Fig. 18), the area of investigation has been divided into three zones.

	Zone		
	A	B	C
Distance in km from the sea	>60	20—60	<20
Number of squares .	831	383	285

Fig. 19 A shows this in detail.

Within the three zones the squares are distributed as below with reference to number of species with a frequency exceeding zero:

Zone	No. of species							
	0	1	2	3	4	5	6	7
A	556	**244**	21	8	1	1	.	.
B	116	86	**103**	57	18	3	.	.
C	86	27	53	**63**	31	17	7	1

No occurrence of blackberries is registered in two thirds of the squares belonging to the inland category, while this applies to only one third of the squares closer to the sea. Although comprising more than half of the total number of squares the inland category has less than 10 % of the squares with two species or more. Of the squares with four species or more, 71 % occur along the coast, 27 % belong to the intermediate category, while as little as 2 % are met with in the inland parts of the area investigated. All the eight squares with six species or more are located along the coast.

Fig. 20 gives the distribution as percentages of the total of each category.

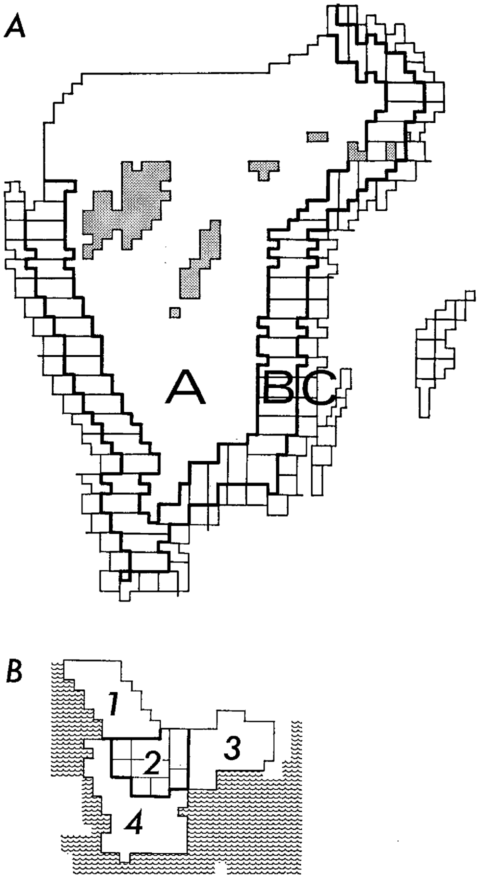


Fig. 19. A: The area investigated divided into three zones (A, B, C) with respect to distance from sea. — B: The south-westernmost part of the area investigated divided into four regions, as described on p. 61. — Blocks of squares for mean number calculations also indicated.

Regional Differences

In order to expose any possible regional differences as regards coastal preference, two of the three zones have been divided into blocks of squares, those in Zone C normally comprising four standard squares, while the blocks in Zone B are normally made up of eight standard squares.

There are 122 blocks of squares, 14 on the islands of Öland and Gotland, a fur-

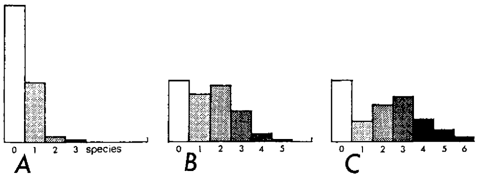


Fig. 20. The squares investigated according to Number of Species per square, distributed in the three zones of Fig. 19 A. The Number of Squares is represented by relative values, the totals of the three zones being equal.

ther 60 in the coastal category and 48 in the intermediate category. Fig. 19 A shows details of the division of the coastal and intermediate categories into blocks.

The mean number of species has been calculated for each block as shown in Fig. 21 A.

The common features of the regional variation of the coastal and intermediate categories, can be expressed in four points as follows:

(1) The islands of Öland and Gotland have considerably lower means of number of species per square than the blocks of squares in the coastal category on the same latitude on the mainland.

(2) The means are higher within the coastal category than in the intermediate one, apart from SW Skåne and one block of squares in the E part of the same province.

(3) The amplitude of the means is greater in the coastal than in the intermediate category, but the variation between adjacent blocks does not seem to be greater in the coastal category as a whole.

(4) There seems to be a certain degree of geographical covariation between the means of the two categories with respect to distance from the sea, but there are several exceptions and some of them are, moreover, rather conspicuous.

Based on the means of the coastal category exclusively the variation in number of species could be described as follows, sequentially from northwest to northeast:

Starting at two farthest in the northwest the mean number of species increases to almost four in the middle of Bohuslän. The mean then falls gradually through the province of Halland, again reaching two in the southernmost part of that province. A sharp rise in north-western Skåne to five, the maximum mean for the total stretch of coast, is followed by a rapid reduction to about one in the six blocks of squares in the south-western parts of the same province. With the exception of one of the blocks in eastern Skåne, which has a mean below two, twenty successive blocks comprising the coastal regions of Blekinge and eastern Småland and up to southern Östergötland have means as high as between three and almost five species per square. The high-

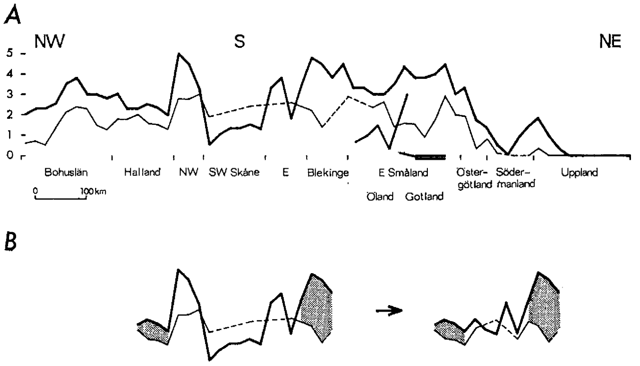


Fig. 21. A: Profile, following the coastline, showing the number of species as means of blocks of squares (cf. Fig. 19 A). — B: Left: A section of the same profile. Right: The same section after introducing the artificial parts of Zone B and C in northern Skåne (cf. Fig. 19 B). The blank part of the section represents Skåne. — Broad line: Zone C. Narrow line (whole or broken): Zone B.

est values for these regions have been registered in Blekinge and north-eastern Småland. Farther north there is a gradual decline of the means through the province of Östergötland. Not until halfway up the coast of Södermanland do we find a block of squares on the coast where there are no blackberry species with a frequency of 1 or more. In the Stockholm archipelago, on the boundary between Södermanland and Uppland, we get the last peak representing almost two species per square. The northern limit of the coastal occurrences of Swedish blackberries seems to be reached halfway up the coast of Uppland.

In all but one of the five blocks of squares on the island of Öland the mean number of species is around one, while the northernmost part of the island has a mean of three species. The mean lies just above zero in the southernmost part of Gotland, while the rest of the island lacks squares with blackberry species exceeding a frequency of zero.

PENINSULAR SKÅNE

The tendency towards an increasing number of species seawards is broken only in one of the mainland provinces, namely Skåne. Although it is the southernmost province in the area investigated, the south-western parts of Skåne have the lowest number of species along the coast, excluding the island of Gotland and the eight north-easternmost blocks of squares preceding the definite limit of coastal occurrence.

One interpretation of the anomalies indicated derives from Skåne's character of a peninsula, and reads as follows: The coastal preference shown by blackberries on the mainland is due to a gradient of climate from the sea to the interior. The area of the peninsula in question is too small to uphold a corresponding gradient of its own, and consequently the general gradient of climate referred to will be found in the mainland north of the peninsula, so that, in the interior of northern Skåne in particular, the frequency of blackberries is higher than would normally be expected.

For the purpose of testing the above hypothesis the gap between the coastal regions of southern Halland and western Blekinge was bridged by altering the location of the blocks of squares of the coastal and intermediate zones as indicated in Fig. 19 B.

By moving the categories of squares concerned northwards the total number of squares within the three zones has been reduced by 73, as shown below:

A	B	C
—18	—27	—28

Theoretically, a corresponding reduction in the number of squares with reference to number of species, within the three zones, would have the following outcome if proportionate to the original distribution (cf. p. 58):

Theoretical values

Zone	No. of species							
	0	1	2	3	4	5	6	7
A	544	239	20	8	1	1	.	.
B	108	80	96	53	16	3	.	.
C	78	24	48	57	28	15	6	1

The distribution obtained on moving the zones northwards is as shown below:

Actual values

Zone	No. of species							
	0	1	2	3	4	5	6	7
A	556	242	15	.	.	.	.	.
B	114	85	94	47	15	1	.	.
C	77	19	48	66	29	15	3	.

The difference between the actual values and the theoretical values:

Zone	No. of species							
	0	1	2	3	4	5	6	7
A	+12	+3	−5	−8	−1	−1	.	.
B	+6	+5	−2	−6	−1	−2	.	.
C	−1	−5	0	+9	+1	0	−3	−1

Thus the introduction of these artificial parts of the coastal and intermediate regions of northern Skåne, and the exclusion of the remainder of the peninsula, results in a disproportionately sharp reduction of the number of squares that have more than one species with a frequency exceeding zero in the inland and intermediate zones. Similarly, the reduction of the number of squares in the coastal zone is now relatively high in the two groups with no species or one, as well as in the two other extreme groups containing squares with six or seven species. The most pronounced effect of the removal of the three zones northwards in Skåne is found in the inland category — 18 squares of a total of 831 disappear, resulting in the loss of all ten squares having more than two species with a frequency exceeding zero!

Another way of evaluating the effects of moving the zones in Skåne as to the number of species in the squares concerned, is to compare distributions within the coastal and intermediate zones before and after the adjustment. The figures are given below:

	0	1	2	3	4	5	6	7	Σ	m
B Before ...	2	3	18	23	4	2	.	.	52	2.6
After		2	9	13	1	.	.	.	25	2.5
C Before ...	9	9	12	6	4	3	4	1	48	2.4
After		1	7	9	2	1	.	.	20	2.8

The difference between the means is remarkably small, whichever the zone both before and after moving the squares, and never exceeds a half species per square. This outcome of the comparison between the original location of the coastal and intermediate zones in Skåne, and the artificial location of the two zones in the northern part of the same province, could be regarded as a reason for not changing the location of the two zones themselves, but rather to broaden their area in this province.

There are, however, two independent facts apparent in the data presented that speak against such a proposal. Firstly, the coastal zone becomes markedly homogeneous when moved northwards. Secondly, but none the less significant, the ratio between the coastal and intermediate categories favours the coastal zone after the adjustment, as opposed to before.

For the remainder of the mainland coast the rule is that in every pair of blocks of squares the coastal zone is richer in species than the intermediate zone (cf. p. 59). Hence, as regards the province of Skåne, the character of being an exception to the rule is less pronounced after moving the two zones in question (Fig. 21 B).

In order to get a clear picture of the position of the province of Skåne, the author decided to make a special analysis which included the adjoining parts of the provinces of Halland and Blekinge, using frequency data from all the wild blackberry species occurring in the area.

The area in question consists of four different regions (cf. Fig. 19 B):

(1) Halland, except the northern part, and adjoining parts of Småland, in all 48 squares within the coastal and intermediate zones.

(2) Northern Skåne, as defined by the artificial coastal and intermediate zones, consisting of 45 squares.

(3) Blekinge, except the easternmost part, and adjoining parts of Småland, as well as minor parts of NE Skåne, in all 50 squares from the coastal and intermediate zones.

(4) Skåne, outside the artificial coastal zone, forming the actual peninsula, consisting of 73 squares.

A kind of mean frequency of each occurring species has been calculated for the four regions separately, and this deviates from the concept previously defined (cf. p. 48), in being the quotient of the Total Frequency and the **total** Number of Squares. (The frequencies of the squares in question, which constitute the raw material for the calculations, are to be found

Table 4. Quotients of Total Frequency and **total** Number of Squares in the four regions shown in Fig. 19 B, treated separately.

Rubus species	1 Halland	2 N Skåne	3 Blekinge	4 Peninsular Skåne
corylifolius agg.	.08	.67	4.28	2.32
plicatus	5.38	7.93	6.74	3.66
nessensis	3.40	4.56	3.08	1.08
thyrsanthus	.	.	.22	.07
lindebergii	.	.16	.08	1.03
radula	.	.	.40	.21
scissus	.21	.71	.02	.
insularis	.	.	.	.12
sprengelii	.	.	.	.01
axillaris	.	.	.	.10
nitidus	.	.	.	.01
vestitus	.	.	.	.01

in Figs. 5—15.) Table 4 gives the quotients.

Let us first compare the values obtained from regions 1—3. Thus the number of species found in northern Skåne is two less than in the adjacent region in Blekinge, but one more than in the corresponding region in Halland. The mean frequencies of four of the five species found in northern Skåne seem to be at least equivalent to the means in the two regions it is compared with. The fifth species, *corylifolius,* is decidedly more frequent in Blekinge than in the other two regions, while the two remaining species have only been found in the province of Blekinge. All facts point to northern Skåne as being a natural bridge between her two neighbours, both of which adjoin the sea.

In the fourth region, the actual peninsula of Skåne, the corresponding quotient of the Total Frequency and total Number of Squares varies between the different species, as indicated in Table 4, right column.

Compared with the previous three regions in south-westernmost Sweden, which together are double the size (143 squares), peninsular Skåne might be characterized as follows:

(1) Of the three species most frequent in northern Skåne, but also occurring in the other two regions of the mainland, *plicatus* and *nessensis* both have a markedly lower frequency on the peninsula than in each of the three mainland regions, while *scissus* seems to be absent from the peninsula.

(2) Of the three species most frequent in the Blekinge region, *corylifolius* has a markedly higher frequency on the peninsula than in Halland and N Skåne; *thyrsanthus* and *radula* have both been found on the peninsula, but not in the mainland regions number 1—2, Halland and N Skåne, respectively.

(3) Five blackberry species are found exclusively on the peninsula, though their frequency is low, while *lindebergii,* a species also reported from N Skåne and Blekinge, has a markedly higher frequency in peninsular Skåne.

Hence, peninsular Skåne seems to be rather dissimilar to the three adjacent mainland regions even if a certain connection with Blekinge is worth noting.

To sum up, northern Skåne seems to form a natural bridge between the two neighbouring regions of Halland and Blekinge (based on frequency of species), both adjoining the sea. The explanation may well be that the gradient of climate

Table 5. Total Frequency divided into six geographical regions.

Rubus species	Mainland proper			Peninsular Skåne	Islands	
	Inland	Intermediate	Coastal		Öland	Gotland
corylifolius agg.	7	329	**1197**	169	79	1
plicatus	34	752	**1295**	267	11	0
nessensis	517	**737**	441	79	3	0
thyrsanthus	1	15	**80**	5	1	0
lindebergii	0	1	10	**75**	0	0
radula	0	3	**59**	15	0	0
scissus	0	**33**	15	0	0	0
bellardii	0	6	**25**	0	0	0
scheutzii	0	1	**6**	0	0	0
sulcatus	0	4	**17**	0	0	0
taeniarum	0	2	**9**	0	0	0
insularis	0	0	0	**9**	0	0
hartmanii	0	0	**6**	0	0	0
sprengelii	0	0	**2**	1	0	0
axillaris	0	0	0	**7**	0	0
nitidus	0	0	0	**1**	0	0
vestitus	0	0	0	**1**	0	0
fuscus	0	**2**	0	0	0	0

from the sea inland crosses northern Skåne. Apart from having a milder climate, the peninsula differs from the adjacent mainland proper in being an open agricultural region with fertile soils. These factors might together best explain the difference between the two parts of Skåne.

PRELIMINARY REGIONAL DIVISION

Using observations on regional differences in the Mean Number of species in blocks of squares to determine coastal preference, a more accurate basis for regional division has been worked out than that originally used. Accordingly, the islands of Öland and Gotland as well as peninsular Skåne are treated as separate regions, while the original division of the mainland proper into three zones with respect to distance from the sea has been retained, with the exception of the squares that were moved northwards (cf. Fig. 19).

Table 5 gives the values of Total Frequency of the 18 *Rubus* species concerned divided into six geographical regions.

Mainland Proper

Fourteen blackberry species are reported from the mainland proper.

Seven of these *Rubus* species have been found neither on the islands of Öland and Gotland nor in peninsular Skåne, viz. *scissus, bellardii, scheutzii, sulcatus, taeniarum, hartmanii* and *fuscus.*

INLAND REGION

In the inland region (which comprises squares situated more than 60 km from the sea), frequencies are distributed as follows: *nessensis* makes up as much as 93 % of the Total Frequency of all species in this region, while the remainder is shared among three species, *plicatus,* with 6 %, and *corylifolius* and *thyrsanthus* with 1 and 0 % respectively.

As regards the Total Frequency of the species individually, *nessensis* is also remarkably well represented in this region, 29 % of its Total Frequency being accounted for here.

INTERMEDIATE REGION

Twelve blackberry species have been found in the intermediate region (where all squares are 20—60 km from the sea, in northern Skåne at most 80 km), two of them being predominant, viz. *plicatus* and *nessensis* which together make up 79 % of the Total Frequency of all species in this region. *Rubus corylifolius* makes up 17 % of the Total Frequency and *scissus* and *thyrsanthus* 2 and 1 % respectively. The remaining 1 % comprises seven species, viz. *lindebergii, radula, bellardii, scheutzii, sulcatus, taeniarum* and *fuscus*.

All the eight species regarded as being most frequent with respect to the whole area investigated have been found in this region, *nessensis* and *scissus* also being represented by the largest proportion of the Total Frequency of individual species, or 42 and 69 % respectively. *Rubus plicatus* comes next with 32 % followed by *corylifolius* and *bellardii,* both with 19 %, and *thyrsanthus,* which has 15 % of its Total Frequency within the intermediate region of the mainland proper. The two remaining species of these eight, *radula* and *lindebergii* are represented by 4 and 1 % of their Total Frequency respectively.

Of the ten species that are less frequent with respect to the whole area investigated one species has been found exclusively in the intermediate region of the mainland proper, viz. *fuscus,* while for the other three species reported from the region 14—19 % of their respective Total Frequencies falls within this region. The species referred to, are *scheutzii, sulcatus* and *taeniarum.*

COASTAL REGION

Thirteen blackberry species have been found in the coastal region (where all squares, with the exception of northern Skåne, are situated less than 20 km from the sea). As was also the case with the intermediate region, two species are predominant, together making up 79 % of the Total Frequency of this region. Here again the one species is *plicatus,* the second now being *corylifolius,* while the species it replaced, *nessensis,* is number three in the coastal region, with 14 % of its Total Frequency. Then come *thyrsanthus* and *radula* with 2 % each followed by *bellardii* and *sulcatus,* both 1 %, while the remaining 1 % of the Total Frequency of the coastal region is shared by six species, viz. *lindebergii, scissus, scheutzii, taeniarum, hartmanii* and *sprengelii.*

All the eight species regarded as most frequent with respect to the whole area investigated occur in the coastal region, five of them being represented by the major part of the Total Frequency of respective species, viz. *thyrsanthus, radula* and *bellardii* (77—81 % in the region), *corylifolius* (67 %) and *plicatus* (55 %). Of the remaining three species *scissus* and *nessensis* are represented by 31 and 25 % of their Total Frequency respectively, while *lindebergii,* a species with its centre of distribution in peninsular Skåne, is also found in the coastal region of the mainland proper with 12 % of its Total Frequency.

Of the ten less frequent species *hartmanii* is the only one occurring exclusively in the coastal region, while the other four species found in this region all have the major part of their Total Frequency here. *Rubus scheutzii, sulcatus* and *taeniarum,* three species also occurring in the intermediate region, are represented in the coastal region by 81—86 % of their respective Total Frequencies, while two thirds of the Total Frequency of *sprengelii* is found in the coastal region of the mainland proper, the remaining third being in peninsular Skåne.

Peninsular Skåne

Since the frequency of the 11 blackberry species in peninsular Skåne, represented by at least one square with a frequency exceeding zero, has already been discussed in detail (cf. p. 62), it remains only to relate the peninsula to the rest of the area investigated.

Of the ten species that are less frequent with respect to the whole area investigated, four species have been found exclusively in the peninsular region, viz. *insularis, axillaris, nitidus* and *vestitus,* while a fifth species, *sprengelii,* appears also in the coastal region of the mainland proper.

From the eight species that are more frequent with respect to the whole area investigated six species are found in peninsular Skåne, only one, *lindebergii,* however, having its centre of distribution on the peninsula, with 87 % of the Total Frequency in the peninsular region. Number two, in this respect, is *radula* (19 %), followed by *corylifolius* and *plicatus* with 10—11 %, and, finally, *nessensis* and *thyrsanthus* having only 4—5 % of their respective Total Frequencies on the peninsula.

The Island of Öland

Rubus corylifolius accounts for 84 % of the Total Frequency of the four blackberry species occurring on the island of Öland, with *plicatus* as number two (12 %), followed by *nessensis* and *thyrsanthus* (3 and 1 % respectively).

Yet, the island of Öland represents only 4 % of the Total Frequency of *corylifolius,* while the other three species are represented by at most 1 % each.

The Island of Gotland

Only one blackberry species was found on the island of Gotland during the investigation, viz. *corylifolius,* and what is more, the species reaches frequency 1 in one square only.

Inferences

As regards Number of Species three regions are about equal, viz. peninsular Skåne, the coastal band of the mainland proper and the intermediate region of the latter area. Of the Number of Species in those regions, considered individually, only one third of them occur in the inland and on the island of Öland. The island of Gotland comes last, with only one species.

Twice as many species as on the peninsula have the major part of their Total Frequency in the coastal band, while the peninsula is superior to the intermediate region of the mainland proper. No species has the major part of its Total Frequency in the inland or on the islands.

EASTERN VERSUS WESTERN DISTRIBUTION

Principle of Division

The area of investigation has been divided into two halves by a vertical line which forms the eastern boundary of the row of standard squares with the two squares numbered 1020 and 5020 in Fig. 1. Thus, in the south the dividing line passes through western Blekinge and farther north runs across the northern part of the lake Vättern.

The eastern half comprises 739 standard squares, while the remaining 760 squares belong to the western half.

Species Occurring in Only One of the Two Halves

Eleven of the 18 *Rubus* species discussed have been found exclusively in one of the two halves of the area investigated, five in the eastern half and six in the western. A list of the species is given below:

Exclusively eastern species

bellardii
scheutzii
sulcatus
hartmanii
fuscus

Table 6. **6 a.** Values of frequency from three different aspects, calculated separately for the eastern and western halves of the area investigated. Quotients also given. **6 b.** Ranking lists according to the quotients in a.

Rubus species	Number of Squares			Mean Frequency			Maximum Frequency			Number of Squares	Mean Frequency	Maximum Frequency
	E	W	E:W	E	W	E:W	E	W	E:W			
corylifolius	162	111	1.5	8.7	3.1	2.8	36	20	1.8	7	1	4
thyrsanthus	53	3	17.7	1.8	2.0	0.9	8	4	2.0	1	7	3
radula	19	9	2.1	3.0	2.2	1.4	12	9	1.3	5	4	5.5
	E	W	W:E	E	W	W:E	E	W	W:E			
plicatus	85	235	2.8	7.1	7.5	1.1	27	27	1.0	4	6	7
nessensis	237	411	1.7	2.4	3.0	1.3	12	15	1.3	6	5	5.5
lindebergii	3	28	9.3	1.3	2.9	2.2	2	12	6.0	3	2	2
scissus	2	25	12.5	1.0	1.8	1.8	1	8	8.0	2	3	1

Exclusively western species

taeniarum
insularis
sprengelii
axillaris
nitidus
vestitus

Species Occurring in Both Halves

The remaining seven species have been found in both halves of the area investigated. These species are identical with species No. 1—7 in the ranking list based on the values of Weighted Frequency (cf. Table 3 e).

In order to investigate the eastern and western features of these seven species values for three different aspects of frequency have been calculated separately for the two halves. The aspects of frequency chosen are Number of Squares, Mean Frequency, and Maximum Frequency i.e. as for Weighted Frequency of the whole area investigated.

The outcome is virtually unambiguous as all but two of the 21 pairs of eastern and western values point to a division into an eastern group with three species and a western group with four species as listed below:

Mainly eastern species

corylifolius
thyrsanthus
radula

Mainly western species

plicatus
nessensis
lindebergii
scissus

That the seven species display distinctive eastern or western features respectively is simply illustrated by the quotient of the values of the two different halves of the area investigated, separately for each aspect of frequency.

Table 6 a gives the values of frequency from the three different aspects dealt with, calculated separately for the two halves of the area investigated, as well as the quotients. In Fig. 16, the dividing line between eastern and western occurrence has been indicated in the Profile of Frequency, an aspect not discussed below.

To begin with Number of Squares, four species have quotients from 1.5—2.8, while the three species *lindebergii, scissus* and *thyrsanthus* have values as high as from 9.3—17.7.

The corresponding quotients of Mean Frequency values are perhaps less convincing as the basis of a division into eastern and western species. *Rubus thyrsanthus* and *plicatus* lie around 1 (0.9—1.1), i.e. they do not belong distinctly to either east or west, whereas the other five species are to be found between 1.3 and 2.8.

Finally, from the aspect of Maximum Frequency three groups of species are discernible. One species, *plicatus,* has equal values in the two halves of the area investigated, the quotient consequently being 1.0, four species have quotients from 1.3—2.0, and the third group, *lindebergii* and *scissus* quotients between 6.0 and 8.0.

It could be added that ten of the twenty-one quotients discussed have a value of 2.0 or more. Also, six of the seven species dealt with, at least from one aspect of frequency, are represented in one of the two halves of the area investigated by a value double or more of that of the other half. And what is more, the two exceptional pairs of values mentioned above, viz. Mean Frequency for *thyrsanthus* and Maximum Frequency for *plicatus,* constitute the quotients 0.9 and 1.0 respectively, which cannot be considered particularly diverging.

Thus, taking all available facts into consideration the division of the seven species that occur in both halves of the area investigated into Mainly Eastern and Mainly Western species, seems to be well-founded.

In an attempt to subdivide these seven species with reference to their eastern and western traits, the relative rank of the quotients has been used (Table 6 b).

Thus, *lindebergii* and *scissus* are two species occurring almost exclusively in one half only of the area, while in *plicatus* and *nessensis* this feature is least pronounced. The first two species are never ranked lower than 3, whereas the latter pair have rank numbers between 4 and 7. One of the Mainly Eastern species also has a rather narrow range of rank numbers but the promising pattern is spoiled by *corylifolius* and *thyrsanthus,* both with rank numbers varying between 1 and 7.

Rating the three different aspects of frequency equal it then might be permissible to subdivide the Mainly Western species into two groups, one containing *lindebergii* and *scissus* being more pronouncedly western in character, and the other, consisting of *plicatus* and *nessensis,* being less so. A corresponding subdivision of the Mainly Eastern species should not be undertaken.

Lastly, the outcome of the quotient calculations will be examined from a somewhat different point of view.

Earlier in this paper it was stated that ". . . Number of Squares, Mean Frequency, and Maximum Frequency are aspects of frequency which result in roughly the same ranking of the Swedish blackberry species" (p. 52). This implies that any species having, for example, a considerably greater Number of Squares than some other species is superior from the two other aspects of frequency, too. If instead we compare the two vertical halves of the area investigated with respect to the seven most frequent species, the same tendency towards co-variation of the values from the three different aspects of frequency is still there, though considerably weaker.

SPECIES NOT INCLUDED

Native Species

(1) Five of the wild blackberry species recognized by HYLANDER (1955) as being native to Sweden (the *Corylifolii* group is omitted here), were not found in a single locality during the investigation. They are:

affinis WEIHE & NEES 1822
pyramidalis KALTENBACH 1844
polyanthemus LINDEBERG 1882
vestervicensis C. E. GUSTAFSSON 1938
dasyphyllus ROGERS 1900

(2) *Rubus langei* G. JENSEN 1887, a wild blackberry species discovered for the first time in Sweden during this investigation at Ystad, in the southernmost part of Skåne (cf. OREDSSON 1966). As there is only a single

locality and the stretch of road investigated in the square concerned is longer than 36 km the frequency is zero.

(3) The two blackberry species related to *villicaulis* KOEHLER 1824 recognized from Bohuslän by WATSON (1958), and briefly discussed by the present author in a previous paper (cf. OREDSSON 1969 p. 455). Two localities have been found, both in the square lying immediately north of the square where the town of Lysekil is situated.

(4) *Rubus caesius* L. 1753, dewberry, found in a sufficiently large number of localities to give a frequency above zero, but regarded as unsuitable for comparison with the other wild members of *Rubus* subgenus *Rubus*. As dewberry is so different from blackberries in its general appearance there is an obvious risk of missing it when making observations by car, so that it is presumably under-represented.

Cultivated Species

Three cultivated species have been found as escapes.

Rubus armeniacus FOCKE 1874, a species cultivated for its fruit, is the only one found in sufficient numbers to attain a frequency above zero. But, as its distribution is due to the activity of man in the first place, and not so much to soil and climate conditions as is the case with wild blackberries, it has not been discussed here.

The other two cultivated species, *laciniatus* WILLDENOW 1806, and *villosus* AITON 1789 or a related species (cf. FOCKE 1914 pp. 89—90), have been met with just two or three times during the investigation, the Total Frequency remaining zero.

Inside gardens only, an unidentified species has also been observed bearing a certain resemblance to the *Corylifolii* group.

WORK PLANNED

The author plans to continue his work on the data presented along five principal lines:

(1) A separation of the frequency maps presented at a maximum of four levels of frequency, the stratified frequency maps thus produced indicating the range according to a given definition, as well as areas of connected squares.

(2) A phytogeographical division of the area investigated will be attempted on the basis of a compilation of the stratified frequency maps.

(3) The possibility of making good predictions of lower levels of frequency from results obtained at a given level of frequency will be investigated.

(4) A comparison will be made between the data presented and the collections of *Rubus* in the four largest Swedish Herbaria to get an idea of comprehensiveness in the data presented. At the same time it will presumably be possible to show that Herbarium collections may give rise to a false picture of the frequency of species.

(5) A comparison will be made between the phytogeographical division, point (2) and other maps of the area investigated, showing various aspects of climate, soil conditions, degree of cultivation and other factors that may be connected with the distribution of blackberries in Sweden.

LITERATURE CITED

FOCKE, W. O. 1910, 1911, 1914. Species Ruborum I—III. — Bibl. Bot. 72 (1—2), 83.

HYLANDER, N. 1955. Förteckning över Nordens växter. 1. Kärlväxter. — Lund.

LINDMAN, C. A. M. 1918, 1926. Svensk fanerogamflora. 1 & 2 uppl. — Stockholm.

NEUMAN, L. M. 1901. Sveriges flora (Fanerogamerna). — Lund.

OREDSSON, A. 1959. Björnbärsinventering i norra Skåne. — Natur i Göinge (Hässleholm).

— 1961. Björnbärsinventering i norra Skåne II. Tillägg och rättelser. — Natur i Göinge (Hässleholm).

— 1966. Rubus langei funnen i Sverige. — Bot. Notiser 119: 371—372.

— 1969, 1970. Drawings of Scandinavian plants 17—44. Rubus L. Subgen. Rubus. — Bot. Notiser 122: 1—8, 153—159, 315—321, 449—456; 123: 1—7, 213—219, 363—370, 447—454.

WATSON, W. C. R. 1958. Handbook of the Rubi of Great Britain and Ireland. — Cambridge.

Taxonomy, Variation and Evolution in Representatives of Leopoldia Parl. (Liliaceae) in the Southern and Central Aegean

By Bengt Bentzer

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

ABSTRACT

BENTZER, B. 1973. Taxonomy, variation and evolution in representatives of Leopoldia Parl. (Liliaceae) in the southern and central Aegean. — Bot. Notiser 126: 69—132.

A taxonomical revision of representatives of *Leopoldia* PARL. (Liliaceae) in the southern and central Aegean is presented. The following taxa are recognized: *L. comosa* (L.) PARL., 2n=18 (27); *L. weissii* (FREYN) FREYN ex HELDR., 2n=18, 36 (54); *L. cycladica* (DAVIS & STUART) GARBARI ssp. *cycladica*, 2n=36, 54; *L. cycladica* ssp. *subsessilis* BENTZER ssp. nov., 2n=36; *L. dionysica* (RECH. FIL.) BENTZER comb. nov., 2n=18, 36; *L. spreitzenhoferi* HELDR., 2n=18, 36.

CONTENTS

INTRODUCTION

The present investigation forms part of the study of the genus *Leopoldia* PARL. in the Aegean. Previous cytological studies on *Leopoldia* have been published (BENTZER 1969, 1972 a, b, c). The aims have been to elucidate the morphological variation, reproductive biology and trends in the evolution in order to present a taxonomical revision of the endemic representatives of the genus. No attempt has been made to make a complete revision of the pan-Mediterranean *L. comosa* complex.

The study of *Leopoldia* is part of the research programme on the Aegean flora initiated by H. RUNEMARK in 1957.

Interpretation of the Aegean *Leopoldia*s has been most confused owing to a high degree of local differentiation, a fact that led RECHINGER (1943 b) to state that — "Die Gattung *Muscari* entwickelt speziell im östlichen Mittelmeergebiet eine grosse Formenmannigfaltigkeit. Sie scheint in dieser Hinsicht z.B. der Gattung *Ophrys* nicht viel nachzustehen".

MATERIAL

This study is based upon both living material and herbarium material. The living material was collected between 1967 and 1972. A number of colleagues have contributed with large bulb collections, viz. I. BJÖRKQVIST (Bt), R. v. BOTHMER (B), L. ENGSTRAND (E), M. GUSTAFSSON (G), A. HANSEN (H), B. HÄGERHÄLL (Hl), J. PERSSON (P), H. RUNEMARK (R), S. SNOGERUP (S) and A. STRID (St). My own collections are designated (Be).

About 1400 bulbs representing some 200 populations from the Aegean have been cultivated in the greenhouses of the Department of Plant Taxonomy, Lund. Cultivated material has been successively dried and is now deposited at LD. The code to the cultivated collections is given in Appendix 1.

Herbarium material has been put at my disposal from the following Herbaria: B, BM, C, E, FI, G, K, LD, LY, W, and WU. Abbreviations are in accordance with the Index Herbariorum (LANJOUW & STAFLEU 1964). Material has also been available from the GOULIMI—GOULANDRIS Herbarium at Kifissia (Athens).

METHODS

(1) All herbarium material that has been referred to in the taxonomy section has been seen unless otherwise mentioned.

(2) In the list of synonyms under each taxon citations from the standard floras of the area are given, i.e. BOISSIER (1884), HALÁCSY (1904), HAYEK (1933), RECHINGER (1943 a, b). Other works are, as a rule, cited only when they are of nomenclatural importance.

(3) Morphological terms are essentially in accordance with STEARN (1966).

(4) The spelling of geographical names mainly follows The Times Atlas (BARTHOLOMEW 1956) and the charts of the British Admiralty.

(5) All figures in the descriptions are based upon a combination of data from measurements of natural living material, cultivated material and herbarium material.

(6) Drawings and photos have been made from living cultivated material.

(7) The morphology of seed surfaces was studied by means of a Cambridge Stereoscan

Mark II:a at the EM lab., Zoological Institute, Lund.

(8) The measurements of seeds were made from seeds collected in the field. Twenty seeds were measured from each locality.

(9) The pollen grains were measured after staining in cotton blue for at least half an hour. Ten grains were measured from each plant. Only grains obtained from cultivated plants were used.

(10) Male fertility was estimated by determining the percentage of stainable pollen using cotton blue (BENTZER 1972 c).

(11) Measurements of the morphological variation in natural populations were carried out in 1969. Ten different characters in the same relative positions and at the same stage of development were measured in 26 natural populations in all, representing all recognized taxa. Measurements of fertile flowers and pedicels of fertile flowers were made on the third lowest fertile flower. Measurements of sterile flowers and of pedicels of sterile flowers were made on the lowest sterile flower. The breadth of the perigon was measured at the broadest part. Twenty plants were usually measured in each population. The plants were chosen in such a way that the probability of measuring two or more plants from the same putative clone was negligible. In some cases it proved impossible to measure all the 10 characters in all 20 plants.

(12) For the crossings 3—7 flowers of the same female parent were emasculated and isolated in paper bags. The emasculated flowers were left for between 3 and 7 days, depending on the taxon, before pollination which was repeated on 3 successive days. After pollination the flowers were again isolated. After fertilization, i.e. when the capsule started to develop, the isolation bags were removed. Crossings have so far only been possible between plants with more or less similar times of flowering. Attempts were made to freeze pollen for future use, but the viability of such pollen was found to be very low or nil after a few days. Unfrozen pollen remained viable for at least two weeks after anthesis.

(13) Forced selfings were carried out in a similar way to crossings, i.e. pollen from one plant was spread by hand over a number of mature stigmas (usually between 5 and 10) of the same plant. In so-called spontaneous selfings the inflorescences were simply isolated. Isolation bags were removed as soon as the capsule started to develop.

(14) In order to determine the length of the flowering period of single flowers and the rate of development of the inflorescence, a number of plants at the same stage of development were selected. The development of the first 14 fertile flowers at least was followed for each plant. Flower initiation was defined as the time when the perigon opened at the apex and at least one of the anthers of the upper whorl had dehisced. Withering was defined as the time when the teeth at the apex of the perigon lost their colour and became soft. The development of the flowers and inflorescences was observed twice a day for three weeks.

(15) In order to measure the degree of protandry a number of plants at the same stage of development were selected, i e. having inflorescences in which all stages were present, from buds to withered flowers.

All flowers were subjected to forced selfing. The pollinated flowers were left overnight and then each stigma was stained in cotton blue, soaked in a weak pectinase solution, squashed, and examined for germinated pollen grains.

The degree of protandry was calculated by means of the rate of inflorescence development and the length of the flowering period of each individual flower. This method is, of course, only applicable when incompatibility does not affect the germination of the pollen grains which apparently is not the case in the present study.

DELIMITATION OF THE GENUS

To date the whole *Hyacinthus-Muscari* complex has mainly been studied from dried material. Very little attention has been given to large-scale observation on living material under natural conditions or in cultivation. Good morphological characters are generally few in living material and drying destroys some of the best ones such as shape and colour of the perigons. The entire complex is in great need of both experimental and field studies in order to elucidate the actual relationships between taxa. The delimitations of taxa hitherto proposed must be regarded as good attempts to demonstrate such relationships but none of them can be considered as final.

In the following, *Leopoldia* PARL. will be treated as a distinct genus. The splitting of *Leopoldia* into sect. *Leopoldia* and sect. *Tenuiflorae* which was proposed by GARBARI and GREUTER (1970) will not be followed. The only character to separate the two sections on is the shape of the fertile flowers. In the present material *L. weissii* displays sufficient variation in this character to be included in both sections (see variation section). Apart from the division of *Leopoldia* into two sections the taxonomical concept that GARBARI and GREUTER (op. cit.) applied to *Leopoldia* and the closely related genera *Muscari* MILL., *Muscarimia* KOSTEL., and *Pseudomuscari* GARBARI & GREUTER will be followed.

The splitting of *Muscari* sensu lato into four separate genera is a hazardous undertaking owing to our very incomplete knowledge of the Asiatic taxa, which may constitute a number of intermediates. On the other hand the maintenance of *Muscari* in the broad sense would imply a very heterogeneous genus in no way equivalent to the generally accepted and allied genera *Bellevalia, Hyacinthella* and *Brimeura* (GARBARI & GREUTER 1970).

GARBARI (1968 a) demonstrated the karyological difference between *Muscari* MILL. sensu GARBARI, *Muscarimia* and *Leopoldia.* These differences were contradicted in GARBARI & MARTINO (1972) and BENTZER (1972 b) where it was shown that *Leopoldia gussonei* PARL. and *Leopoldia bicolor* (BOISS.) EIG & FEINBR. have karyotypes similar to those of members in the genus *Muscari* sensu stricto. The morphological features of these two taxa are, however, in close agreement with those of the genus *Leopoldia.*

Diagnostic differences between the genera *Leopoldia, Muscari, Muscarimia* and *Pseudomuscari* are found in the sterile flowers and in the form and colour of the fertile flowers (see GARBARI & GREUTER 1970):

(1) *Leopoldia* has prominent sterile flowers which are bluish to violet unlike the fertile ones. The other genera usually lack conspicuous sterile flowers which if they occur are usually a paler shade of the basic colour of the fertile flowers.

(2) The fertile flowers of *Leopoldia* are more or less zygomorphic with apophyses of varying shape on the shoulders (Figs. 23, 24, 29). The other genera have actinomorphic fertile flowers.

HISTORICAL OUTLINE

In 1844 KOSTELETZKY divided the genus *Muscari* into three genera, i.e. *Muscari, Muscarimia* and *Etheiranthus,* the last genus corresponding to *Leopoldia* PARL. The two new genera of KOSTELETZKY were nomina nuda, but they do nevertheless serve to support the decision of the author to make a more natural subdivision of the *Muscari* complex.

When PARLATORE (1845) described *Leopoldia,* he based the genus on three species originally described in three different genera, viz. *Hyacinthus comosus* L. (which was selected as lectotype for the genus *Leopoldia* by GARBARI & GREUTER 1970), *Muscari maritimum* DESF. and *Bellevalia pinardii* BOISS. The name *Leopoldia* was, however, not available as it had already been used for a new genus in Amaryllidaceae, *Leopoldia* HERBERT in 1820. GARBARI and GREUTER (op. cit.) proposed *Leopoldia* HERBERT as nomen rejiciendum vs. *Hippeastrum* HERBERT, and proposed *Leopoldia* PARL. as a nomen conservandum, which was supported by the committee for Spermatophyta in 1972 (Taxon 21: 531).

SALISBURY (1866) described *Leopoldia* PARL. as *Comus* SALISB. which will be the correct name of the genus if *Leopoldia* PARL. is not conserved.

Leopoldia PARL. has never been generally accepted as a genus. BAKER (1871) treated *Leopoldia* PARL. as an infrageneric unit within *Muscari* MILL. In 1876 HELDREICH did not treat *Leopoldia* as a separate genus but included it in *Bellevalia* LAPEYR. Two years later (1878) the same author made the only monographic survey of *Leopoldia* in which he included 15 good species and 3 dubious species. HELDREICH (1878) also divided *Leopoldia* into two infrageneric categories, i.e. *Breviflorae* and *Tenuiflorae.*

BOISSIER (1844) did not separate *Leopoldia* from *Bellevalia* and he described *Bellevalia pinardii* [*Leopoldia pinardi* (BOISS.) PARL.]. In Flora Orientalis (1884) BOISSIER altered his opinion and accepted the separation of *Leopoldia* from *Bellevalia.* He then treated *Leopoldia* as a section within *Muscari,* but also kept in the section the two infrageneric categories of HELDREICH 1878. BOISSIER's way of treating *Leopoldia* was followed by others including, for instance, ASCHERSON & GRAEBNER (1905).

RICHTER (1890) treated *Leopoldia* as an infrageneric unit within *Muscari* without defining its taxonomic rank, while KRAUSE (in ENGLER 1930) treated *Leopoldia* as a section of *Muscari.*

HALÁCSY (1904) kept *Leopoldia* as a genus without further division, while HAYEK (1933) and RECHINGER (1943 a, b) did not separate *Leopoldia* from *Muscari* in any way.

Quite recently STUART (1965) and ZAHARIADI (1966) proposed *Leopoldia* as a subgenus in *Muscari* MILL., while GARBARI (1968 a, b; 1969) and GARBARI & GREUTER (1970) keep *Leopoldia* as a distinct genus. GARBARI & GREUTER (op. cit.) accepted the further division of *Leopoldia* into two separate sections, i.e. sect. *Leopoldia* (*Breviflorae* HELDR.) and sect. *Tenuiflorae* (HELDR.) GARBARI & GREUTER, as proposed by HELDREICH (1878).

For further historical data see HELDREICH (1878), GARBARI (1968 b) and GARBARI & GREUTER (1970).

PRINCIPLES USED FOR TAXONOMIC DELIMITATION

In *Leopoldia,* as in any other critical biological complex, the delimitation of taxa is to a certain extent arbitrary. In this study I have chosen to use a broad taxonomic concept in order to make it taxonomically more useful. Rather wide variation in taxa is permitted. *L. weissii* is particularly variable, and the extremes of its range of variation are morphologically separated from each other to the same degree as are other recognized taxa. Between these extremes are, however, a large number of intermediate populations distributed all over the area of investigation but not forming any obvious ecological and geographical pattern.

As a rule cytological data add very little information that is of use in the delimitation of taxa, except in *L. comosa* which has a characteristic karyotype (BENTZER 1972 c). All other taxa have essentially similar basic karyotypes (BENTZER in prep.). Different chromosome numbers constitute sterility barriers which in themselves are sufficient to separate biological units from each other. For practical reasons it would, however, be unwise to use polyploidy as a criterion for taxonomic delimitation in this material, since it is generally not possible to correlate any given morphological feature to a particular chromosome number.

Taxonomic delimitation has mainly been based on: (1) Morphological features, (2) Intermediate form series, (3) Geographical distribution, (4) Preference of habitat.

The crossing experiments carried out have not yet given sufficient results with respect to sterility barriers. When these results are available it may be necessary to some extent to revise the taxa recognized here.

The following taxa are recognized in the area of investigation:

L. comosa (L.) PARL., 2n=18, (27).

L. weissii (FREYN) FREYN ex HELDR., 2n=18, 36, (54).

L. cycladica (DAVIS & STUART) GARBARI ssp. *cycladica,* 2n=36, 54.

L. cycladica ssp. *subsessilis* BENTZER ssp. nov., 2n=36.

L. dionysica (RECH. FIL.) BENTZER comb. nov., 2n=18, 36.

L. spreitzenhoferi HELDR., 2n=18, 36.

GENERAL DESCRIPTION OF THE SOUTHERN AND CENTRAL AEGEAN REPRESENTATIVES OF LEOPOLDIA

All species are perennials with tunicated *bulbs*. The tunics are usually brown, greyish or pinkish. Many taxa proliferate to a varying degree. The bulbils are not covered by a protective layer and they sprout very soon. The *leaves* are usually as long as the scape or longer. They are equitant, entire, striate and more or less canaliculate. The margins are denticulated to a varying degree. The number of leaves varies from 2 to more than 10. They are recurved to flaccid and sometimes more or less erect. The width varies between 1 and c. 50 mm. The apex of the leaves is usually more or less acute. The *scape* is glabrous and usually erect. The height varies from a few centimetres to more than 100 cm. The *inflorescence* is a raceme composed of fertile as well as apical sterile flowers. The inflorescence elongates during flowering and becomes cylindrical to conical and more or less loose when fully expanded. The *bracts* are between 0.5 and 2 mm long and scale-like. The *fertile flowers* are tubular to more or less urceolate with apophyses of varying shape on the shoulders near the apex. In the distal part of the perigon there is a more or less pronounced constriction. At the apex there are usually 6 teeth of somewhat varying shape and size. The colour of the lower part of the perigon is a dirty brown, greenish-yellow or creamy. The upper part of the perigon apart from the teeth is a darker, brown—dirty brown—red-brown, greenish, or dark greenish-brown. The teeth are whitish, creamy or yellow. The perigon dehisces in its proximal part when the capsule expands. The *pedicels* of the fertile flowers are of varying length, i.e. from 0 to 30 mm. In early bud they are suberect to erect but in late bud they are sometimes flaccid or bent downwards. During flowering the pedicels are usually more or less horizontal, sometimes ascending. The *sterile flowers* vary in size and shape. They are usually from 1 to 8 mm long and from 1 to 6 mm broad, tubular, obovoidal to obconoidal and generally bright blue or violet. The *pedicels* of the sterile flowers are more or less horizontal or ascending and from 0 to 30 mm long. The *stamens* are arranged in two whorls of 3 in the upper part of the perigon, the one somewhat higher than the other. The *anthers* are usually red to brownish and dehisce by means of longitudinal slits. The *pistil* is composed of 3 carpels with marginal placentation. The *stigma* is faintly three-lobed. The *capsules* are loculicidal and have a triquetrous outline in transverse section. The *seeds* are spherical to pear-shaped. There are usually two seeds in each loculus. The seeds are dark violet to black, with a bright, more or less heavily ridged to alveolate surface in the equatorial region. The flowering period is from March to June.

The distribution of the entire genus is centred in the Mediterranean region. In the west the genus occurs on the Canary Islands and Madeira, as far north as central Germany and in southern European Russia. It is found in northern Africa and the Middle East, and as far east as Afghanistan.

The genus contains about 20 species. Many more have been described but most of them presumably do not deserve taxonomic recognition.

KEY TO THE RECOGNIZED TAXA

1. Fertile flowers with whitish or creamy teeth. Sterile flowers forming a corymb. Often growing in fields .... *L. comosa*
   Fertile flowers with yellow to yellowish (rarely whitish or creamy) teeth. Sterile flowers not forming a corymb. Rarely growing in fields 2
2. Pedicels of fertile flowers often forming an angle of c. 45° with the stem. Opening of tube in fertile flowers less than 2 mm. Pollen grains usually 36—44 μ long. Endemic to Kriti .... *L. spreitzenhoferi*

Pedicels of fertile flowers usually horizontal. Opening of tube in fertile flowers usually more than 2 mm. Pollen grains usually more than 44 μ long 3

3\. Pedicels of fertile flowers 0—3 mm long. Capsules with valves having an oblong to elliptic outline in transverse section .... *L. cycladica* 4

Pedicels of fertile flowers usually more than 3 mm long. Capsules with valves with an ovate to triangular outline in transverse section 5

4\. Plant usually more than 20 cm. Leaves 5—40 mm broad. Fertile flowers 7—12 mm long. Pollen grains 46—58 μ long. Mainly on cliffs .... ssp. *cycladica*

Plant usually less than 20 cm. Leaves 2—12 mm broad. Fertile flowers 5—9.5 mm long. Pollen grains 42—52 μ long. Mainly in phrygana .... ssp. *subsessilis*

5\. Bulbs 3—6 cm in diameter. Pedicels of fertile flowers usually 10—25 mm. Mainly on small islands and on cliffs .... *L. dionysica*

Bulbs rarely exceeding 3 cm in diameter. Pedicels of fertile flowers usually 2—10 mm. Mainly in phrygana .... *L. weissii*

DESCRIPTIONS OF SPECIES AND SUBSPECIES

Nomina nuda are as a rule not mentioned in the text. The names *Leopoldia graeca* (HELDR.) HELDR. and *Leopoldia neumayrii* HELDR. were validly published in 1876 and 1878 respectively. *L. graeca* is described from Peloponnisos and *L. neumayrii* from Mt. Giona. No material of these taxa has been available, and since they are unlikely to change the present taxonomy they have been left out of consideration in the present study.

Leopoldia comosa (L.) PARL.

PARLATORE, Fl. Palermit. I: 438 (1845); HELDREICH, BSNMosc. 53. I: 64 (1878); HALÁCSY, Consp. Fl. Graec. III: 266 (1904); — *Hyacinthus comosus* LINNAEUS, Sp. Plant. I: 318 (1753); — *Muscari comosum* (L.) MILLER, Gard. Dict. ed. 8 no. 2 p.p. (1768), (not seen); BOISSIER, Fl. Orient. V: 291 (1884); HAYEK, Prodr. Fl. pen. Balc. III: 88 (1933); RECHINGER, Fl. Aeg.: 730 (1943 a); — *Bellevalia comosa* (L.) KUNTH, Enum. Plant. IV: 306 (1843). — Orig. coll.: LÖFLING, LINN no. 438. 15, Hispania no. 268 (LINN lectotype, microfiche seen).

Bellevalia Holzmanni HELDREICH, Sert. Pl. Nov. Fl. Hellenic. in Atti Congr. Firenze p. 228 (1876); — *Leopoldia Holzmanni* (HELDR.) HELDREICH, BSNMosc. 53. I: 65 (1878); — *Muscari Holzmanni* (HELDR.) FREYN, ÖBZ. 28: 88 (1878); BOISSIER, Fl. Orient. V: 292 (1884); — *Leopoldia comosa* var. *Holzmanni* (HELDR.) HALÁCSY, Consp. Fl. Graec. III: 266 (1904); — *Muscari comosum* var. *Holzmanni* (HELDR.) FIORI, Fl. anal. It. I: 192 (1898); VIERHAPPER, ÖBZ. 66: 166 (1916); HAYEK, Prodr. Fl. pen. Balc. III: 88 (1933); RECHINGER, Fl. Aeg.: 730 (1943 a). — Orig. coll.: HELDREICH et HOLZMANN, Herb. Fl. Hellenic no. 49, In colle Turcobuni prope Athenas, 19.4. 1875 (FI lectotype, G, W, WU).

Muscari Charrelii HAL. & NADJI in NADJI, Emp. Ott. Geogr. Bot.: 42 (1892); RECHINGER, Fl. Aeg.: 729 (1943 a); — *Leopoldia Charrelii* (HAL. & NADJI) HALÁCSY, Consp. Fl. Graec. III: 266 (1904); — *Muscari tenuiflorum* TSCH. ssp. *Charrelii* (HAL. & NADJI) HAYEK, Prodr. Fl. pen. Balc. III: 87 (1933). — Orig. coll.: HELDREICH Herb. Graec. Norm. no. 1084, in dumosis vallis Toumba prope Thessalonicam, 15.5. 1889, Leg. L. CHARREL (W Herb. Hal. lectotype, B, E, K, L). — Note: The selected type sheets of *Leopoldia charrelii* (HAL. & NADJI) HAL., i.e. HELDREICH Herb. Graec. Norm. no. 1084, all belong to *L. comosa*. They agree well with the original description of *L. charrelii*. However, a later collection by CHARREL (Salonique, collines arides, 5.5. 1892, E, FI), determined as *L. charrelii* and probably available to HALÁCSY and NADJI when describing *L. charrelii* is somewhat heterogeneous. Some specimens are *L. comosa* but some of the specimens are rather similar to a collection from Thasos (no. 336), grown in cultivation during this investigation (see under *L. weissii*).

Muscari Cousturieri GANDOGER, Fl. Cret.: 101 (1916); — *Muscari comosum* var. *Cousturieri* (GANDOG.) HAYEK, Prodr. Fl. pen. Balc. III: 88 (1933); RECHINGER, Fl. Aeg.: 730 (1943 a). — Orig. coll.: GANDOGER, Herb. creticum no. 13033, Mirabello, in agrestis Lassithi, 10.5. 1918 (LY lectotype). — Note: The type specimen was received by GANDOGER in 1914 as a bulb. It was grown in his garden and he obviously made the description from living material which was dried in 1918. According to the description, the sterile flowers are pinkish. In other characters the type specimen agrees well with typical *L. comosa.*

DUBIOUS SYNONYMS: *Leopoldia curta* HELDREICH, BSNMosc. 53. I: 65 (1878). — Orig. coll.: HELDREICH, rara in colle aprico petroso Turcobuni prope Athenas, ubi d. 17.4. 1875 (not seen). — Note: A sheet determined as *L. curta* from W, Herb. Hal. was seen: ad Elissum prope Athenas, 27.3. 1879, Leg. HELDREICH (W Herb. Hal. neotype). This collection definitely belongs to *L. comosa*. The original description agrees reasonably well with a not fully developed *L. comosa*.

Leopoldia Sartoriana HELDREICH, BSNMosc. 53. I: 66 (1878). — Orig. coll.: HELDREICH, Parnethis Atticae prope Dekeleiam, date not given (not seen). — Note: A specimen collected in May 1879 from locus classicus and determinated by HELDREICH was seen (W Herb. Hal. neotype). This specimen belongs to *L. comosa*. It is not clear from the original description whether the type sheet is an abnormal *L. comosa*, a poorly developed *L. comosa*, an atypical *L. weissii* or a good taxon of its own.

ILLUSTRATIONS: Figs. 29 A (inflorescence), 23 A (fertile flowers), 11 A (capsules), 25: 1—2 (seed surface).

Bulbs (1—)1.5—2.5(—3) cm in diam., usually at a depth of 10—30 cm. Tunics pinkish. *Scapes* (10—)20—45(—100) cm long. *Leaves* (2—)3—4(—5), green, linear, from half as long to 1.5 times as long as the scape, (3—)5—15(—22) mm broad, erect to more or less recurved. *Racemes* (5—)10—15(—25) cm long. Number of fertile flowers from 10 to c. 100. *Fertile flowers* (5—)7—9(—10) mm long, 4—8 mm in diam., tubular to subcampanulate with conspicuous shoulders varying in shape, contracted near apex. Colour in bud violet, during anthesis lower part of perigon light greenish-brown, upper part dirty brown to dark brown. Teeth at apex white to creamy. *Pedicels* of fertile flowers 4—20(—30) mm long, horizontal. *Sterile flowers* 10—c. 50, (2—)3—6(—9) mm long, 1—4(—5) mm in diam., tubular to turbinate to pear-shaped. Colour usually dark blue to violet, occasionally pink. *Pedicels* of sterile flowers (5—)10—25 (—30) mm long, horizontal to ascending, usually forming a conspicuous corymb. *Anthers* 0.7—0.9 mm long when dehisced. *Pollen grains* reniform to ellipsoidal, 42—52(—62) μ long. *Capsules* 0.5—0.8 cm in diam., broadly ovoidal. Each valve with an ovate to triangular outline in transverse section. *Seeds* 1.5—2.8 mm in diam., spheroidal to pear-shaped, surface composed of a number of wavy peaks. *Chromosome number* 2n=18, (27).

DISTRIBUTION: Common in Europe from central Germany and France southwards and common throughout Greece (Fig. 1). Also found in northern Africa, the Canary Islands, Madeira, southern Russia and the Middle East.

HABITAT: Mainly in disturbed habitats. Generally found in extensively cultivated tracts. Appears to have no special demands on soil conditions.

GENERAL REMARKS: On the islands of the south and central Aegean and at lower altitudes in Attiki and Peloponnisos the species is morphologically rather homogeneous. In southern Greek Macedonia a form series is found with narrow leaves, small capsules and comparatively few, somewhat smaller, fertile flowers. This form series has been described as a species under the name of *L. charrelii*. However, TURRILL (1932) even then pointed out that continuous transitions between *L. charrelii* and typical *L. comosa* were frequent and that he was unable to distinguish the former as a species. Material of *L. charrelii* has not been cultivated or investigated cytologically.

In northern Macedonia and in Dalmatia another form series is found with unusually long sterile flowers. It approaches *L. tenuiflora* (TAUSCH) HELDR. but does not have the blackish teeth on the perigon of the fertile flowers. No material of this form series has been cultivated.

From Peloponnisos and Attiki, *L. holzmanni* has been recorded. This taxon is said to be very similar to *L. comosa* but somewhat smaller, probably owing to modifications or ecotypic adaptation since it grows at relatively high altitudes. When

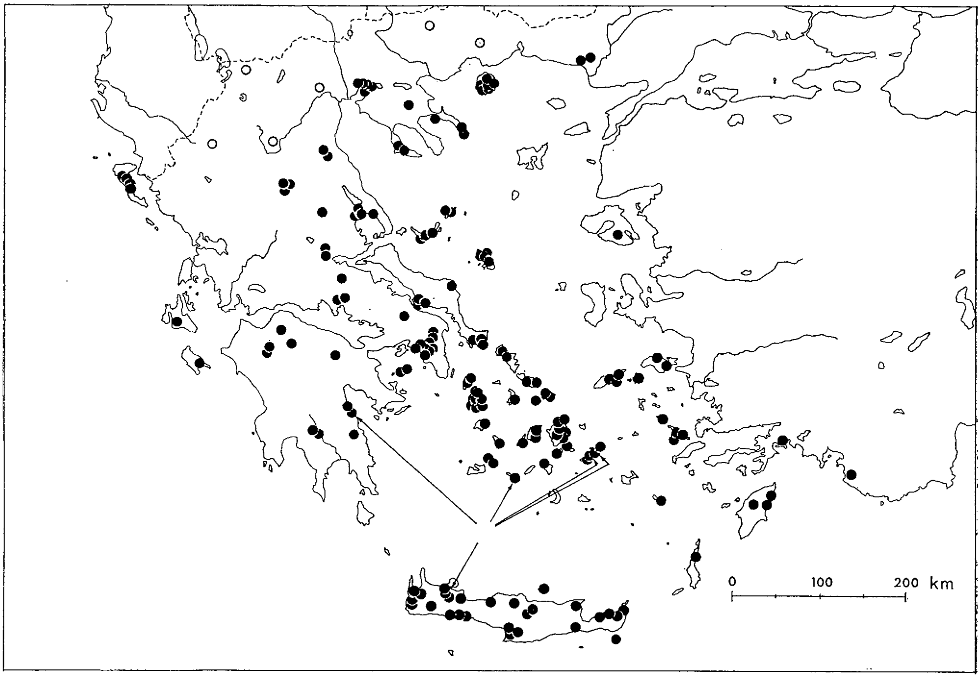


Fig. 1. *Leopoldia comosa.* Collecting sites for cultivated material and herbarium material investigated. Dots=normal forms. Rings=aberrant forms in N Greek Macedonia. Arrows indicate populations used for morphological measurements in nature.

L. comosa from the Kikladhes is grown under greenhouse conditions it is indistinguishable from typical *L. holzmanni,* a fact that indicates a high degree of modification in *L. comosa.*

As a rule *L. comosa* is fairly constant in certain characters such as length of pedicels and colour of fertile flowers, throughout its wide area of distribution. The bulbs have been used medicinally for more than 2000 years (cf. TÄCKHOLM & DRAR 1954) and they have probably been occasionally dispersed by man, which might account for the fact that morphologically similar types are found in remote areas. On the other hand, there is the fact of the geographical differentiation of *L. comosa* on the Greek mainland, for example.

The main characteristics of *L. comosa* are the dirty brown colour of the fertile flowers, the white to creamy teeth of the fertile flowers and the sterile flowers on long ascending pedicels usually forming a very conspicuous corymb.

Leopoldia weissii (FREYN) FREYN ex HELDR.

HELDREICH, BSNMosc. 53. I: 67—68 (1878); HALÁCSY, Consp. Fl. Graec. III: 268 (1904); — *Muscari Weissii* FREYN, ÖBZ. 28: 87—88 (1878); BOISSIER, Fl. Orient. V: 293—294 (1884); HAYEK, Prodr. Fl. pen. Balc. III: 89 (1933); RECHINGER, Fl. Aeg.: 730—731 (1943 a). — Orig. coll.: WEISS, Syro, April 1867 (G lectotype, microfiche seen).

Leopoldia Theraea HELDREICH, BSNMosc. 53. I: 69 (1878); HALÁCSY, Consp. Fl. Graec. III: 266 (1904); — *Bellevalia theraea* (HELDR.) NYMAN, Consp. Fl. Europ.: 733 (1882); — *Muscari Theraeum* (HELDR.) BOISSIER, Fl. Orient. V: 290 (1884); HAYEK, Prodr. Fl. pen. Balc. III: 87 (1933); RECHINGER, Fl. Aeg.: 730 (1943 a). — Orig. coll.: J. F. SCHMITH, in insula Thera, Mart. 1866, Herb. HELDREICH (W Herb. Hal. lectotype).

Leopoldia Gussonei PARL. sensu HELDREICH (1878) non PARLATORE (1852); HELDREICH, BSNMosc. 53. I: 68 (1878).

Muscari Weissii var. *karpatanum* VIERHAPPER, VZBG. 69: 301 (1919); HAYEK, Prodr. Fl. pen. Balc. III: 89 (1933); RECHINGER, Fl. Aeg.: 731 (1943 a). — Orig. coll.: PICHLER, no. 628, Karpathos, inter Pigadia et Aperi, 24.4. 1883 (WU lectotype, K).

Muscari Weissii var. *Sartorianum* (HELDR.) HAY. sensu HAYEK (1933) et RECHINGER (1943 a) p.p. non HELDREICH (1878); HAYEK, Prodr. Fl. pen. Balc. III: 89 (1933); RECHINGER, Fl. Aeg.: 731 (1943 a). (See under *L. comosa*.)

DUBIOUS SYNONYM: *Leopoldia Pharmacusana* HELDREICH, BSNMosc. 53. I: 66 (1878). — Orig. coll.: HELDREICH, Megali Kyra, in freto Salamis, 2.4. 1877 (not seen). — Note: Sheets collected by HELDREICH from locus classicus in 1878 (FI neotype, K, W Herb. Hal.) show a certain similarity to *L. weissii* as well as *L. comosa* and even to some extent to *L. dionysica*. However, *L. pharmacusana* may be a large *L. weissii* or perhaps a hybrid between *L. weissii* and *L. comosa*.

ILLUSTRATIONS: Figs. 29 B—C (inflorescence), 23 B—C (fertile flowers), 10 A—B (capsules), 25: 3—8 (seed surface).

Bulbs 1—3(—4) cm in diam., often at a depth of 2—15 cm. Tunics brownish—pink to greyish. *Scapes* (6—)10—30(—45) cm long. *Leaves* 3—5(—6), green to greenish-blue, linear, from half as long as the scape up to 50 % longer, (2—)3—15(—21) mm broad, more or less recurved, sometimes flaccid. *Racemes* 5—30 cm long. Number of flowers from 10 to c. 100. *Fertile flowers* (5—)6—10(—11) mm long, 3—6(—7) mm in diam., tubulate to suburceolate to subcampanulate usually with distinct shoulders of varying shape, contracted near apex. Colour in bud violet to light blue, sometimes light green, particularly on Attiki more or less distinctly striated, during anthesis lower part of perigon greenish-yellow, upper part brown to reddish-brown. Teeth at apex usually bright yellow, on Rodhos, Karpathos and Attiki somewhat creamy. *Pedicels* of fertile flowers (0—)3—8(—14) mm long, horizontal during flowering, sometimes somewhat ascending in fruit. *Sterile flowers* 5 to more than 50, (1—)2—6(—8) mm long, (1—)2—4(—5) mm in diam., tubular to turbinate to obovoidal. Colour usually blue to light blue. *Pedicels* of sterile flowers (0—)1—8(—12) mm long, usually horizontal, occasionally forming a loose inconspicuous corymb. *Anthers* 0.7—1.1 mm long when dehisced. *Pollen grains* 42—52 (—62) μ long, reniform to ellipsoidal. *Capsules* 6—9(—11) mm in diam., more or less conoidal to ovoidal. Each valve with a triangular to ovate outline in transverse section. *Seeds* 1.5—3 mm in diam., usually spherical, surface ridged. *Chromosome number* $2n=18, 36, (54)$.

DISTRIBUTION: Common on most Aegean islands except the small islands in the SE and in the Paros—Andiparos area. Rare on Kriti. Infrequent on the Greek mainland, Peloponnisos and the Anatolian west coast (Fig. 2).

HABITAT: A form series of large types grows in disturbed habitats, e.g. roadsides, margins of cultivated areas etc. (the field ecotype). Another form series of smaller types grows in phrygana communities apparently on calcareous as well as volcanic soil, more seldom on schist (the phrygana ecotype). Intermediate form series are mainly found in somewhat disturbed habitats.

GENERAL REMARKS: The species is polymorphic and displays considerable variation in a number of morphological characters such as colour and shape of the perigon of the fertile flowers, length of pedicels of the fertile as well as the sterile flowers, number of sterile and fertile flowers, shape of capsules, size of plants, etc.

Many islands have more or less characteristic local populations, such as: (1) Serifopoula (E of Serifos) where the sterile part of the raceme has a conspicuous

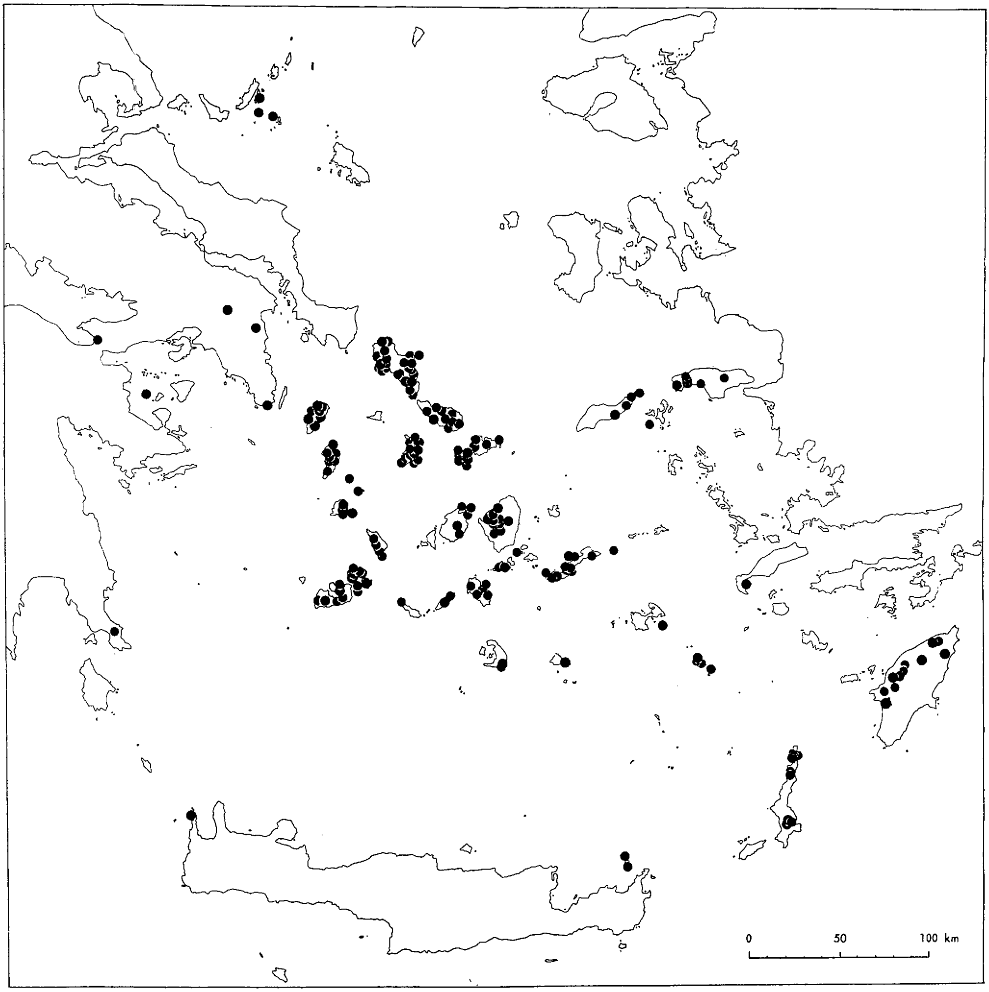


Fig. 2. *Leopoldia weissii*. Collecting sites for cultivated material and herbarium material investigated.

triangular form; (2) the islet of Ampelos near Siros (population no. 367) where the fertile flowers are exceptionally large (Fig. 23 no. 16); (3) the island of Tinos (population no. 328) where the apophyses on the perigon of the fertile flowers are very conspicuous (Fig. 23 no. 14). (4) In many populations from the Siros area the fertile flowers have short pedicels and dense racemes. In this respect they approach *L. cycladica* ssp. *subsessilis* but differ from the latter mainly in the size and shape of the capsules.

L. weissii is chiefly characterized by the yellowish teeth on the perigon of the fertile flowers, by the sterile flowers which do not form a conspicuous corymb, by the pedicels of the fertile flowers which are usually as long as the perigon or a few mm shorter, and by the valves in the capsules which have a triangular to ovate outline in transverse section.

SOME DEVIATING POPULATIONS

Population no. 336 from the island of Thasos was first referred to *L. comosa* because of the shape and colour of the perigon of the fertile flowers. It has creamy teeth, dirty-brown shoulders and a dirty greenish-brown lower part. However, the sterile flowers do not form the characteristic corymb of *L. comosa.* The karyotype was similar to that of *L. weissii* except for the attachment of the satellites (Bentzer in prep.) Morphologically this population falls somewhat outside the normal range of variation of *L. weissii.* Mainly on cytological grounds, I consider it most appropriate at present to place population no. 336 in *L. weissii.* When more is known about the variation of *Leopoldia* in N Greece it may perhaps prove necessary to unite this collection with part of Charrel's collection of *L. charrelii* (Salonique, collines arides, 5.5. 1892, E, FI) and a collection from Samos by E. Gathorne-Hardy (no. 225, E) to form a new taxon.

A population from Hagion Oros (no. 334) has greenish teeth on the perigon of the fertile flowers, and dark blue to violet sterile flowers. The karyotype is similar to that of population no. 336 in that the attachment of the satellites is similar.

Populations from Rodhos, Karpathos and Loutraki (Attiki) in cultivation (nos. 69, 99, 32, 67, 38 and 51) have pale yellow to creamy teeth on the perigon of the fertile flowers. In other characters they are essentially similar to typical *L. weissii.* Material collected by Rechinger on Rodhos (nos. 7014 L, W, 7357 W, 7230 W) was determined as *L. pinardi* (Boiss.) Parl., and seems to correspond rather well with my material, but differs from the type of *L. pinardi* (in G) in the breadth of the leaves and the shape of the perigon of the fertile flowers. According to Boissier (1884), *L. pinardi* has a distribution from western Turkey to Lebanon. I consider that the Rodhos, Karpathos and Loutraki material should be retained in *L. weissii,* at least until more is known about possible sterility barriers between it and more typical *L. weissii.* It is not possible at present to state whether the material from Rodhos, Karpathos and Attiki is linked together in a natural way by means of similar form series on Kriti and Peloponnisos, since living material from the last two areas is lacking.

TRANSITIONS BETWEEN L. WEISSII AND L. DIONYSICA

One population from Amorgos (no. 426) approaches *L. dionysica* in some vegetative characters, e.g. size of flowers and breadth of leaves. The population grows on a high cliff and in its vicinity. The pedicel length of the sterile as well as the fertile flowers, and the size of the sterile and fertile flowers (Fig. 17) agree more with *L. weissii* than with *L. dionysica.* These features together with the narrower leaves have caused me to place this population in *L. weissii.* It is not possible to distinguish *L. weissii* from *L. dionysica* on cytological grounds.

TRANSITIONS BETWEEN L. WEISSII AND L. COMOSA

In a number of localities populations of *L. weissii* are found adjacent to populations of *L. comosa.* In some localities the two species are found intermixed, as on Amorgos, Kithnos and Sirna for example. In such localities hybridization between the species is common. Cytological data support spontaneous backcrossing of such hybrids at least to *L. weissii* on Sirna (Bentzer 1969). Thus introgressive hybridization gives rise to a complete mixture of morphological characters in such localities.

It is very possible that introgressive products have been given taxonomic rank by earlier workers, e.g. *L. bouriana* Heldr., *L. graminifolia* Heldr. & Holzm., *L. andria* Heldr. These are unpublished names on herbarium sheets.

Leopoldia cycladica (DAVIS & STUART) GARBARI

GARBARI, Webbia 27: 289—297 (1972); — *Muscari cycladicum,* DAVIS & STUART, The Lily Year Book 30: 123—124 (1967). — Orig. coll.: DAVIS no. 1380, Greece, Cyclades: Amorgos, Langhada, 10.4. 1940 (E holotype).

Leopoldia cycladica (DAVIS & STUART) GARBARI ssp. **cycladica**

Orig. coll.: See under the species.

ILLUSTRATIONS: Figs. 29 D (inflorescence), 24 (fertile flowers), 11 C (capsules), 25: 9 (seed surface).

Bulbs 3—6 cm in diam., usually at a depth of 2—10 cm. Tunics brownish to pinkish. *Scapes* (10—)15—30(—45) cm long. *Leaves* (2—)3—5(—6), green, linear to lanceolate, as long as the scape or up to 50 % longer, (5—)10—25(—38) mm broad, suberect to recurved. *Racemes* 5—15(—23) cm long. Number of fertile flowers usually 15—40. *Fertile flowers* 7—10.5(—12) mm long, 5—7 mm in diam., tubular to suburceolate with shoulders often not very conspicuous, contracted near apex to a varying degree. Colour in bud usually bluish, during anthesis lower part of perigon greenish-yellow to light greenish, upper part dark brown to dirty brown. Teeth at apex yellow. *Pedicels* of fertile flowers 0—2 (—4) mm long, horizontal. *Sterile flowers* c. 10—20, 3—8 mm long, 2—4.5 mm in diam., usually obovoidal. Colour blue to light blue. *Pedicels* of sterile flowers 1—13 mm long, horizontal. *Anthers* 0.9—1.2 mm long when dehisced. *Pollen grains* usually ellipsoidal or ovoid, 48—54(—58) μ long. *Capsules* 9—17 mm in diam., broadly conoidal to broadly elliptical. Each valve with a narrowly ovate to triangular outline in transverse section. *Seeds* 2.5—3.5 mm in diam., usually spherical, surface ridged. *Chromosome number* 2n= 36, 54.

DISTRIBUTION: A central Aegean endemic, restricted to a few islands in the southern Kikladhes (Fig. 3).

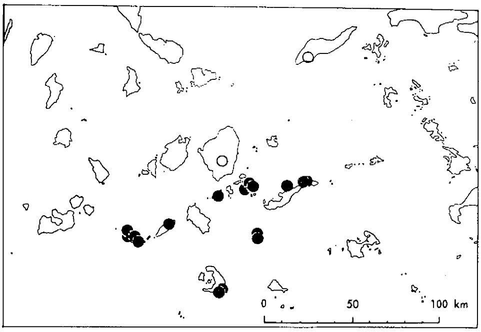


Fig. 3. *Leopoldia cycladica* ssp. *cycladica.* Collecting sites for cultivated material and herbarium material investigated. Dots = normal forms. Rings = dubious determinations.

HABITAT: Preferably on limestone cliffs. Sometimes growing in phrygana communities close to cliffs.

GENERAL REMARKS: The subspecies is usually quite distinct, but some populations are intermediate between this subspecies and ssp. *subsessilis* and are thus difficult to determine. Such transitional form series are mainly found on islands between eastern Paros and Amorgos, e.g. Iraklia and Karos.

When describing *L. cycladica,* DAVIS and STUART (1967) regarded it as the only uniformly hexaploid species in the area. However, on Nikouria (N of Amorgos) and in the western part of Folegandros tetraploid populations were found which are almost indistinguishable from the hexaploid ones.

In locus classicus, the morphological variation of the population is considerable and introgressive hybridization with *L. dionysica* has probably taken place. Many plants in the population are similar to *L. dionysica,* and of particular interest is that most plants have a fragile stem, a character which they share with *L. dionysica* from Anafi (nos. 48 and 421). This character seems to be unique for these two populations.

The main characteristics for the subspecies are the short or almost lacking pedicels of the fertile flowers, the large capsules which usually drop off while still containing seeds, the broad leaves and the comparatively large seeds.

Leopoldia cycladica (DAVIS & STUART) GARBARI ssp. **subsessilis** BENTZER ssp. nov.

Orig. coll.: BENTZER, Greece, Kikladhes, Paros: 1.5 km SE Korifi Karomboli, phrygana, limestone, 150—200 m.s.m., 28.4. 1969 (LD holotype).

Similis *L. cycladicae* ssp. *cycladicae* sed floribus, capsulis et seminibus minoribus.

ILLUSTRATIONS: Figs. 5 (habit, bulb, fertile flower, capsule), 29 E (inflorescence), 24 (fertile flowers), 11 B (capsule), 25: 10—11 (seed surface).

Bulbs 1—2.5 cm in diam., usually at a depth of 2—10 cm. Tunics greyish to pale pink. *Scapes* 5—20(—26) cm long. *Leaves* (2—)3—5, green, linear, as long as the scape or up to 50 % longer, 2—8(—12) mm broad, usually recurved. *Racemes* 2.5—9(—11) cm long. Number of fertile flowers usually 15—30. *Fertile flowers* 5.5—8(—9.5) mm long, 3—5.5 mm in diam., tubular to suburceolate with shoulders of varying shape, contracted near apex. Colour in bud usually blue to violet, during anthesis lower part of perigon pale greenish-yellow, upper part dark brownish. Teeth at apex yellow. *Pedicels* of fertile flowers 0—2(—3) mm long, horizontal. *Sterile flowers* usually less than 10, 3—6(—7) mm long, 1.5—3(—3.5) mm in diam., obovoidal to obconoidal. Colour blue to light blue. *Pedicels* of sterile flowers 0—3(—5) mm long, horizontal to somewhat ascending. *Anthers* 0.7—1.1 mm long when dehisced. *Pollen grains* usually more or less ellipsoidal, 44—50(—52) μ long. *Capsules* 0.8—1.1 cm in diam., usually broadly conoidal. Each valve with a narrowly ovate to triangular outline in transverse section. *Seeds* 1.5—2.5 mm in diam., more or less spherical, surface ridged. *Chromosome number* 2n=36.

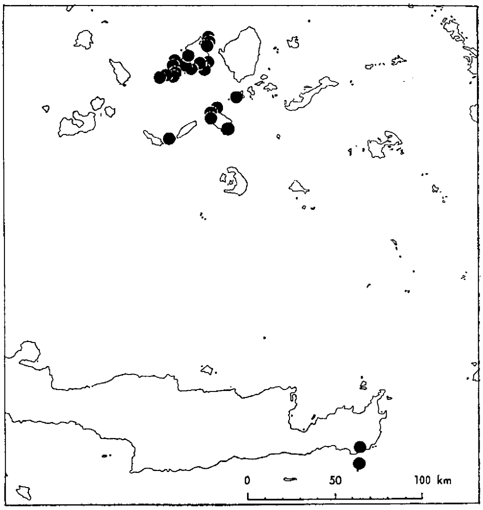


Fig. 4. *Leopoldia cycladica* ssp. *subsessilis*. Collecting sites for cultivated material and herbarium material investigated.

DISTRIBUTION: Endemic to S Kikladhes and SE Kriti. Common in the Paros—Andiparos—Strongilo area, on Ios, Iraklia and on Kardiotissa (between Sikinos and Folegandros). Found in one locality on southeasternmost Kriti and in one locality on the island of Koufonisi (SE of Kriti). (Fig. 4).

HABITAT: Mainly in phrygana communities, sometimes on sandy soil close to the sea.

GENERAL REMARKS: This subspecies shares distinct characters with ssp. *cycladica,* e.g. pedicel length and shape of capsule. The differences are mainly of a quantitative nature.

The subspecies is mainly characterized by the short or lacking pedicels of the fertile flowers, the small number of sterile flowers, the narrow leaves, its comparative smallness and the small seeds.

Leopoldia dionysica (RECH. FIL.) BENTZER comb. nov.

Muscari dionysicum RECHINGER, Neue Beitr. Fl. Kreta: 167—168 (1943 b). — Orig. coll.: RECHINGER, no. 12880; Kreta: Distr.

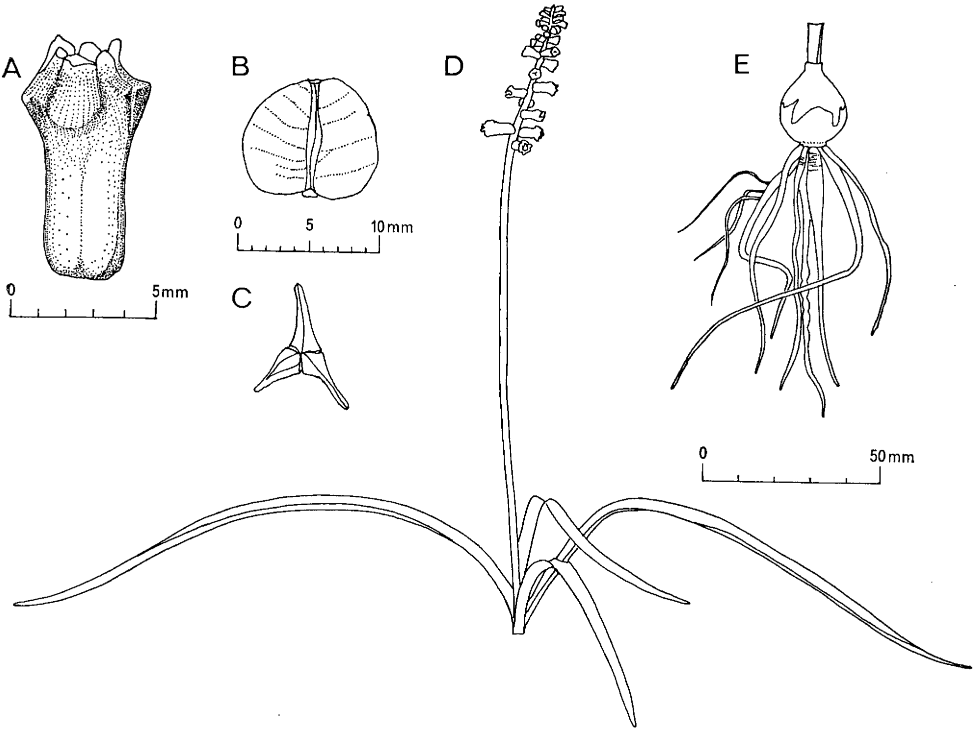


Fig. 5. *Leopoldia cycladica* ssp. *subsessilis*. Drawings of the type specimen. — A: Fertile flower. — B: Side-view of mature capsule. — C: Mature capsule seen from above. — D: Habit. — E: Bulb and roots.

Sitia, Insulae Dionysades, in saxosis calc. litoreis insulae Paximadi, 14.5. 1942 (W holotype).

ILLUSTRATIONS: Figs. 29 F (inflorescence), 23 D (fertile flowers), 11 D (capsules), 26 (seed surface).

Bulbs 3—6 cm in diam., usually at a depth of 5—10 cm. Tunics reddish-brown. *Scapes* (15—)25—40(—60) cm long, very stiff and stout. *Leaves* (3—)4—6(—9), green to bluish-green, linear to lorate, as long as the scape or somewhat shorter, (6—)10—25(—50) mm broad, often slightly recurved. *Racemes* (6—)10—25 (—35) cm long. Number of fertile flowers 50—c. 100. *Fertile flowers* 7—10(—12) mm long, 5—8 mm in diam., tubular to obovoidal, often with conspicuous shoulders, more or less strongly contracted near apex. Colour in bud violet to light blue, sometimes markedly striped with blue, during anthesis lower part of perigon greenish-yellow to dirty brownish-yellow, upper part dark reddish-brown or brown. Teeth at apex bright yellow to creamy. Flowers often strong smelling. *Pedicels* of fertile flowers (7—)10—25 (—27) mm long, in early bud erect, in late bud usually curving downwards, during anthesis horizontal. *Sterile flowers* usually 20—35, 3—8 mm long, 1—5 mm in diam., obconoidal to obovoidal. Colour light blue to blue. *Pedicels* of sterile flowers 5—20 mm long, horizontal to suberect. *Anthers* 0.9—1.5 mm long when dehisced. *Pollen grains* more or less reniform, 46—56(—62) μ long. *Capsules* usually (6—) 8—12 mm in diam., conoidal to ovoidal.

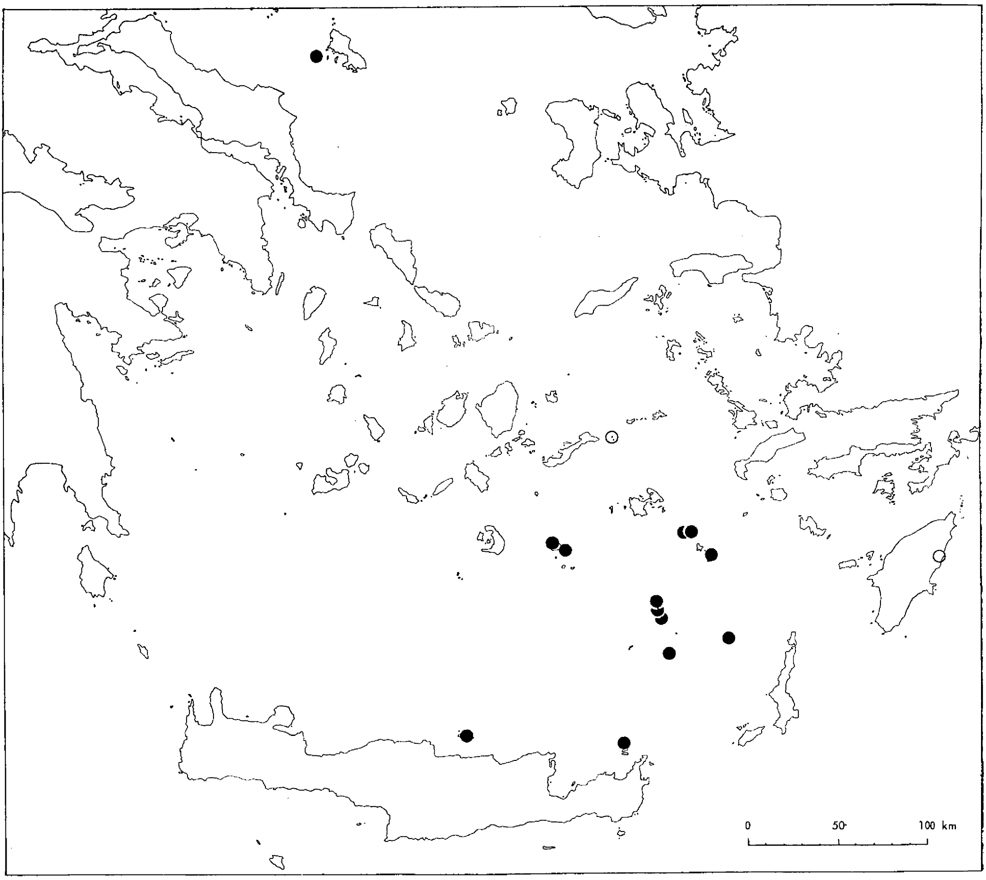


Fig. 6. *Leopoldia dionysica*. Collecting sites for cultivated material and herbarium material investigated. Dots=normal types. Rings=dubious determinations.

Each valve with a more or less ovate to triangular outline in transverse section. *Seeds* 2.3—4 mm in diam., usually almost spherical, surface ridged with a reticulate pattern. *Chromosome number* 2n=18, 36.

DISTRIBUTION: Mainly on small islands in the SE Aegean. Similar plants, such as *Muscari haradjianii* RECH. FIL. and *Muscari atropatanum* SCHLICHIAN are found on Cyprus, in Anatolia, Syria and Persia. Their mutual relationships have not been worked out. The distribution of *L. dionysica* is given in Fig. 6.

HABITAT: Mainly on small islands, but occasionally on cliffs.

GENERAL REMARKS: Except for the material from Unia Nisia (no. 50) and to some extent Astakidha (no. 97), *L. dionysica* is relatively constant in quantitative morphological features in contrast to many other species from small islands and cliffs in the Aegean.

The perigon of the fertile flowers is more uniform in colour (brown—dirty brown) in the diploid populations (from Unia Nisia and Astakidha) than in the tetraploid populations. The diploids have a karyotype approaching that of *L. weissii* from N Greece, i.e. populations nos. 334 and 336 (see under *L. weissii*). Tetraploid populations of *L. dionysica* have karyotypes which are indistinguishable from those of other tetraploid *Leopoldia* taxa in the area (BENTZER in prep.).

The species is characterized by its large general size, the large fertile flowers, the broad leaves and the long pedicels of the fertile flowers.

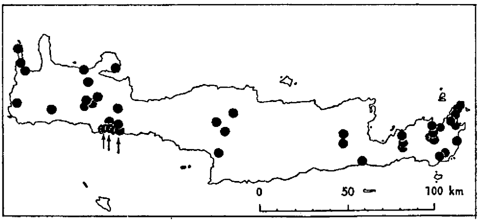


Fig. 7. *Leopoldia spreitzenhoferi*. Collecting sites for cultivated material and herbarium material investigated. Arrows indicate populations used for morphological measurements in nature.

Leopoldia spreitzenhoferi HELDR.

HELDREICH in OSTERMEYER, VZBG. 40: 299 (1890); HALÁCSY, Consp. Fl. Graec. III: 268 (1904); — *Muscari Spreitzenhoferi* (HELDR.) VIERHAPPER, ÖBZ. 66: 167 (1916); HAYEK, Prodr. Fl. pen. Balc. III: 89 (1933); RECHINGER, Fl. Aeg.: 731 (1943 a). — Orig. coll.: SPREITZENHOFER, iter Creticum 1882, Kreta, prope Mavrous Lakkous, 22.7. (WU lectotype, W Herb. Hal.).

Muscari creticum VIERHAPPER, ÖBZ. 66: 166 (1916); HAYEK, Prodr. Fl. pen. Balc. III: 89 (1933); RECHINGER, Fl. Aeg.: 731 (1943 a). — Orig. coll.: WETTSTEIN, Kreta, Südküste, Tybaki—Klima, 13.4. 1914 (WU lectotype).

Muscari amoenocomum RECHINGER, Neue Beitr. zur Fl. von Kreta: 168 (1943 b); — *Leopoldia amoenocoma* (RECH. FIL.) GARBARI, Webbia 27: 289—297 (1972). — Orig. coll.: RECHINGER no. 14361, Kreta, Lassithi, Mt. Lazaro, 12.7. 1942 (W lectotype).

Muscari creticum var. *inconspicuum* RECHINGER, Neue Beitr. zur Fl. von Kreta: 169 (1943 b). — Orig. coll.: RECHINGER no. 12459, Kreta, Distr. Sitia: Verkarstete Kalkhügel bei Limin Sitias, blühend und mit jungen Früchten am 2 Mai 1942 (W lectotype, BM, G).

Note: The name *Muscari maritimum* DESF. has been used incorrectly in different combinations for *L. spreitzenhoferi* by a number of workers. They have based the name on a HELDREICH collection from Kriti, i.e. HELDREICH, Kreta, Sphakia, Frankokastron, 8.4. 1846 (FI), which is morphologically indistinguishable from *Leopoldia spreitzenhoferi* HELDR. True *Muscari maritimum* DESF. (PC lectotype, microfiche seen) occurs in N Africa.

ILLUSTRATIONS: Figs. 29 G (inflorescence), 23 E (fertile flowers), 11 E (capsule), 25: 12 (seed surface).

Bulbs 1—2(—3) cm in diam., usually at a depth of 1—4 cm. Tunics brown to pinkish. *Scapes* 6—20 cm long. *Leaves* (2—)3—4(—5), green to bluish green, linear, as long as the scape or up to 30 % longer, (2—)3—9(—15) mm broad, more or less recurved. *Racemes* (2—)3—7(—15) cm long. Number of fertile flowers usually 10—30. *Fertile flowers* (4—)5—7 mm long, 2—4 mm in diam., more or less tubular with inconspicuous shoulders, usually slightly contracted near apex. Colour in bud greyish blue-green, during anthesis lower part of perigon brownish-green, upper part deeper brown. Teeth at apex yellow. *Pedicels* of fertile flowers (1—) 2—5(—6) mm long, usually suberect forming an angle of c. 45° with the scape. *Sterile flowers* usually less than 10, 1—3 mm long, 0.5—2 mm in diam., tubular to obconoidal. Colour bright blue to light blue or pink. *Pedicels* of sterile flowers 0—6 mm long, usually horizontal. *Anthers* 0.7—0.9 mm long when dehisced. *Pollen grains* more or less reniform, 36—44 (—48) µ long. *Capsules* 0.5—0.8 cm in diam., broadly conoidal to ellipsoidal. Each valve with a more or less ovate outline in transverse section. *Seeds* 1.6—2.3 mm in diam., ovoidal, surface ridged. *Chromosome number* $2n = 18, 36$.

DISTRIBUTION: Endemic to Kriti except for one locality in Algeria (BALANSA no. 167, 1851, K) (Fig. 7).

HABITAT: Usually found in phrygana communities on calcareous ground from sea level up to 2100 m.; also on seashores on the south coast.

GENERAL REMARKS: Two different form series have been recognized on Kriti; one low-land form series and one montane. The former has been given the names *M. creticum* VIERH. and *M. creticum* var. *inconspicuum* RECH. FIL. and the latter has been given the names *L. spreitzenhoferi* HELDR. and *M. amoenocomum* RECH. FIL. The main differences between the form series seems to be that as a rule the low-land form has fewer fertile flowers and sometimes smaller capsules than the montane form. I do not consider the differences sufficiently great to maintain two species especially as the variation in each form series is considerable and intermediate types are frequent.

The species is mainly characterized by the suberect pedicels of the fertile flowers, the small fertile flowers with an inconspicuous constriction near the apex and the small pollen grains.

REPRODUCTIVE BIOLOGY

Flowering Period

The onset and duration of the flowering period were observed in the same cultivated populations for three years. A similar trend was found all years.

There are clear-cut differences between different populations as regards the commencement and duration of the flowering periods. These differences do not seem to be correlated with taxonomic limits, however. In the cultivated material of *L. weissii* from the Milos area the two diploid populations start flowering c. 10—30 days after the two tetraploid ones. There is some overlapping of the flowering periods. A similar discrepancy was found between two tetraploid populations of *L. dionysica* from the neighbouring islands of Zafora and Karavi respectively, where the former start flowering c. 20 days before the latter.

Table 1. *Leopoldia.* Order of development in the inflorescence from different populations with regard to sterile and fertile flowers. Observations made on cultivated material. The number of specimens per population varies from 2 to 27; usually c. 7.

Taxon	Number of populations		
	sterile fl. first developed	inter-mediate	fertile fl. first developed
L. comosa (2x)	4	1	4
L. weissii (2x, 4x)	2	13	47
L. cycladica			
ssp. *cycladica* (4x, 6x)	.	4	2
ssp. *subsessilis* (4x)	.	4	4
L. dionysica (2x, 4x)	3	1	3

Flower Development

The flowering sequence of a *Leopoldia* inflorescence is acropetal with the fertile flowers and the sterile flowers developing independent of each other.

The order in which the sterile and fertile flowers commence their development from bud to mature flower, i.e. the sterile flowers become bluish and their pedicels begin to elongate, and the fertile flowers open, often varies between different populations of the same taxon (Table 1). The trend seems to be that in *L. comosa* and *L. dionysica* there is no definite order of flower development, while in the other taxa the fertile flowers usually develop first, or more or less simultaneously with the sterile ones. The two populations of *L. weissii* which develop the sterile flowers first (Table 1), i.e. nos. 300 and 342, are both tetraploid. All plants in a given population seem to have a more or less similar sequence of flower development. In those populations of *L. weissii* where the fertile flowers were developed first, the sterile flowers usually developed after a lapse of between 2 and 5 days. A similar time lapse was found in corresponding populations of the other taxa.

A brief investigation was carried out

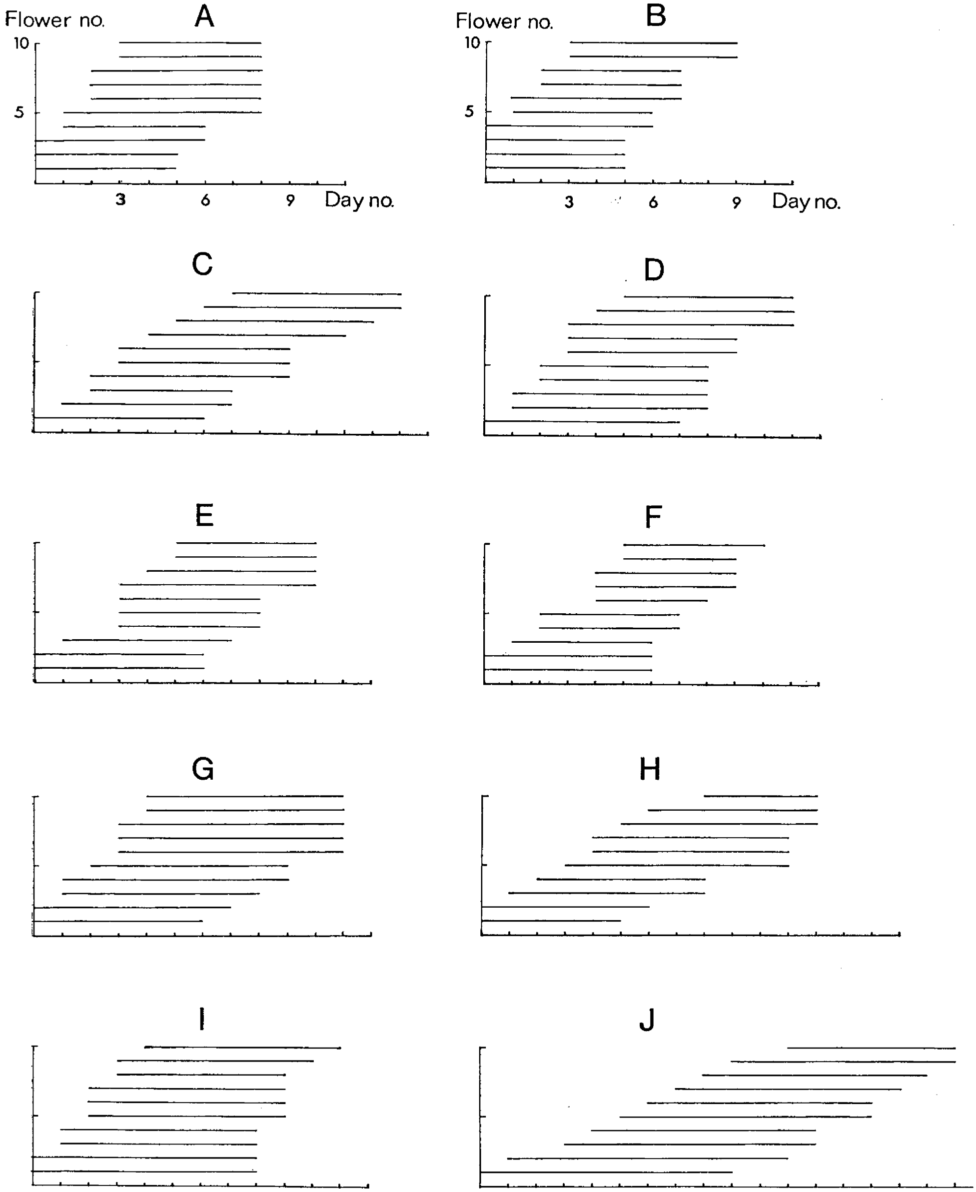


Fig. 8. *Leopoldia.* Rate of development of ten successive fertile flowers in one inflorescence and the duration of anthesis in each flower. Each horizontal line represents one single flower. — A—B: *L. comosa* (2x). — C—D: *L. weissii* (2x). — E—F: *L. weissii* (4x). — G: *L. cycladica* ssp. *cycladica* (6x). — H: *L. cycladica* ssp. *subsessilis* (4x). — I: *L. dionysica* (4x). — J: *L. spreitzenhoferi* (2x).

on cultivated material to study the rate of development of the fertile flowers in an inflorescence. In *L. comosa, L. cycladica* ssp. *cycladica* and *L. dionysica* flower initiation was reached in c. 5—6 days in 14 flowers. In *L. weissii* (2x, 4x) and *L. cycladica* ssp. *subsessilis* it required 7—10 days for 14 flowers to reach flower initiation and *L. spreitzenhoferi,* finally, was slow and developed only c. 1 flower per day (Fig. 8).

L. cycladica ssp. *subsessilis, L. spreitzenhoferi* and to some extent *L. weissii,* which have a low rate of development, also have comparatively few fertile flowers. The rate of development in these taxa may be regarded as being a mechanism to ensure that the flowering period lasts as long as possible.

The anthers of *Leopoldia* species mature in a position somewhat above the stigma. As the style grows during anthesis the stigma passes the anthers and becomes receptive for pollen when level with or above the upper anthers. The time lapse between the onset of anther dehiscence and the stigma receptivity seems to be between 2 and 6 days. Four observations were made on *L. weissii* (2—4 days lapse), two on *L. comosa* (4—5 days lapse) and two on *L. cycladica* ssp. *cycladica* (4—6 days lapse).

The length of anthesis varied rather considerably even between flowers in the same inflorescence, perhaps as a result of slightly varying growth conditions in the greenhouse with respect to temperature, humidity etc. (Fig. 8). Anthesis generally lasted between 6 and 10 days. There seems to be a slight tendency for taxa with a slow rate of development to remain in flower somewhat longer than the other taxa. The material studied is, however, too limited to permit of any general conclusions.

Table 2. *Leopoldia.* Seed-setting response after selfing. Consideration is not taken to the number of seeds obtained. Each attempt at forced selfing includes 5—10 flowers, n = number of attempts. The results obtained from each individual attempt were considered rather uncertain owing to the possibility of technical mistakes. It was therefore considered more reliable to present the results as sums.

Taxon	Per cent seed-setting plants after selfing			
	Spontaneous	n	Forced	n
L. comosa (2x)	20	10	77	27
L. weissii (2x)	70	20	80	44
L. weissii (4x)	44	41	54	71
L. cycladica				
ssp. *cycladica* (4x, 6x)	60	5	69	13
ssp. *subsessilis* (4x)	13	8	43	21
L. dionysica (2x)	100	1	80	5
L. dionysica (4x)	63	8	46	13
L. spreitzenhoferi (2x, 4x)	60	5	60	10

Pollination

In the greenhouse it was sometimes observed that pollen from the same flower was stuck to the stigma within the perigon tube especially when the flower collapsed and the anthers came into closer contact with the stigma. Since pollen is viable for at least two weeks after the flower withers, self-pollination is theoretically possible. The above phenomenon has not been observed in nature.

Self-pollination in cultivated material indicates that mechanical self-pollination is not a characteristic feature since forced selfings, with the exception of *L. dionysica,* tended to display a higher percentage of seed setting compared with spontaneous selfings (Table 2). Such discrepancies were especially pronounced in *L. comosa* and *L. cycladica* ssp. *subsessilis.*

The general composition of a *Leopoldia* inflorescence with fertile as well as sterile flowers seems to favour cross-pollination. Knoll (1921) made experimental studies on the attraction stimuli of the inflorescence to some insects, such as honey bees and flies. He used *L. comosa* where the morphological distinction between sterile and fertile flowers is most pronounced. According to KNOLL (op. cit.) the colour of the sterile flowers functions as a primary visual stimulus to the insects. Subsequently the visitors are attracted by the colour of the fertile flowers and move down the inflorescence. Nectar is only found in the fertile flowers.

The buds of the fertile flowers are blue—violet, while the mature flowers below them are greenish—yellowish to brownish in most populations of the different taxa. The colour of the buds above may play a role similar to that of the sterile flowers, emphasizing the attraction stimulus of the latter.

Since the flowering sequence in *Leopoldia* is acropetal and since each flower within an inflorescence is protandrous one may expect visitors to transfer pollen from a flower with non-receptive stigma to one with receptive stigma in the same inflorescence as they move downwards. Each insect visits a number of plants during a short period of time (KNOLL 1921) so that it is likely that at least some pollen from different plants adheres to it and is carried from one plant to another. A certain amount of cross-pollination by insects certainly does take place in *Leopoldia* species, but unless there is some sort of barrier to self-fertilization it is more likely that insects mainly aid self-pollination.

Seed Setting after Selfing and Crossing

There are certain sources of error in the experimental selfings and crosses due to greenhouse conditions, isolation bags, technique of emasculation etc. (Table 3 and p. 113). The result obtained must therefore be treated with caution. Comparisons within the material should, however, be relatively reliable since the experimental factors were kept as constant as possible during the entire study.

All taxa were capable of producing seeds after selfing, at least to some extent. The most unsuccessful taxon was *L. cycladica* ssp. *subsessilis* (Table 2). The number of successful forced as well as spontaneous selfings was greater in diploid *L. weissii* than in tetraploid, which may indicate a higher degree of self-incompatibility in the latter. This contrasts with what is known from certain members of Solanaceae, Scrophulariaceae and Leguminosae, for example, where the diploid species tend to be self-incompatible and the natural polyploid species self-compatible (D. LEWIS 1943, 1966).

Table 3. *Leopoldia.* Seed setting after selfing of the same plant in 1970 and 1972. Identical reaction: the same plant either sat seed both years or neither year. Opposite reaction: seed setting one year, but not the other.

Taxon	No. of plants	Identical reaction	Opposite reaction
L. weissii (2x)	9	9	.
L. weissii (4x)	11	8	3

The response to selfing was as a rule ambiguous within a population. In some plants self-pollination was possible, in others not. Two populations of *L. dionysica,* viz. no. 48 from the island of Anafi (4x), and no. 50 from the island of Unia Nisia (2x) were, however, completely self-compatible.

Crosses between populations within *L. weissii* (2x, 4x) gave a higher percentage of seed setting than did selfings (Table

Table 4. *Leopoldia.* Comparison between seed-setting ability after selfing and crossing respectively. No consideration was taken to the number of seeds obtained, n = number of attempts. In the selfings 5—10 flowers were used from each plant; in the crosses 3—5 flowers were usually used.

Taxon	Per cent successful forced selfings	n	Per cent successful interpopulation crosses	n
L. weissii (2x) . .	80	44	96	23
L. weissii (4x) . .	54	71	77	74

Table 5. Dormancy in seeds obtained from crosses between and within taxa in *Leopoldia*.

Crosses		No. of seeds obtained and sown	No. of germinated seeds	
female	male		1st season	2nd season
L. comosa (2x)	× *L. comosa* (2x)			
Kithnos (330-4)	×Peloponnisos (451-2)	14	6	8
Siros (347-3)	×Peloponnisos (451-2)	6	.	1
L. weissii (4x)	× *L. weissii* (4x)			
Andros (359-2)	×Tinos (319-4)	19	2	5
Andros (365-9)	×Karpathos (67-3)	26	17	1
L. weissii (4x)	× *L. comosa* (2x)			
Naxos (3-8)	×Peloponnisos (451-2)	14	.	5
Sirna (74-9)	×Siros (347-1)	23	15	1
L. weissii (4x)	× *L. spreitzenhoferi* (2x)			
Kimolos (41-2)	×Kriti (405-9)	1	.	1
L. weissii (4x)	× *L. dionysica* (4x)			
Milos (9-1)	×Anafi (48-4)	34	31	2
L. cycladica ssp. *cycladica* (6x)	× *L. weissii* (4x)			
Santorin (60-10)	×Siros (361-1)	28	12	9
L. cycladica ssp. *subsessilis* (4x)	*L. cycladica* ssp. *subsessilis* (4x)			
Andiparos (80-6)	×Tsimindiri (56-1)	10	1	4
Makronisi (75-2)	×Dhespotiko (96-2)	17	12	2
Sum of seeds obtained from intraspecific crosses		92	38 (41 %)	21 (23 %)
Sum of seeds obtained from interspecific crosses		100	58 (58 %)	18 (18 %)

4). The number of crosses and/or selfings within the other taxa are too few to permit of comparison between selfings and crosses.

Crosses between plants within populations were carried out only exceptionally, hence it is impossible to compare the seed-setting ability after cross-pollination with that after self-pollination, at the population level.

One may conclude that to judge from available facts, i.e. reduced seed setting after selfing but a comparatively increased seed setting after crosses between populations, some sort of self-incompatibility system seems to operate to a varying degree in *L. weissii* and perhaps in the other taxa as well. Balanced structural heterozygosity at chromosomal level may be a participating factor in decreasing the possibility of autogamy. Structural heterozygosity seems to be a common phenomenon in many populations (cf. BENTZER 1969, 1972 a, c).

Germination

In greenhouse tests seeds of *L. comosa, L. weissii, L. cycladica* ssp. *subsessilis* and *L. spreitzenhoferi* collected in nature germinated after 1.5—2.5 months, while the larger seeds of *L. cycladica* ssp. *cycladica* and *L. dionysica* (Fig. 9) and crosses in which either of these participate germinated after 1—1.5 months. The seedlings of the last two taxa are considerably more vigorous than those of the other taxa, a feature which might be of adaptive importance.

It was observed that a certain number of the seeds obtained from some crosses lay dormant till the second season at least (Table 5). A similar tendency was observed in seeds obtained from some selfings. The tendency to seed dormancy seems to be more or less similar in the seeds obtained from both inter- and intraspecific crosses (Table 5).

The adaptive significance of seed dormancy has been discussed by HARPER (1966) and others.

Table 6. Distribution of plants in populations according to pollen stainability in cultivated material of *Leopoldia*.

Taxon and area	50	55	60	65	70	75	80	85	90	95	100 %
L. comosa (2x)											
Tria Nisia (no. 92)	1	.	.	.	.	.	.	.	.	2	4
Naxos (no. 320)	.	.	.	1	.	.	.	.	.	.	6
Kithnos (no. 322)	.	.	.	.	.	.	.	.	.	1	6
Kithnos (no. 330)	.	.	.	.	.	.	.	.	1	3	4
Mt. Giona (no. 335)	.	.	1	.	.	.	.	.	.	.	5
Total	1	.	1	1	.	.	.	.	1	6	25
L. weissii (2x)											
Milos (no. 73)	1	2	1	.	2	1	.	.	1	1	6
Poliaigos (no. 49)	1	.	.	.	.	.	1	.	.	3	11
Kimolos (no. 54)	.	.	.	.	.	.	.	.	.	2	9
Piperi (no. 47)	.	.	.	.	.	.	.	.	2	1	4
Kithnos (no. 303)	.	.	.	.	.	.	.	.	.	.	6
Mikonos (no. 306)	1	.	.	1	1	.	1	.	.	.	2
Mikonos (no. 309)	.	.	.	.	.	.	.	.	1	1	5
Dhilos (no. 314)	.	.	.	.	.	.	.	.	1	.	4
Rhinia (no. 307)	2	.	.	.	.	.	.	.	.	.	1
Tinos (no. 326)	.	.	.	.	1	.	1	1	.	1	1
Tinos (no. 333)	.	2	.	.	1	.	.	1	.	1	2
Kea (no. 409a)	1	.	.	2	.	.	1	.	1	.	.
Total	6	4	1	3	5	1	4	1	6	10	51
L. cycladica											
ssp. **cycladica** (4x, 6x)											
Nikouria (no. 17), (4x)	.	.	1	.	.	.	.	1	.	2	1
Folegandros (no. 31), (6x)	.	.	.	.	.	.	.	.	.	1	2
Santorin (no. 60), (6x)	.	.	.	.	1	.	.	.	.	.	9
Total	.	.	1	.	1	.	.	1	.	3	12
ssp. **subsessilis** (4x)											
Makronisi (no. 75)	.	.	.	.	.	.	.	.	1	2	11
Paros (no. 13)	.	1	.	.	.	.	.	.	2	.	2
Andiparos (no. 57)	.	.	.	.	.	.	.	.	.	.	4
Andiparos (no. 80)	.	.	.	.	.	.	.	1	1	1	5
Strongilo (no. 72)	.	.	.	.	.	.	.	.	.	.	4
Total	.	1	1	.	.	.	.	1	4	3	26
L. dionysica (2x, 4x)											
Unia Nisia (no. 50), (2x)	.	.	.	.	.	.	.	.	.	1	1
Karavi (no. 30), (4x)	.	.	.	.	.	.	.	.	.	.	6
Dio Adelfi (no. 25), (4x)	.	.	.	.	.	.	.	.	.	.	2
Anafi (no. 48), (4x)	.	.	.	.	.	.	.	1	2	.	1
Total	.	.	.	.	.	.	.	1	2	1	10
L. spreitzenhoferi (2x, 4x)											
Kriti (no. 405), (2x)	.	.	.	.	.	.	.	.	.	.	6
Kriti (no. 402), (4x)	.	.	.	.	.	.	.	.	.	.	2
Total	.	.	.	.	.	.	.	.	.	.	8

Table 7. Distribution of plants in populations of *Leopoldia weissii* (4x) according to pollen stainability in cultivated material.

Taxon and area	50	55	60	65	70	75	80	85	90	95	100 %
L. weissii (4x)											
Karpathos (no. 67)	.	.	.	.	.	.	.	.	3	1	5
Rodhos (no. 32)	1	.	.	.	1	.	.	.	.	.	4
Rodhos (no. 69)	.	.	.	.	.	.	.	1	.	2	2
Rodhos (no. 99)	.	.	.	.	.	.	1	.	.	.	4
Sirna (no. 66)	.	.	.	.	.	.	.	.	1	2	1
Sirna (no. 74)	1	.	.	.	1	.	.	.	1	2	10
Amorgos (no. 19)	.	.	.	.	1	.	.	.	1	2	1
Milos (no. 68)	.	.	.	.	.	.	.	.	.	2	5
Kimolos (no. 45)	.	.	.	.	.	.	.	2	1	.	5
Kimolos (no. 61)	.	.	.	.	.	.	.	.	4	.	5
Naxos (no. 3)	.	.	1	1	.	1	1	4	1	1	1
Naxos (no. 44)	1	.	.	2	.	.	.	.	.	2	4
Naxos (no. 53)	.	.	1	.	.	.	.	1	.	1	2
Naxos (no. 329)	.	1	1	1	.	.	.	.	.	1	1
Serifos (no. 10)	.	.	.	.	.	.	.	.	.	.	5
Serifos (no. 77)	1	.	.	.	.	.	.	.	3	.	1
Siros (no. 342)	.	.	.	.	.	.	.	.	.	.	5
Tinos (no. 300)	.	.	.	.	.	.	.	1	.	.	5
Tinos (no. 328)	.	.	.	.	.	.	.	.	.	.	5
Tinos (no. 332)	.	.	.	.	.	.	.	.	.	4	6
Andros (no. 338)	.	.	.	.	.	.	.	.	.	1	4
Andros (no. 340)	.	.	.	.	.	.	.	.	.	2	4
Andros (no. 346)	.	.	.	.	.	.	1	.	.	.	5
Andros (no. 357)	.	.	.	.	.	.	.	.	.	.	5
Andros (no. 365)	.	.	.	.	.	.	.	.	.	.	9
Attiki (no. 38)	.	.	.	1	.	1	2	.	.	.	1
Attiki (no. 51)	.	.	.	1	.	.	.	2	.	.	2
Total	4	1	3	6	3	2	5	11	15	23	107

Pollen Stainability

The reduction in pollen stainability was found to be substantial, i.e. more than 10 % of the plants had less than 90 % stainable pollen in all taxa except *L. spreitzenhoferi*, of which very little material was available (Tables 6, 7).

In diploid *L. weissii* 34 % of the plants had less than 90 % stainable pollen, while in tetraploid *L. weissii* 28 % of the plants had a similar reduction (30 % $>$ P $>$ 10 %) (Tables 6, 7).

The reduction in pollen stainability agrees well with the frequent occurrence of structural chromosome heterozygosity in the large chromosomes (BENTZER 1969, 1972 a, c) although it is not possible to demonstrate a general correlation.

Asexual Reproduction

Proliferation under natural conditions was only occasionally observed by the author, viz. in *L. weissii* and *L. cycladica* ssp. *subsessilis*. BJÖRKQVIST, BOTHMER and SNOGERUP (personal communication) have, however, observed a frequent occurrence of bulbils in some populations of *L. comosa* and *L. weissii* from Kriti and Andros respectively.

In cultivation all taxa except *L. spreitzenhoferi* were found to produce bulbils (Table 8). The available material of *L. spreitzenhoferi* was very limited and no general conclusions can be drawn regarding its proliferation capacity.

The percentage of cultivated populations in which there were at least some

Table 8. Frequency of proliferation in taxa of *Leopoldia*.

Taxon	Total number of populations	Per cent proliferating populations	Total number of plants in the proliferating populations	Per cent proliferating plants
L. comosa (2x)	39	41	120	75
L. weissii (2x)	37	27	52	29
L. weissii (4x)	76	47	237	30
L. cycladica				
ssp. *cycladica* (6x)	7	29	29	28
ssp. *subsessilis* (4x)	17	88	130	38
L. dionysica (2x, 4x)	12	25	19	21
L. spreitzenhoferi (2x, 4x) ..	4	0	.	.

proliferating plants was about twice as high in *L. cycladica* ssp. *subsessilis* as in any other taxon (Table 8), but the percentage of proliferating plants was about twice as high in *L. comosa* as in the other taxa. In no taxon does there seem to be any correlation between the capacity to proliferate in cultivation, and the extent of morphological variation within populations in nature.

In a few cases there are indications that proliferation is of significance in plants with a poor capacity to reproduce sexually. On Anafi (no. 422) five specimens proved to be hybrids between *L. comosa* (2x) and, presumably, *L. weissii* (4x). The pollen stainability of the hybrids varied between 25 % and 40 %. One of the hybrids produced a few bulbils in cultivation. It seems likely that these plants have been produced by means of proliferation from one triploid founder hybrid.

Population no. 500 of *L. comosa* from Kriti is probably composed of one or a few clones of autotriploids (BENTZER 1972 c). The pollen stainability was 64 % and 74 % respectively in the two plants studied. Three out of eight plants proliferated in cultivation.

No general correlation between pollen stainability and proliferation capacity seems to exist in *Leopoldia*.

The liberated bulbils of *L. comosa* were usually small, i.e. 3—10 mm long, and numerous (Table 9). In the other taxa the bulbils were, as a rule, larger, i.e. 5—30 mm, but tended to be fewer.

The bulbils of *Leopoldia* sprout when still covered by the storage leaves of the main bulb, unlike *Allium* (BOTHMER in prep.) for instance. In *L. comosa* the bulbils are released early while still very small. In the other proliferating taxa the bulbils remain enclosed by the tunics of the main bulb for fairly long periods of time.

No proliferating population of *L. comosa* has produced any flowering plant from bulbils during four years of cultivation. It is possible that the smaller amount of nutrient supply in the bulbils of *L. comosa* does not permit of such rapid development as in other taxa. The most effective population as regards proliferation was no. 75 of *L. cycladica* ssp. *subsessilis*. One plant in this population produced eight new flowering plants during three years in cultivation.

Proliferation seems to be an effective mode of reproduction under unfavourable external conditions. Some plants of *L. comosa* from Paros (no. 11) did not do well in cultivation and only exceptionally developed inflorescences, i.e. in all, 2 inflorescences were developed on 22 plants during four years in cultivation. In nature no bulbils were observed in this population, but in cultivation proliferation frequency was high (Table 9). The same

Table 9. *Leopoldia.* Number of plants producing different numbers of bulbils during a total of 4 years in cultivation.

Taxon and population	0	1	2	3	4	5	6	7	8	9	10	15	20	25	30	
L. comosa (2x)																
Tria Nisia (no. 92) ..	4	3	3	.	.	.	.	1	.	.	.	.	.	.	.	.
Poliaigos (no. 55) ...	2	3	3	.	.	1	2	1	1	.	1	3	1	.	.	1
Naxos (no. 16)	4	3	2	.	1	.	.	.	.	.	.	.	.	.	.	.
Paros (no. 11)	.	.	.	1	1	.	.	.	1	3	2	3	5	2	4	.
L. weissii (4x)																
Milos (no. 68)	9	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Naxos (no. 3)	7	1	3	1	2	.	.	.	.	.	.	.	.	.	.	.
Naxos (no. 329)	3	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Serifos (no. 327)	7	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
L. cycladica ssp. *cycladica* (6x)																
Santorin (no. 60) ..	12	1	.	1	.	.	2	.	.	.	.	1	.	.	.	.
L. cycladica ssp. *subsessilis* (4x)																
Andiparos (no. 63) ..	4	4	1	.	.	2	.	1	.	.	.	1	.	.	.	.
Makronisi (no. 75) ..	4	2	3	4	1	2	1	.	.	.	1	1	1	.	.	.
Tourlos (no. 89) ...	5	2	.	1	.	1	.	1	.	.	.	.	.	.	.	.

tendency prevailed in other proliferating populations of all taxa although they did somewhat better in cultivation.

The potential proliferation capacity of *L. comosa* may be of adaptive value in the prevailing biotope for that species. The production of small bulbils that separate early should be an effective mode of reproduction in extensively cultivated biotopes where there may be considerably less chance for seedlings to survive and to become established. Proliferation in the other taxa does not seem to be as clearly adapted to a given biotope.

Dispersal

L. comosa, L. weissii, L. dionysica and *L. spreitzenhoferi* are all essentially spread by means of single seeds. The size of the seeds differs considerably even within taxa (Fig. 9).

In *L. cycladica* ssp. *cycladica* and ssp. *subsessilis* the whole capsules are dispersed while still containing seeds. The dry capsules of both taxa have large surfaces, which might be seen as an adaptation to wind dispersal (Fig. 11).

In one population of *L. dionysica* (no. 48) and in one heterogeneous population of *L. cycladica* ssp. *cycladica* (no. 430) whole inflorescences are often dispersed due to the extreme fragility of the stem.

Vertical movements of bulbs and bulbils are effected by means of contractile roots (GALIL 1958). In *L. comosa* and *L. weissii* at least, bulbils occasionally migrate from the main bulb by means of elongating horizontal rhizomes. According to field observations (BJÖRKQVIST, BOTHMER and SNOGERUP, personal communication), bulbils can move in this way some 10 cm from the main bulb.

Dispersal by means of bulbils is not likely to be of any importance in *Leopoldia* since: (1) Proliferation seems to be restricted in nature, at least under normal conditions; (2) If bulbils are liberated from the main bulb above the appropriate growth level, as might happen in cultivated areas, they develop contractile roots and migrate downwards.

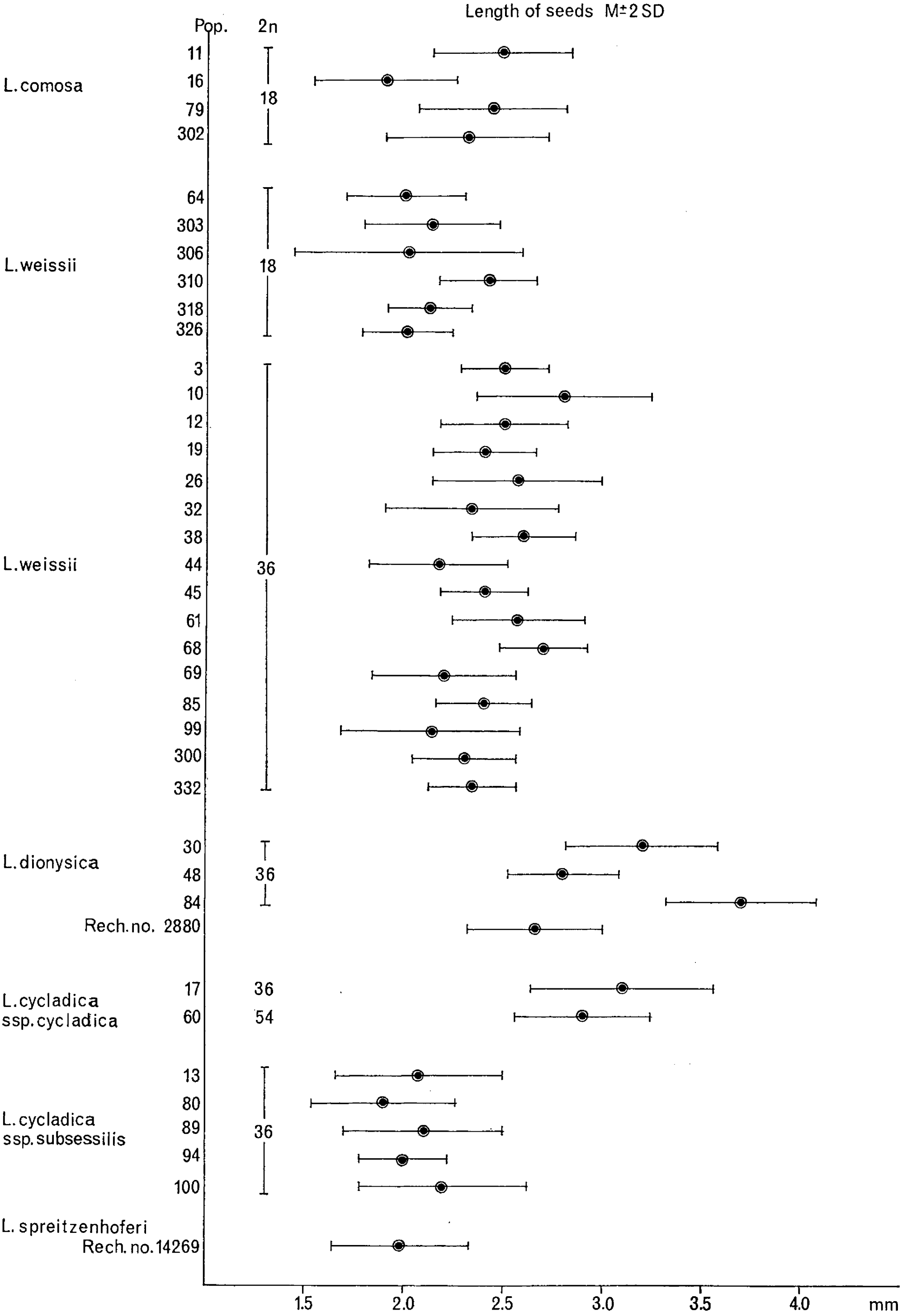


Fig. 9. *Leopoldia*. Variation in length of seeds. 20 seeds measured in each sample.

Conclusion

Although self-pollination is theoretically likely to occur either mechanically (*L. dionysica*) or through the agency of insects, cross-pollination seems to be prevalent in all taxa. Mechanisms that favour cross-pollination are: (1) Protandry; (2) Some sort of partially operating self-incompatibility; (3) The colour and conspicuousness of the inflorescence which serves to attract insects.

The importance and frequency of proliferation in natural populations is difficult to estimate at present. It seems, however, reasonable to assume that proliferation occurs in most natural populations to varying degrees. Proliferation frequency may possibly be determined by external factors, as it seems to be higher under unfavourable conditions.

Indications of proliferation are: (1) The extensive proliferation in cultivated material demonstrates a common potential capacity to proliferate; (2) The high frequency of structural chromosome heterozygosity (p. 92) which certainly decreases capacity for sexual reproduction. The plant would be faced with the risk of rapid elimination unless it reproduced asexually. (3) The high percentage of plants with reduced pollen stainability (p. 92) would likewise presumably be eliminated unless they reproduced asexually.

On the other hand, proliferation in nature has only been observed in a few natural populations.

MORPHOLOGICAL VARIATION

Variation within as well as between populations of different taxa has been studied. Herbarium material has been used to a certain extent but many characters such as shape and colour of perigon, shape and size of capsules, etc. are difficult or impossible to observe in dried material. The investigations on variation are consequently chiefly based on field studies and on cultivated material.

The variation patterns of the different taxa of *Leopoldia* in the Aegean are very complicated and difficult to elucidate. The members of the genus merge as a whole into a more or less diffuse polymorphic complex. The morphological complexity is accompanied by a high degree of cytological variation (Bentzer 1969, 1972 a, c), although without apparent covariation. No quantitative morphological characters constitute a clinal variation pattern along geographical gradients. They appear to vary discontinuously, mainly as a result of apparent non-adaptive radiation in the sense of Cain (1944).

Many morphological characters which have been used for the discrimination of taxa by a number of earlier botanists such as Halácsy (1904), Hayek (1933) and Rechinger (1943 a, b) have proved less diagnostic than was earlier believed. Such characters are, for instance, length of pedicels of fertile as well as sterile flowers, shape of perigon, height of stem, etc.

Variation within Plants

Variation within a single plant is as a rule restricted, and confined to the inflorescence and the leaves. The entire inflorescence elongates during the flowering period and so do the pedicels of the sterile and fertile flowers. The full length of the inflorescence is reached when the stigmas on the last fertile flower to develop mature. This also applies to the individual pedicels which cease growing when their respective stigmas become receptive for pollen.

The pedicels of the fertile flowers are more or less of equal length, sometimes with a slight tendency for the lowest ones to be somewhat shorter than the others.

The fertile flowers are usually similar in outline within a single inflorescence but the apophyses on the shoulders vary between individual flowers.

The outer sterile flowers are always larger than the inner ones and the pedi-

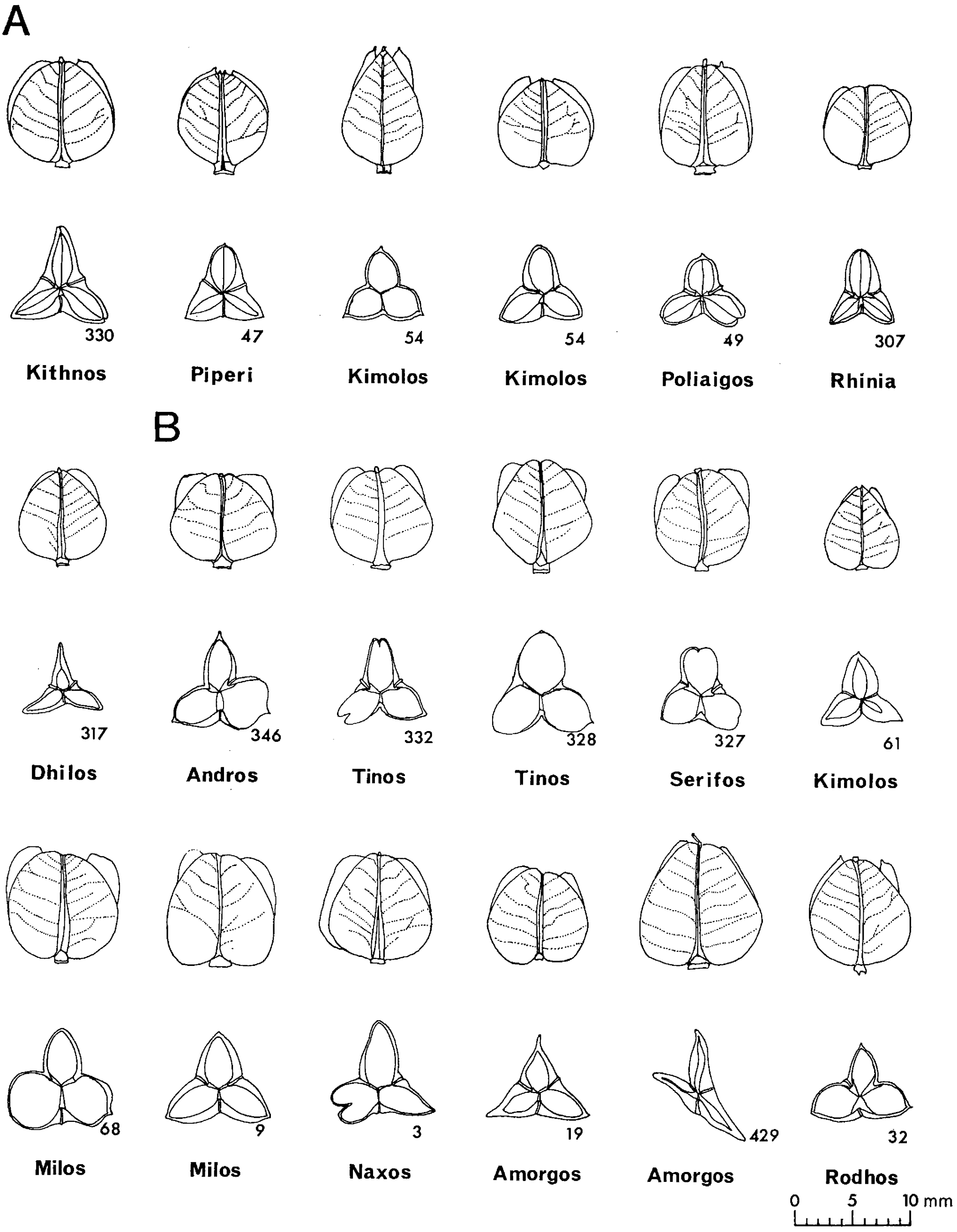


Fig. 10. *Leopoldia.* Variation in dry capsules; side-views, and seen from above (N.B. the latter variation depending to a great extent on the degree of opening of the valves). — A: *L. weissii* (2x). — B: *L. weissii* (4x) (no. 429 drawn from a hybrid plant).

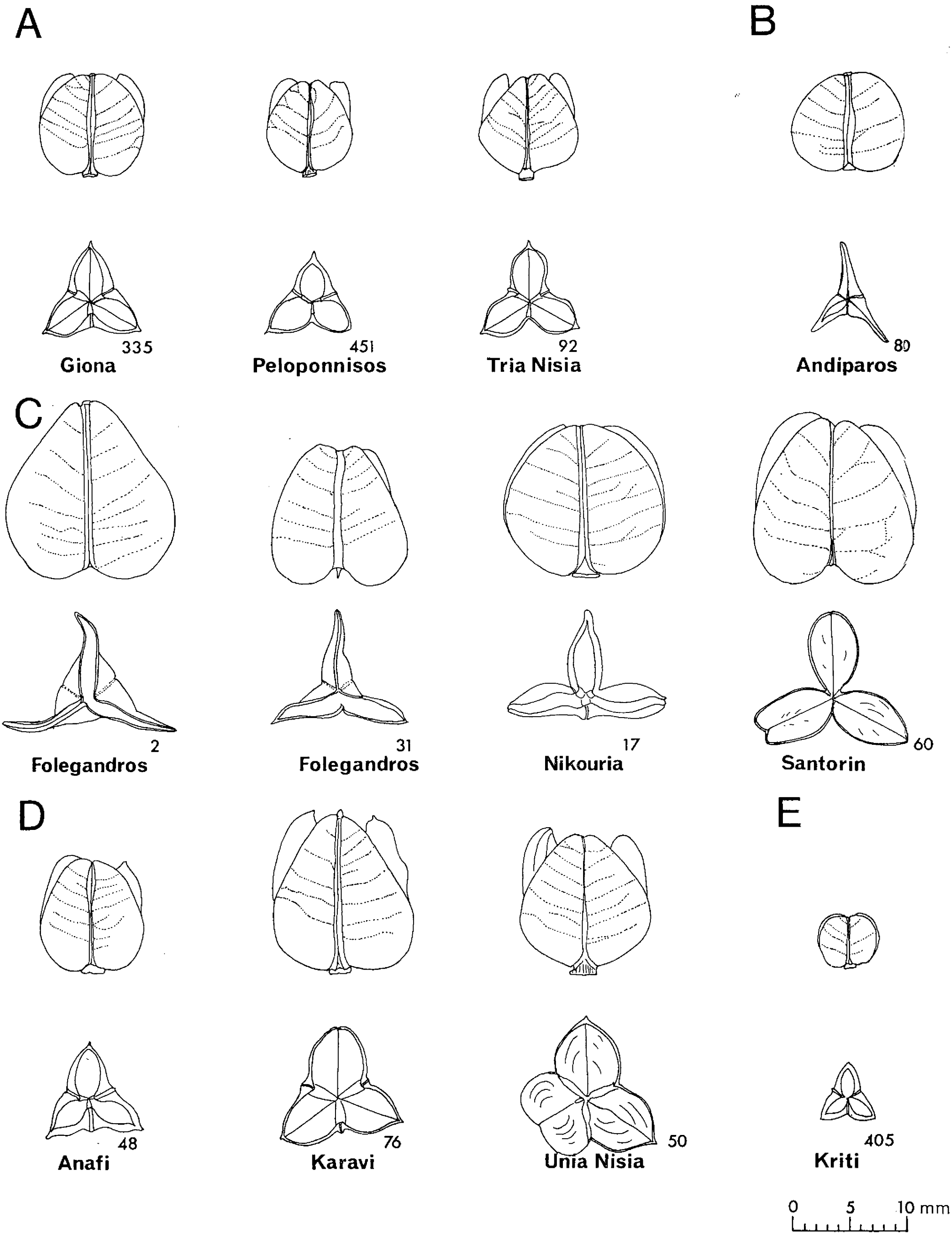


Fig. 11. *Leopoldia.* Variation in dry capsules; side-views, and seen from above (N.B. the latter variation depending to a great extent on the degree of opening of the valves). — A: *L. comosa* (2x). — B: *L. cycladica* ssp. *subsessilis* (4x). — C: *L. cycladica* ssp. *cycladica* [no. 17 (4x), nos. 2, 31 and 60 (6x)]. — D: *L. dionysica* [no. 50 (2x), nos. 48 and 76 (4x)]. — E: *L. spreitzenhoferi* (2x).

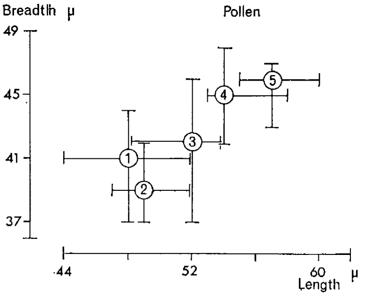


Fig. 12. *Leopoldia comosa* (2x). Variation in pollen size in 5 plants from the same population, i.e. no. 512. Mean and extreme values. 10 pollen grains measured from each plant.

cels of the former are usually longer than those of the latter.

The size of pollen grains often varies within a flower. The variation within a flower in five plants of *L. comosa* (2x) is shown in Fig. 12. The variation in *L. comosa* in this respect is similar in the other taxa (Fig. 13). The plants of *L. comosa* in Fig. 12 originate from a population in which structural heterozygosity has been found (BENTZER 1972 c p. 411).

Since cytological abnormalities are frequent in the other taxa as well, one may assume that the variation in pollen size is at least partly caused by such phenomena.

Capsules and seeds appear to be relatively constant on the whole.

The breadth of the leaves varies considerably, with the innermost leaf often being less than 1/3 as broad as the outermost.

Variation within Populations

The intrapopulational variation is usually considerable in almost all quantitative characters in the field. It is difficult to state to what extent the variation is caused by modifications due to slightly varying environmental factors. It seems,

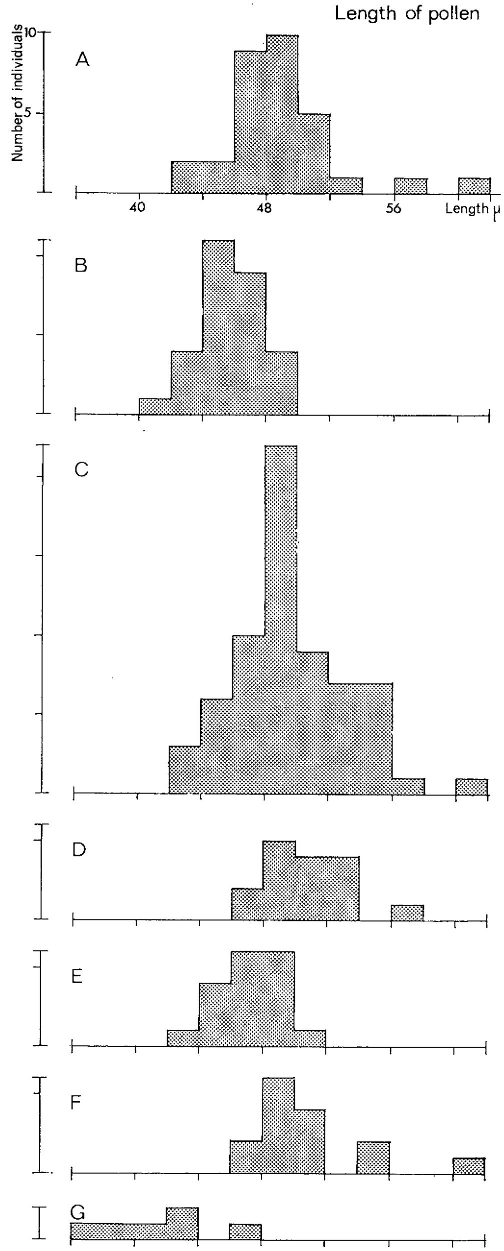


Fig. 13. *Leopoldia*. Variation in pollen length. 10 pollen grains measured from each plant. Not more than 2 plants from the same population were used. The histograms are constructed from mean values. — A: *L. comosa* (2x). — B: *L. weissii* (2x). — C: *L. weissii* (4x). — D: *L. cycladica* ssp. *cycladica* (4x, 6x). — E: *L. cycladica* ssp. *subsessilis* (4x). — F: *L. dionysica* (2x, 4x). — G: *L. spreitzenhoferi* (2x, 4x).

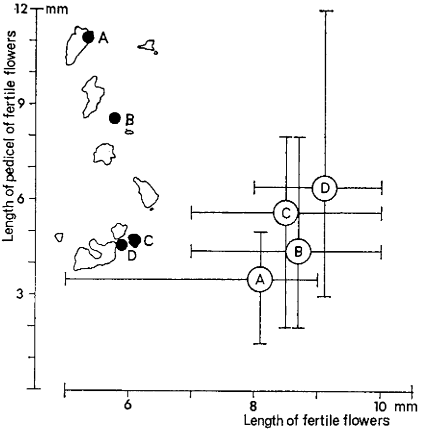


Fig. 14. *Leopoldia weissii* (2x), phrygana ecotype. Variation in the length of the pedicels of the fertile flowers (vertical) and the length of the fertile flowers (horizontal). Mean and extreme values. A and B measured in nature, C and D measured on cultivated material. — A: Kea, no. 410 (20 plants). — B: Piperi, no. 413 (20 plants). — C: Poliaigos, no. 49 (17 plants). — D: Kimolos, no. 54 (11 plants).

however, that a considerable amount of the natural variation is genetically determined. When *L. weissii* (2x), for instance, is grown in a greenhouse, the amplitude of variation in pedicel length and length of fertile flowers between different plants is as large as in natural populations (Fig. 14).

Qualitative characters such as colour of perigon, outline of perigon, outline of capsules, etc. are with few exceptions (Figs. 10, 11, 23, 24) relatively constant within populations.

L. COMOSA

The species appears mainly as a weed in disturbed habitats, i.e. fields, old terraces, etc., and a higher degree of modificative plasticity than in the other taxa might be expected. The variation in the characters measured was very great indeed (Figs. 15—17). The impression one gets from cultivated material is that the populations are fairly homogeneous, which would imply a high modificative plasticity in the natural populations. Since measurements could not be made on sufficient cultivated material owing to scarcity of flowering plants, no definite statement can be made.

The variation is of slightly different magnitude in different populations. Population no. 429 from Amorgos tends to be more homogeneous than no. 424 from the same island (Figs. 15—17) although the

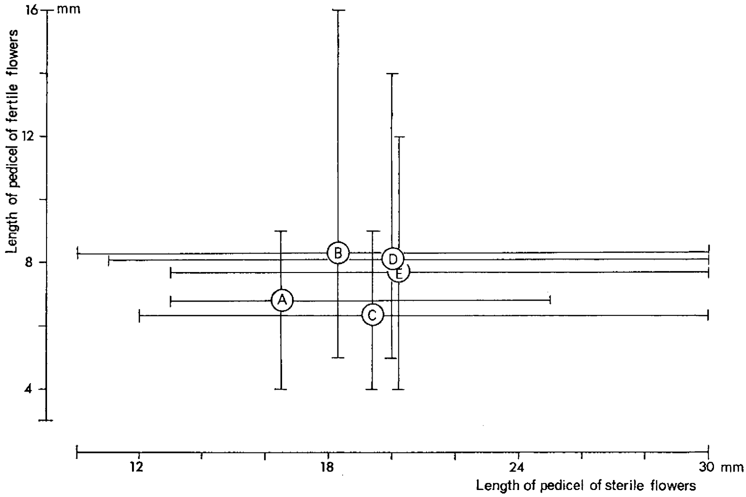


Fig. 15. *Leopoldia comosa* (2x). Variation in the length of the pedicels of the fertile flowers (vertical) and the length of the pedicels of the sterile flowers (horizontal). Mean and extreme values. — A: Folegandros, no. 415. — B: Kriti, no. 401. — C: Peloponnisos, no. 437. — D: Amorgos, no. 424. — E: Amorgos, no. 429. All measurements were made in nature on 20 plants from each population.

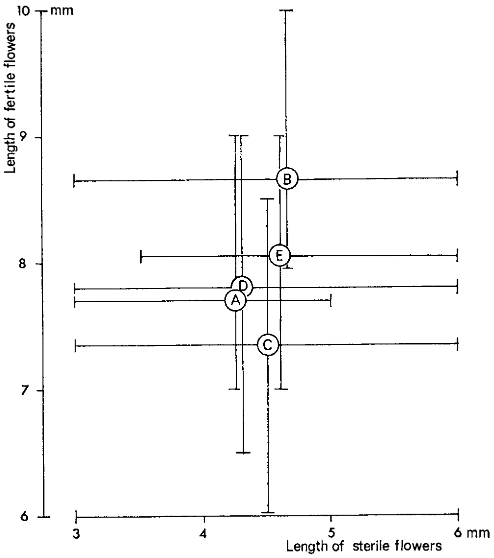


Fig. 16. *Leopoldia comosa* (2x). Variation in the length of the fertile flowers (vertical) and the length of the sterile flowers (horizontal). Mean and extreme values. The same populations as in Fig. 15. All measurements were made in nature on 20 plants from each population.

difference is small. A similar tendency is shown in population no. 415 from Folegandros, which is more homogeneous than the other populations studied (Figs. 15, 16). The biotopes of the more homogeneous populations comprise open fields, while the other populations grow in more heterogeneous habitats, another fact that supports the assumption of modificative plasticity.

Pollen grains seem to be very variable in size (Figs. 12, 13). There is reason to believe that this variation is genetically determined.

L. WEISSII

Some populations display limited variation in one character but greater variation in another. Population no. 427 (Fig. 17) has, for instance, more or less similar fertile flowers while the sterile flowers show considerable variation in size. In population no. 428 (Fig. 17) the length of the pedicel of the fertile flowers is fairly constant, while both the fertile and the sterile flowers are more variable in size.

There are no apparent differences in amplitude of variation between diploid and tetraploid populations as regards any given character. This is exemplified in Fig. 18, where population no. 432 (4x) has a variation range that in both characters agrees well with those of the diploid populations. Population nos. 411 (2x) and 427 (4x) both show considerable variation (Fig. 18).

Within *L. weissii* it is possible to recognize two somewhat different ecotypes which remain more or less distinct in cultivation: one larger, which is found growing in field margins, in shady places, on roadsides, on old terraces, etc., biotopes which are also inhabited by *L. comosa,* and a smaller one which grows in pure phrygana communities.

Populations of the larger field ecotype show greater variation in characters such as length of stem, length of leaves, number of flowers as compared with populations of the phrygana ecotype (Fig. 19). The differences in these respects are mainly modificative and are less pronounced in cultivation. In other characters, such as length of pedicel of the sterile flowers, length of sterile flowers, etc. there are no clear-cut differences in the variation range between the ecotypes. These latter characters also seem to be as variable in cultivation as in nature.

It seems reasonable to presume that in the phrygana ecotype there is a restricted range within which variation can be tolerated, at least in characters that affect total plant size. The phrygana biotope certainly constitutes a rather extreme habitat especially from the point of limited water supply.

With the field ecotype, on the other hand, the limiting factor of the water supply is not so pronounced, and it may consequently tolerate a larger variation in general size.

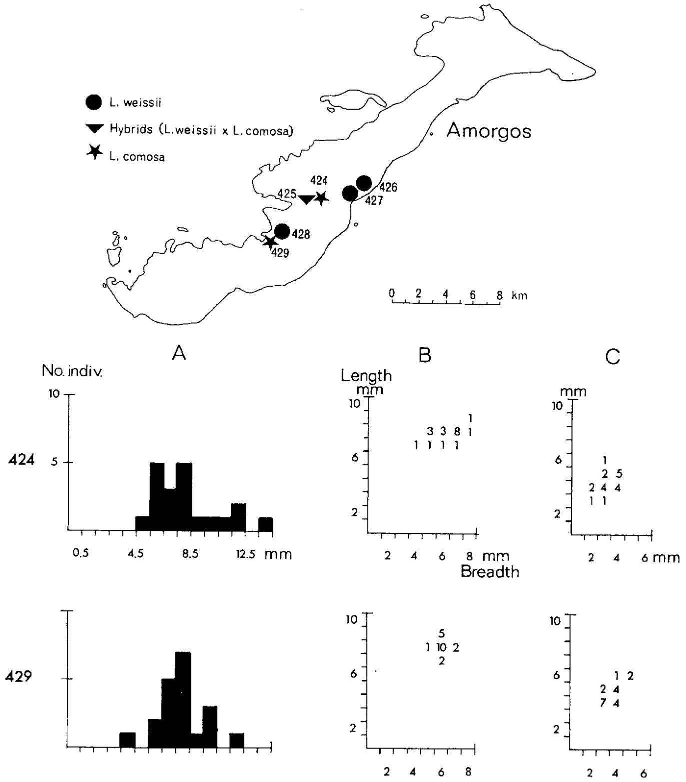


Fig. 17. Variation in: A: the length of the pedicels of the fertile flowers; — B: the length and breadth of the fertile flowers; — C: the length and breadth of the sterile flowers. — All measurements were made in nature on 20 plants from each population.

Since much of the variation in size in the respective ecotypes disappears in cultivation, one may conclude that modifications are somewhat more pronounced in the field ecotype than in the phrygana ecotype. To what extent the degree of plasticity in size characters is genetically determined is impossible to state from the present material.

It was observed in some localities that the two ecotypes merged, forming a small cline in vegetative appearance, along a gradient from a field into the pure phrygana vegetation. One such population is shown in Fig. 19 C.

L. CYCLADICA

The variation patterns of ssp. *cycladica* and ssp. *subsessilis* are essentially similar to that of *L. weissii* (Figs. 20, 21).

In population no. 417 of ssp. *subsessilis* there seems to be a discontinuity in the variation of the pedicel length of the sterile flowers (Fig. 20). Since this population was found to proliferate in nature as well as in cultivation, it constitutes an exceptional case in which clonal subdivision of a population is indicated. A similar discontinuity is, however, not met with in other characters of the same population.

In many populations of ssp. *cycladica* as well as ssp. *subsessilis* the length of the pedicel of the fertile flowers is more or less constant, a fact which is especially evident in population no. 60 (6x) and population no. 414 (6x) (Fig. 21) of ssp. *cycladica*.

In ssp. *cycladica*, hexaploid populations do not seem to be more variable than tetraploids.

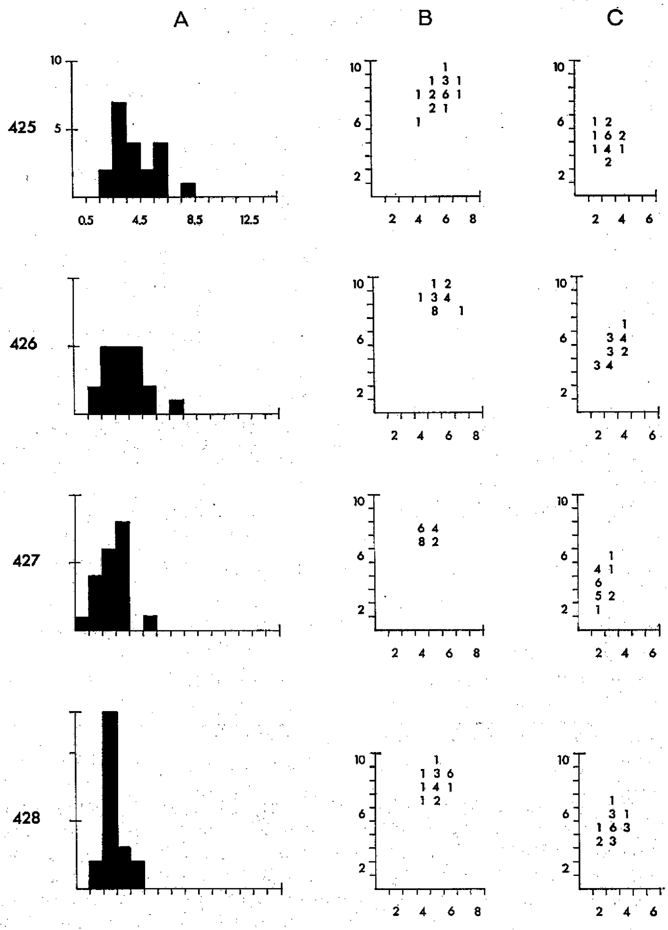


Fig. 17 (cont.). Variation in: A: the length of the pedicels of the fertile flowers; — B: the length and breadth of the fertile flowers; — C: the length and breadth of the sterile flowers. — All measurements were made in nature on 20 plants from each population.

L. DIONYSICA

Since the species is normally comparatively large, variation is also great in absolute figures, but hardly greater than in the other taxa, relatively seen. A distinct feature of population no. 50 (2x) from Unia Nisia is that two entirely different shapes of the fertile flowers exist (Fig. 23 D no. 26). This is remarkable since the fertile flowers, although variable in size, are usually constant in general appearance within populations.

L. SPREITZENHOFERI

Variation is more or less similar to that in the other taxa with a slight tendency for the flowers to be somewhat more constant in size (Fig. 22). It appears that this taxon has a comprehensive plasticity. In shrubs of *Sarcopoterium spinosum* (L.) SPACH strongly etiolated plants were often found. In cultivation the populations seem to be homogeneous. The variation range of diploid populations seems to be the same as that of tetraploid populations (Fig. 22).

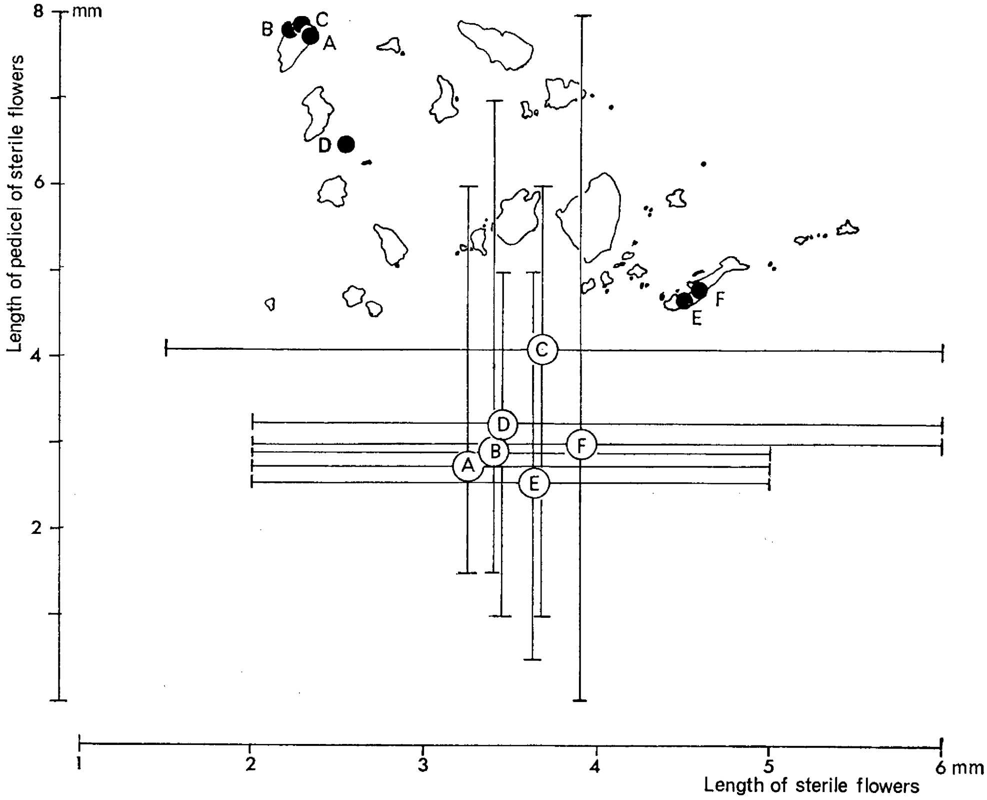


Fig. 18. *Leopoldia weissii* (2x, 4x), phrygana ecotype. Variation in the length of the pedicels of the sterile flowers (vertical) and the length of the sterile flowers (horizontal). Mean and extreme values. — A: Kea, no. 410 (2x). — B: Kea, no. 409 a (2x). — C: Kea, no. 411 (2x). — D: Piperi, no. 413 (2x). — E: Amorgos, no. 432 (4x). — F: Amorgos, no. 427 (4x). — All measurements were made in nature. A, B, D and F are each based on 20 plants, C and E are based on 16 plants each.

Variation between Populations

As pointed out above, no geographical clines have been found within the material. The interpopulational variation is therefore difficult to elucidate in a simple but comprehensive way.

The variation patterns of the different taxa, especially those between populations from different islands, are in a number of cases similar to those described by SNOGERUP (1967 b) in *Erysimum* sect. *Cheiranthus,* and by STRID (1970) in *Nigella,* i.e. discontinuities in different characters occur even between islands which may be situated very close to each other. Examples of such local but very striking differentiation are, for instance: (1) The conspicuously triangular appearance of the mature sterile part of the inflorescence of *L. weissii* (4x) from the islet of Serifopoula NE of Serifos. The sterile flowers are numerous and have long horizontal pedicels on the lower flowers. The pedicels become successively shorter higher up until they are sessile at the apex; (2) The fragile stem of *L. dionysica* (4x) from the cliffs of Kalamos on the island of Anafi. Some kilometres W of

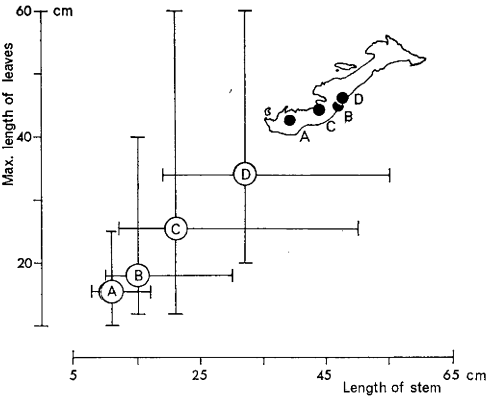


Fig. 19. *Leopoldia weissii* (4x), phrygana ecotype, intermediate and field ecotype. Variation in the maximum length of the leaves (vertical) and the length of the stem (horizontal). Mean and extreme values. — A: no. 432 (phrygana ecotype). — B: no. 427 (phrygana ecotype). — C: no. 428 (intermediate). — D: no. 426 (field ecotype). — All measurements were made in nature on 20 plants from each population in B, C and D. In A, 16 plants were measured.

Kalamos the taxon has the usual more or less tough stem; (3) The distinct smell of brewery from the fertile flowers of *L. dionysica* (2x) from the island of Unia Nisia; (4) The very light greenish lower part of the fertile flowers of *L. dionysica* (4x) from Dio Adelfi; (5) The large size and the high proliferation capacity of *L. cycladica* ssp. *subsessilis* from the island of Makronisi E of Paros. On Paros some kilometres away the same taxon is considerably smaller in similar biotopes.

In all the above cases, the populations consist of a restricted number of plants, i.e. up to some hundreds, and one may assume that the unique characters have been fixed by chance (genetic drift).

L. COMOSA

Within *L. comosa* in Greece four different form series can be recognized: (1) A small form with few flowers which grows in montane habitats on Peloponnisos and Attiki; (2) A low-land form on the southern Greek mainland and the southern and central Aegean islands with numerous comparatively large fertile flowers; (3) A NE Greek form series with comparatively few and small flowers, and with long narrow leaves; (4) A N Macedonian form, which is large and has long sterile flowers.

Living material has been available from the southern and central Aegean area only, and to a very limited extent from Peloponnisos.

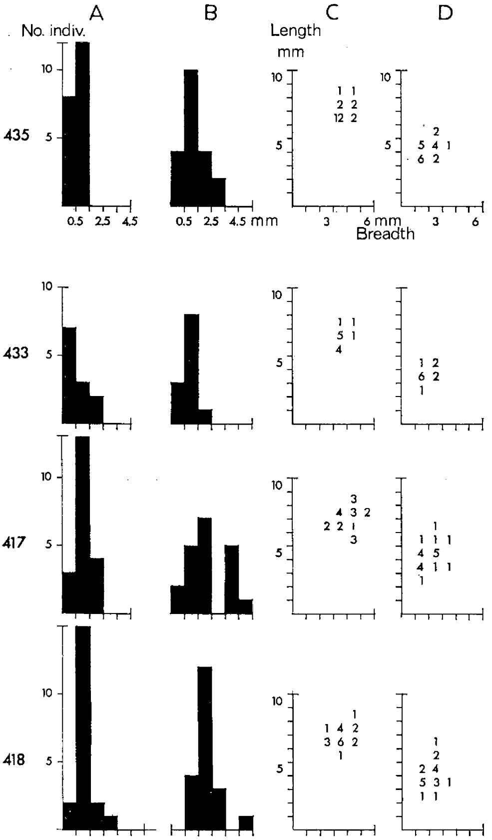
Within the area investigated *L. comosa* has a fairly restricted interpopulational variation, not at all as pronounced as the intrapopulational variation (Figs. 15—17). The fertile flowers are larger on Kriti than on Peloponnisos, the material from the Kikladhes being intermediate. A similar tendency is shown in the length of the pedicels of the fertile flowers. It is, however, not possible to generalize from any such pattern of variation since the available material is too limited and the intrapopulational variation too extensive.

The variation range of a given character can be small in one population while being considerably wider in another. This phenomenon is demonstrated in Fig. 15, where the variation range of the pedicel length of the fertile flowers is almost twice as great in population no. 401 as in no. 415 and no. 437. In other characters the variation range can be similar in different populations, e.g. length of fertile as well as sterile flowers (Fig. 16). There is no apparent difference between populations from Amorgos and a population from Folegandros (Figs. 15, 16).

A certain amount of variation is displayed in the general shape of the fertile flowers (Fig. 23) and the capsules (Fig. 11 A) in the area investigated.

L. WEISSII

The species is polymorphic and several populations constitute transitional forms while others have conspicuously characteristic features (see pp. 78—79). It is also



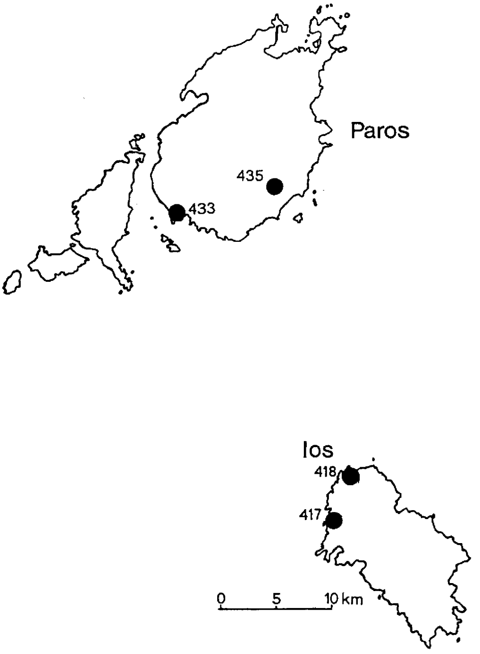


Fig. 20. *Leopoldia cycladica* ssp. *subsessilis* (4x). Variation in: A: the length of the pedicels of the fertile flowers; — B: the length of the pedicels of the sterile flowers; — C: the length and breadth of the fertile flowers; — D: the length and breadth of the sterile flowers. — All measurements were made in nature on 20 plants from each population.

possible to recognize two ecotypes, i.e. a phrygana ecotype and a field ecotype as mentioned on p. 101.

The variation in characters seems to be similar to that of *L. comosa*, i.e. the interpopulational variation is to a large extent camouflaged by the intrapopulational one. The variation between populations on a single island is, in some characters at least, just as large as the variation between populations from different islands (Fig. 18). Other characters seem to be more or less typical for a restricted group of islands, e.g. the almost sessile fertile flowers in the Siros area, the pale yellow to creamy teeth of the fertile flowers from Rodhos, Karpathos and Attiki.

A given character may be fairly constant in one population while being much more variable in another. The length of the pedicels of the fertile flowers in population no. 410 (2x) from Kea is, for instance, fairly constant while the variation range of the same character is twice as large in population no. 54 (2x) from Kimolos (Fig. 14 A. D).

Different chromosome numbers do not seem to imply differences in morphological characters (Figs. 10, 18, 23) except certain tendencies in seed size (Fig. 9) and pollen size (Fig. 13).

L. CYCLADICA SSP. CYCLADICA

In natural populations extensive measurements have only been carried out in

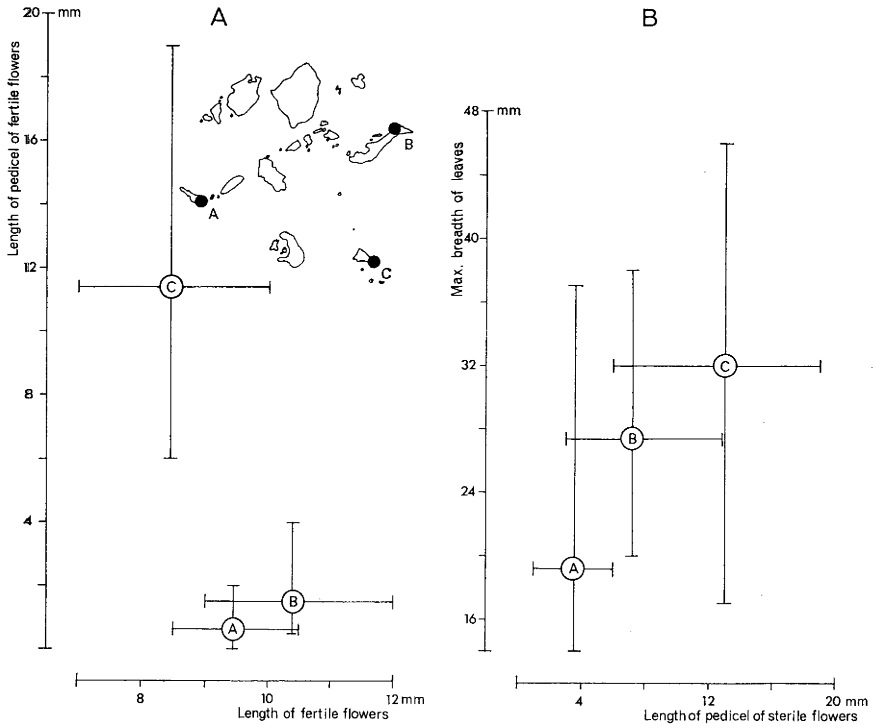


Fig. 21. *Leopoldia.* A: Variation in the length of the pedicels of the fertile flowers (vertical) and the length of the fertile flowers (horizontal). — B: Variation in the maximum breadth of the leaves (vertical) and the length of the pedicels of the sterile flowers (horizontal). — Mean and extreme values. In each diagram: A: *L. cycladica* ssp. *cycladica* (6x), Folegandros, no. 414. — B: *L. cycladica* ssp. *cycladica* (4x), Amorgos, no. 430. — C: *L. dionysica* (4x), Anafi, no. 421. — All measurements were made in nature on 20 plants from each population.

populations no. 414 and 430 (Fig. 21). The former of these populations is typical ssp. *cycladica* while the latter, which happens to be the population to which the type belongs, is intermediate between normal ssp. *cycladica* and *L. dionysica* (see p. 81). The resemblance to *L. dionysica* is mainly restricted to characters of general size, i.e. height of stem, length of leaves etc. In the length of the pedicels of the sterile flowers and the maximum breadth of the leaves, the mean values as well as the variation ranges of population no. 430 are intermediate between *L. dionysica* and *L. cycladica* ssp. *cycladica* (Fig. 21 B). The main characters that keep population no. 430 in ssp. *cycladica* are the shape and size of the capsules and the short pedicels of the fertile flowers (Fig. 21 A).

Except for certain tendencies in pollen size it is impossible to distinguish the tetraploid populations from the hexaploid on morphological characters. Cultivated material of population no. 17 (4x) from Nikouria (N of Amorgos) is, for instance, apart from its distinctive capsular shape, similar to population no. 60 (6x) from Santorin, while they both differ from population no. 414 (6x) from Folegandros in having a longer stem and a larger number of flowers than the latter.

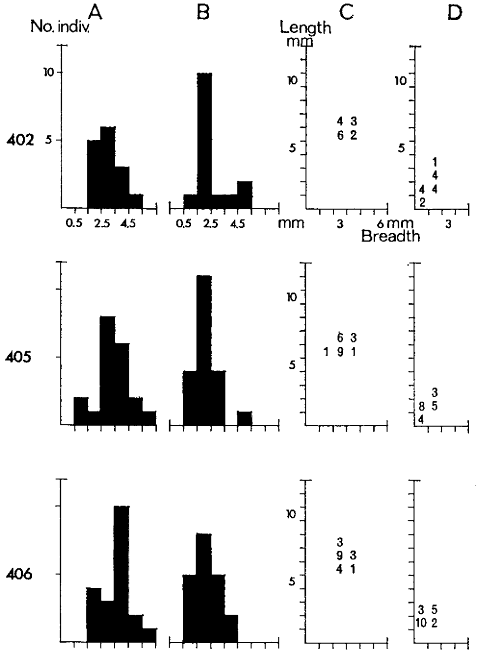


Fig. 22. *Leopoldia spreitzenhoferi* (2x, 4x). Variation in: A: the length of the pedicels of the fertile flowers; — B: the length of the pedicels of the sterile flowers; — C: the length and breadth of the fertile flowers; — D: the length and breadth of the sterile flowers. — All measurements were made in nature on 20 plants from each population.

On the islands of Iraklia and Karos (between Amorgos and Naxos) intermediate populations between ssp. *cycladica* and ssp. *subsessilis* seem to occur. As observations were made on dried material only from these areas, it is difficult to estimate the actual appearance of representatives from these populations.

L. CYCLADICA SSP. SUBSESSILIS

Living material has been available from the central Kikladhes only. According to the herbarium material studied from SE Kriti these populations seem to be essentially similar to the central Aegean ones.

Within the main area of distribution in the Kikladhes (Fig. 4) ssp. *subsessilis* is fairly homogeneous with a few exceptions, e.g. population no. 75 (see p. 105) (Figs. 20, 24). However, the pedicels of the fertile flowers display a slight tendency to be somewhat shorter in the Paros area than on Ios (Fig. 20).

L. DIONYSICA

The species is a taxon occurring in small populations mainly confined to cliffs and small islands, and this has undoubtedly affected the degree of differentiation between populations in mainly qualitative characters. On p. 105 some local morphological characteristics are given. Other characters also vary between the populations, e.g. the time of flowering (see p. 86) and the degree of self-compatibility (see p. 89).

On the whole one may conclude that *L. dionysica* is locally very differentiated in varying respects, but in gross morphology the species is fairly homogeneous.

L. SPREITZENHOFERI

Very limited natural material has been studied, and it has not been possible to compare the two form series earlier recognized (see p. 86) from living material. In the Sfakion area on SW Kriti the species is uniform, independent of chromosome number and biotope (Fig. 22). Judging from observations on dried material from a number of populations on Kriti, there undoubtedly seem to be certain differences, mainly between populations from different altitudes. Characters which change with altitude are, for instance, number of flowers, height of stem, breadth and length of leaves, etc. All these characters seem to be easily modifiable characters. Other characters such as length of pedicels, shape of capsules, etc. are essentially constant in the whole material.

HYBRIDS

Hybrids between *L. weissii* (4x), field ecotype, and *L. comosa* (2x) seem to be common where these taxa occur together. The morphology of the hybrids is on the whole intermediate between that of the parents (Fig. 17) but some plants usually more closely resemble one or other of the parents, indicating introgressive hybridization. The morphological indications of introgression are also supported by cytological data (BENTZER 1969).

There are morphological indications of hybridity between *L. weissii* (2x) and *L. comosa* (2x) in one locality on Kithnos (population nos. 408 a, b). The karyotypes of several plants from the locality are strikingly heterozygous, but it has not been possible to prove the origin of the genomes.

Variation in Seed Morphology

Only a very limited amount of seed material was used for scanning studies on seed surface morphology and the results are consequently tentative. *L. weissii* is the most variable taxon as to seed surface morphology the other taxa being relatively constant (Figs. 25, 26). Of particular interest is the constancy showed by *L. dionysica* (2x, 4x). This taxon is certainly exposed to a great deal of apparently non-adaptive radiation in other characters, cf. p. 105.

There is considerable variation in seed length within populations, particularly in *L. weissii* (Fig. 9). The extent of the variation range can probably be accounted for in part by sampling errors, i.e. in some populations seeds have been collected from a number of plants, while in other populations seeds have been collected from only a few plants. In *L. weissii* there is a tendency for the diploids to have smaller seeds than the tetraploids although overlapping is considerable. In the two populations of *L. cycladica* ssp. *cycladica* the situation is the opposite, i.e. the population with the lowest chromosome number has the largest seeds (Fig. 9). While populations of *L. dionysica* were constant in seed surface morphology the seed length tends to vary a great deal (Fig. 9).

Conclusion

It seems obvious that the intrapopulational variation in quantitative characters is wider than the interpopulational variation at least in those characters which have been studied. The trend is similar within all taxa and within the ecotypes of *L. weissii.*

Allogamy undoubtedly plays an important role in the creation and maintenance of a large intrapopulational variation. Vegetative propagation may be a supplementary mode of preserving a wide gene-determined intrapopulational variation, i.e. in plants that have a characteristic genotype but which are inadequately adapted, the effects of selection are neutralized to a great extent, and they propagate by means of proliferation. Since bulbils are unlikely to be widely distributed a population may consist of a large number of small clones that are at least partly interfertile.

The similarity between populations within a natural area, i.e. an island or a group of islands which are situated close to one another, is usually not greater than the similarity between populations situated far apart.

Many populations of *L. weissii* and *L. dionysica* in particular are characterized by some conspicuous feature that makes them stand apart.

CROSSING EXPERIMENTS

The results that can be obtained from the present crossing experiments are expected to elucidate two phenomena: (1) To what extent different genomes are related; (2) To what extent introgressive hybridization is possible between the different taxa and populations.

Genomic relationships and interfertility between taxa and between populations is

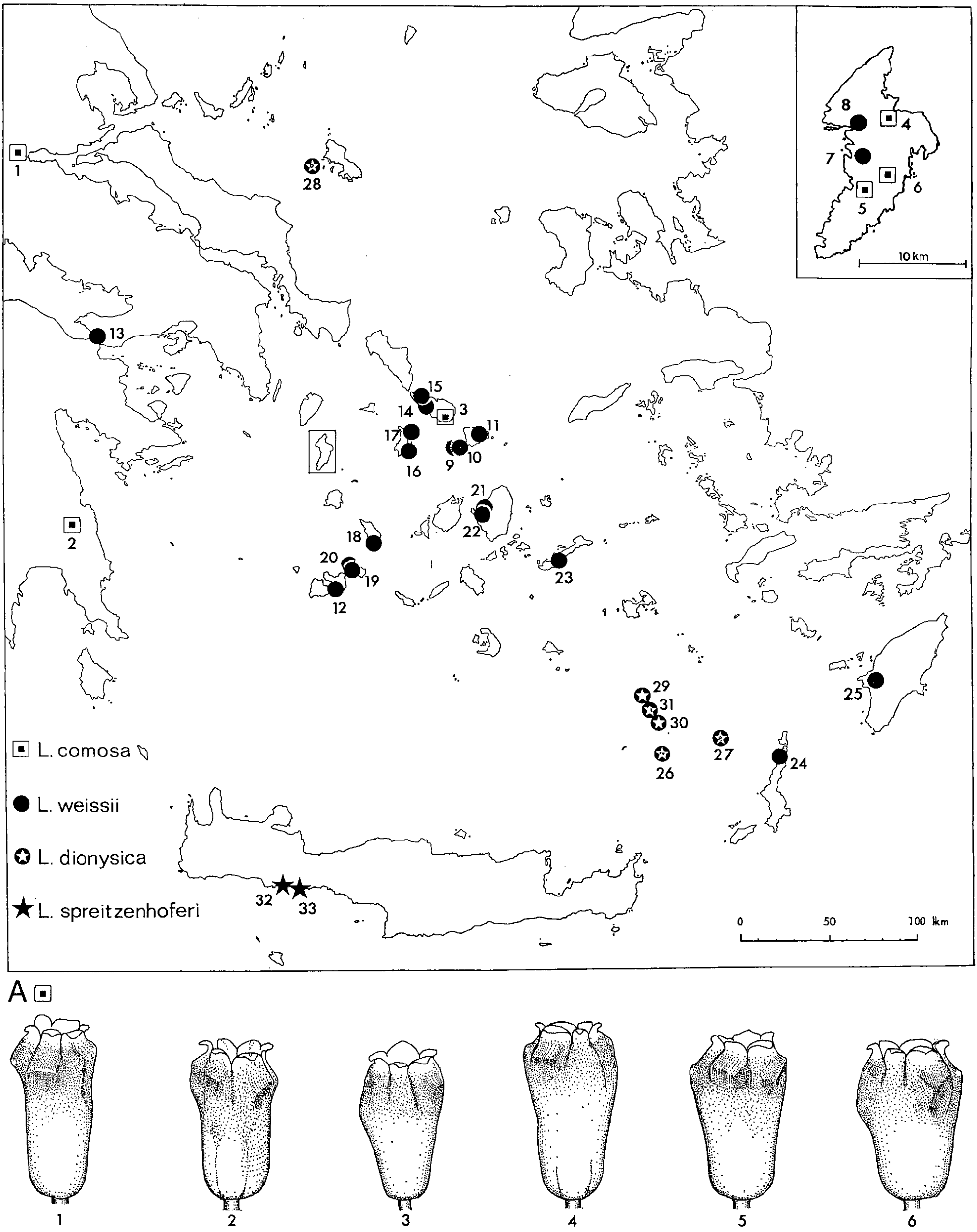
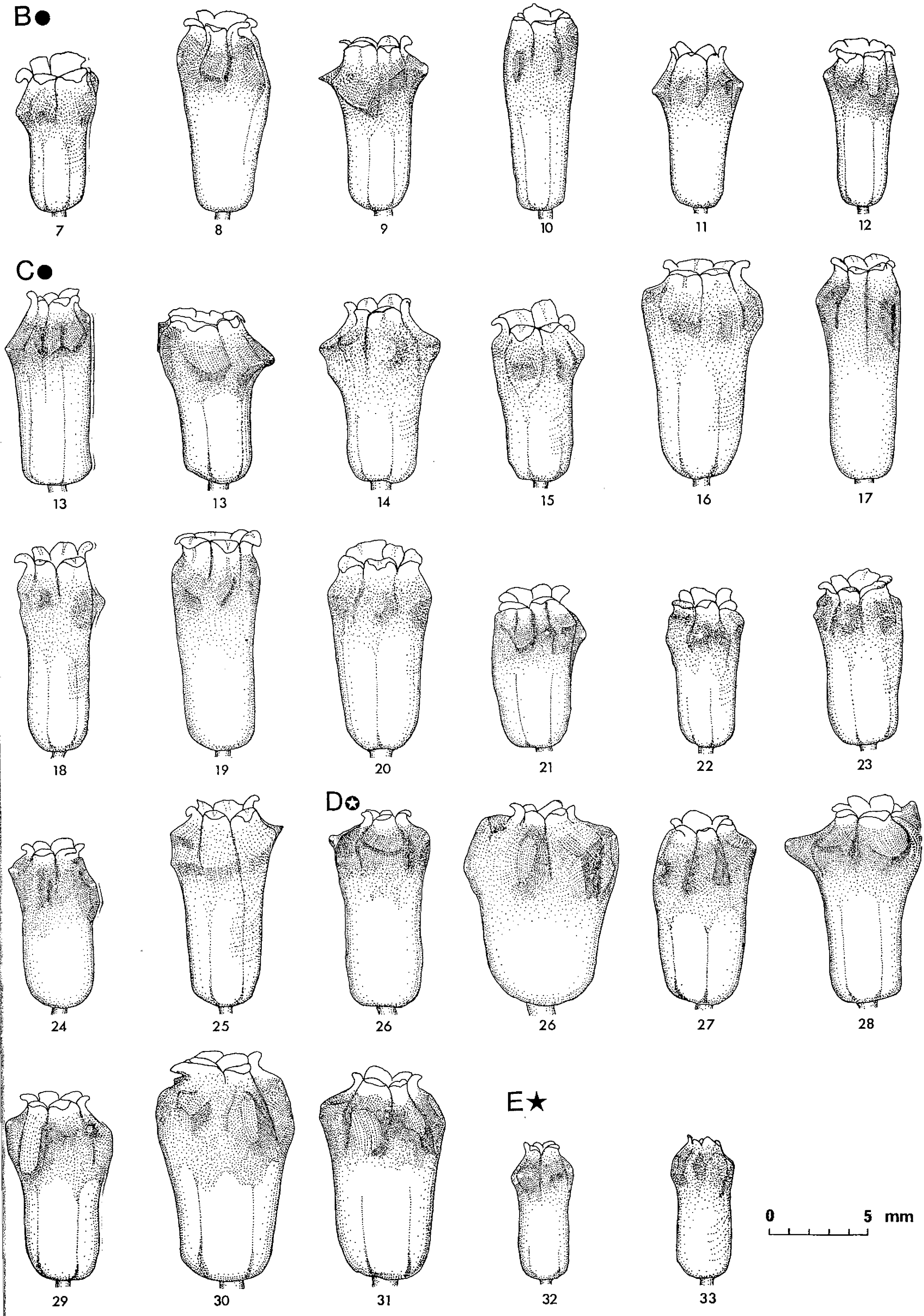


Fig. 23. *Leopoldia.* Variation in outline of fertile flowers. Note that the flowers shown are not necessarily absolutely typical. The appearance is, however, fairly constant within populations. — A: *L. comosa* (2x). — B: *L. weissii* (2x). — C: *L. weissii* (4x). — D: *L. dionysica* (2x, 4x). — E: *L. spreitzenhoferi* (2x, 4x).


B●
7
8
9
10
11
12
C●
13
13
14
15
16
17
18
19
20
21
22
23
24
25
D✪
26
26
27
28
29
30
31
E★
32
33
0
5 mm

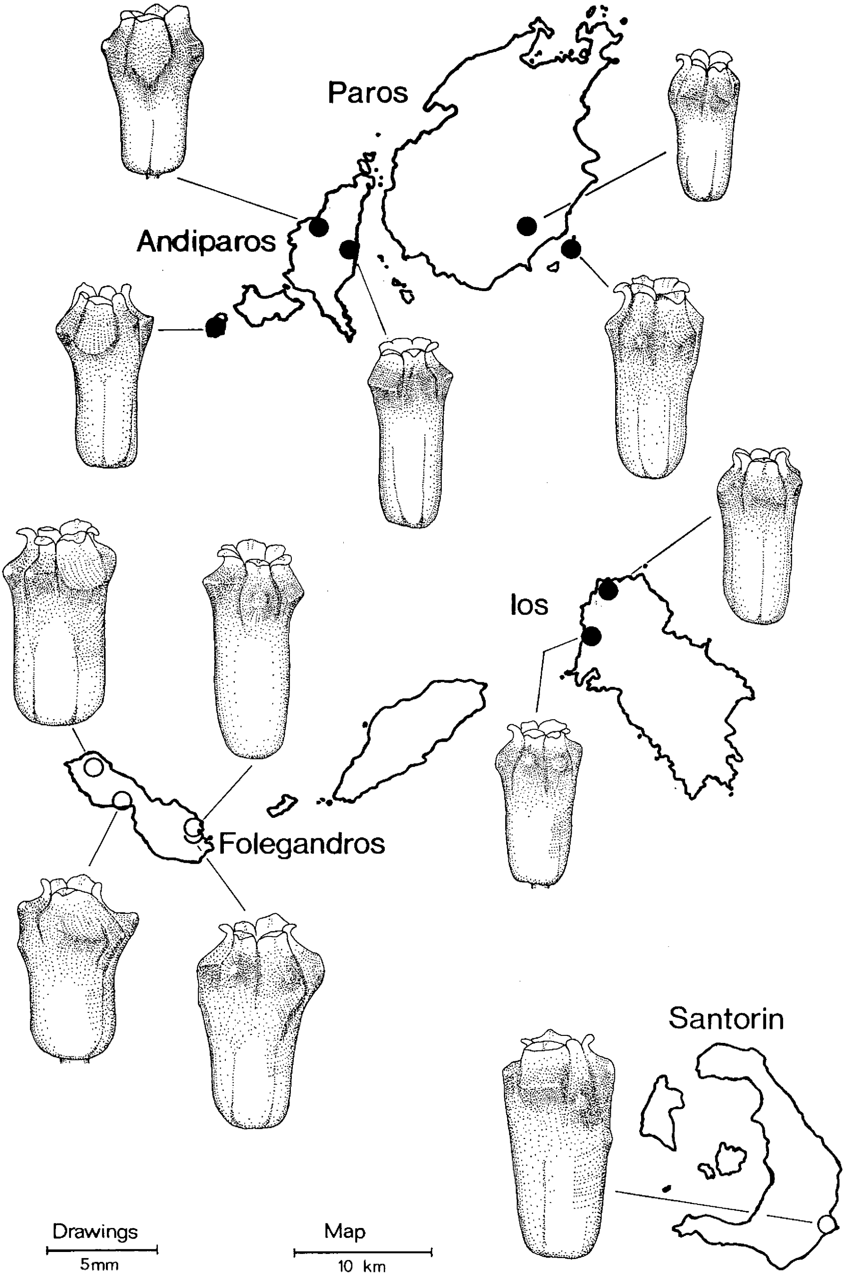


Fig. 24. *Leopoldia.* Variation in outline of fertile flowers. Dots=*L. cycladica* ssp. *subsessilis* (4x). Rings=*L. cycladica* ssp. *cycladica* (4x, 6x). The western-most population of *L. cycladica* ssp. *cycladica* is tetraploid, while the others are hexaploid.

most appropriately investigated by studying the pollen stainability and chromosome pairing affinities of the F_1 and F_2 hybrids. At the present stage of this investigation it is not possible to make precise analyses of genomic relationships since the F_1 hybrids have just completed their third season of growth without flowering. It is expected that they will commence flowering in 1974.

The ability of a particular cross to produce seeds that germinate, with a subsequent normal development of the seedlings, can only be regarded as an extremely rough estimate of the genetic similarities between the parents. In much of the material investigated by others, it has been shown that there is no correlation between crossability and interfertility (ORNDUFF 1969), nor is there necessarily any correlation between the germinating capacity of hybrid seeds and subsequent pollen stainability in the hybrids (STRID 1970).

Crossability between two taxa indicates the possibility of natural introgressive hybridization provided the parents occur sympatrically. The potential ability to proliferate is widespread in Aegean *Leopoldia* and cases of proliferation in natural hybrids between *L. weissii* (4x) and *L. comosa* (2x) have been observed in cultivation (see p. 93). One may therefore assume that if hybrid seeds germinate and grow to maturity, the plants may subsequently proliferate and may ultimately give rise to a number of new plants, i.e. a clone. Triploid hybrid clones may persist for long periods of time and may serve as bridges across which a given gene exchange may occur (MÜNTZING 1937, ZOHARY & NUR 1959).

The crossings were performed by means of the same technique of emasculation, isolation and pollination during the entire investigation. However, negative crosses (see Appendix 2) may in fact be due to minor technical mistakes. The significance of the values for seeds obtained from successful crosses and seeds that germinated are very difficult to estimate. Obvious discrepancies are sometimes found between identical crosses, e.g. crosses nos. 135 and 136 (see Appendix) between the same two plants of *L. weissii* (4x) and *L. cycladica* ssp. *subsessilis* (4x) crossed in two successive years. The first of these resulted in 3 seeds, none of which germinated, while the second resulted in 11 seeds of which 10 germinated.

As a rule it seems to be easy to cross populations of the same taxon and get seeds that germinate and grow well. In Fig. 27 B and C, some crosses within *L. weissii* are shown. There are apparently no pronounced barriers to crossability in diploid and tetraploid *L. weissii.*

Crosses between taxa with the same chromosome number were generally almost as easy to make as crosses between populations of the same taxon. This is exemplified in Fig. 27 A, where crosses between *L. dionysica* (4x) and tetraploid *L. weissii* indicate good general crossability.

Crosses between plants with different levels of ploidy within as well as between taxa, tend to give lower seed production and seed germination than similar crosses at the same level of ploidy (see Appendix 3).

L. comosa falls somewhat outside the normal scheme of crossability as would be expected from its deviating chromosome morphology. It seems to be rather difficult to cross intraspecifically as well as interspecifically, at least at the diploid level (see Appendix 3, crosses nos. 158—168). The few attempts at crosses between *L. comosa* and tetraploid *L. weissii* that were carried out seem to indicate that such crosses are easier to perform, facts that are also supported by the many hybrids between *L. comosa* and *L. weissii* (4x) that are found in nature.

In the Aegean, *Leopoldia* seems to comprise a complex of populations which are more or less interfertile from the point of actual crossability but which might nevertheless prove to be genetically more

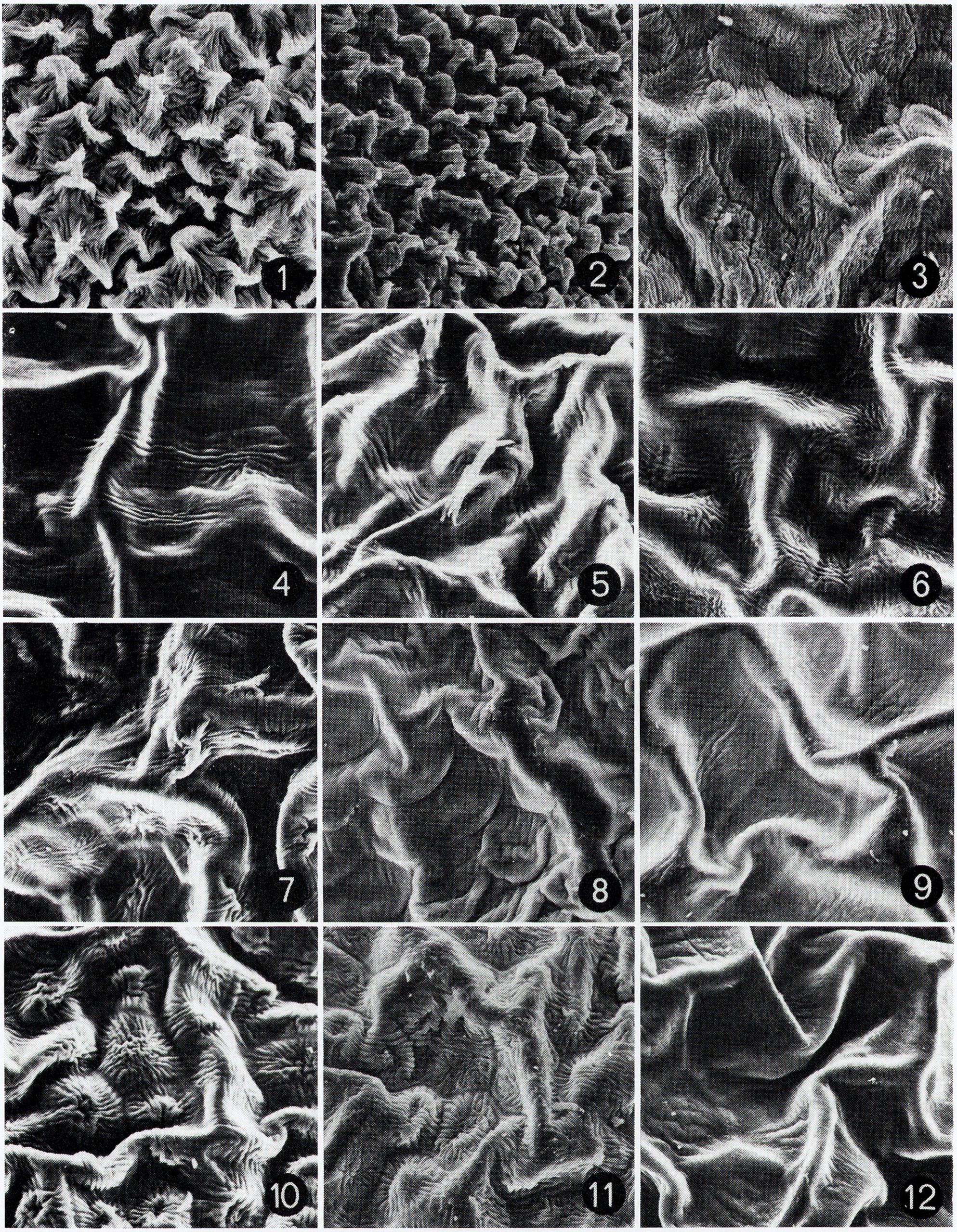
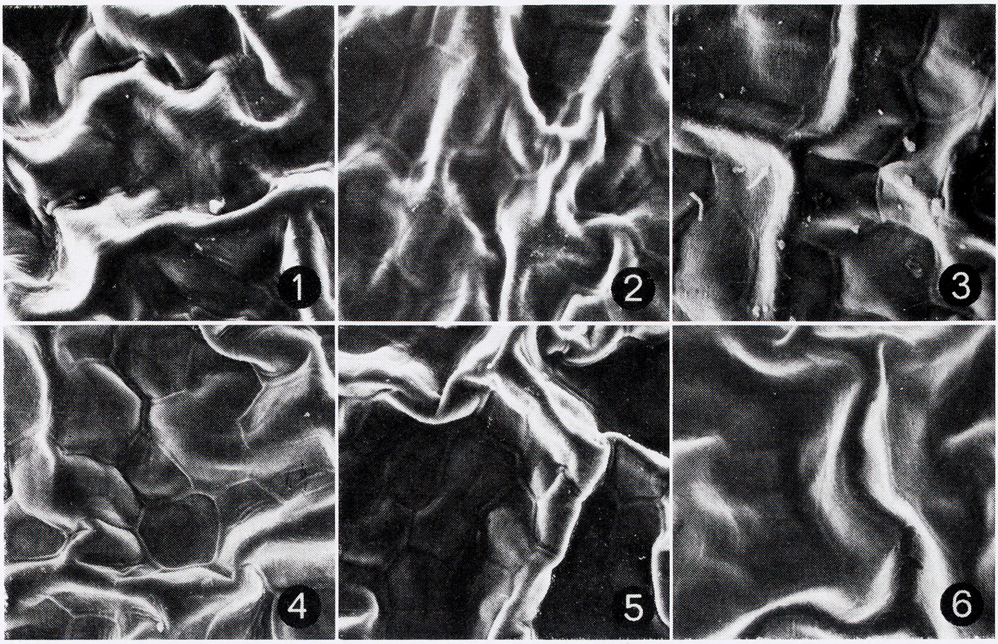


Fig. 25. *Leopoldia.* Variation in the equatorial part of seed surfaces (×c. 160). — 1—2: *L. comosa* (2x). — 3—6: *L. weissii* (2x). — 7—8: *L. weissii* (4x). — 9: *L. cycladica* ssp. *cycladica* (6x). — 10—11: *L. cycladica* ssp. *subsessilis* (4x). — 12: *L. spreitzenhoferi* (4x). — 1 (no. 16), 2 (no. 79), 3 (no. 303), 4 (no. 313), 5 (no. 314), 6 (no. 49), 7 (no. 67), 8 (no. 32), 9 (no. 60), 10 (no. 100), 11 (no. 80), 12 (no. 404).



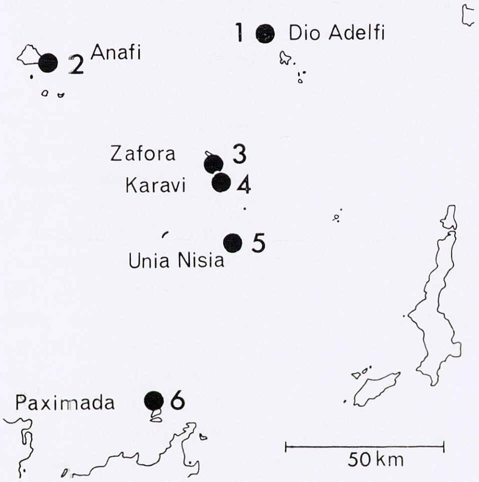


Fig. 26. *Leopoldia dionysica* (2x, 4x). Variation in the equatorial part of seed surfaces (×c. 160). No. 5 diploid, no. 6 unknown chromosome number, the others tetraploid.

or less distinct. At present it does not seem possible to use data from the crossing programme to support the proposed taxonomic subdivision of the Aegean material, even if a certain tendency to limited crossability is found, for instance between levels of ploidy. Barriers to crossability are not necessarily of any taxonomic importance (ORNDUFF 1969). A number of barriers to crossing among populations of the same taxon are pointed out by ORNDUFF (op. cit.) and he even suggests that rigid species definitions based on crossability and/or interfertility are impracticable in flowering plants.

EVOLUTIONARY TRENDS IN AEGEAN LEOPOLDIA

Paleogeography and Phytogeography

The paleogeographical development and the phytogeographical subdivision of the Aegean region has been outlined by a number of workers, e.g. PFANNENSTIEL 1954, CREUTZBURG 1963, 1966, MEULENKAMP 1971, SONDAAR 1971, RECHINGER 1950, 1951, SNOGERUP 1967 b, RUNEMARK 1969, 1970, 1971, STRID 1970, 1972, GREUTER 1970, 1971, 1972, STORK 1972.

During the Pliocene, a land bridge connected southern Greece with Anatolia via the central Aegean. During the Pleistocene this land bridge subsequently subsided leaving a number of islands. During Pleistocene times, the sea level in the Mediterranean fluctuated considerably, i.e. maybe up to c. 200 m, between periods of glaciation and the interglacial stages. The geographical isolation of some closely situated islands was consequently at times interrupted.

Further south, Peloponnisos was connected with Anatolia via a land bridge over the present islands of Kithira, Kriti, Karpathos and Rodhos during the mid-Tertiary. This bridge partially collapsed and the present islands have probably been isolated from one another since the Pliocene.

The phytogeographical subdivision of the central and southern Aegean was originally proposed by RECHINGER (1950). The main outlines of this subdivision is given in Fig. 30. The different *Leopoldia* taxa fit only partly into RECHINGER's subdivision.

L. comosa is a pan-Mediterranean weed and it is consequently not restricted by any local phytogeographical boundaries in the area studied.

L. weissii is mainly restricted to the Aegean region but not to a particular phytogeographical area. There are, however certain tendencies in the differentiation of the taxon that agree with the paleogeographical development of the area such as the similarity of material from Rodhos, Karpathos and Attiki, cytologically deviating populations from the Northern Sporades and other northern Aegean islands (BENTZER in prep.).

The range of *L. cycladica* ssp. *cycladica* agrees well with the central Aegean phytogeographical region if a dubious locality on Ikaria is left out of account.

L. cycladica ssp. *subsessilis* is also mainly a central Aegean element with outposts on SE Kriti. Similar distributions are known from other plant species, e.g. *Amaracus tournefortii* (SIBTH.) BENTH., *Eryngium amorginum* RECH. FIL., *Seseli crithmifolium* (DC.) BOISS.

L. dionysica may belong to an east Mediterranean element that appears in isolated localities that were originally part of an extensive continuous distribution. The small islands between Astipalaia and Karpathos, which are inhabited by *L. dionysica*, are difficult to fit into a phytogeographical scheme, and RUNEMARK (1971) presumed that they are remnants of a former larger system of islands.

The species shows close morphological resemblance to *Leopoldia* collections seen from Cyprus and E Anatolia. A number of plant species seem to share a similar distribution type, e.g. *Nigella fumariifolia* KOTSCHY, *Lithospermum hispidulum* S. & S., *Bromus caroli-henrici* GREUTER.

L. dionysica has an extraordinary outpost on the N Sporades. A similar jump over the central Aegean is seen in, e.g. *Amelanchier cretica* (WILLD.) DC., the *Symphyandra cretica* DC. complex.

The range of *L. spreitzenhoferi* agrees well with the southern Aegean phytogeographical region, being endemic to Kriti. The single locality in Algeria, based upon a single collection from 1851, is certainly provoking but further studies are needed to elucidate possible relationships between North African *Leopoldia* and *L. spreitzenhoferi*.

As the present distribution of *Leopoldia* taxa does not wholly agree with the phytogeographical regions one would assume

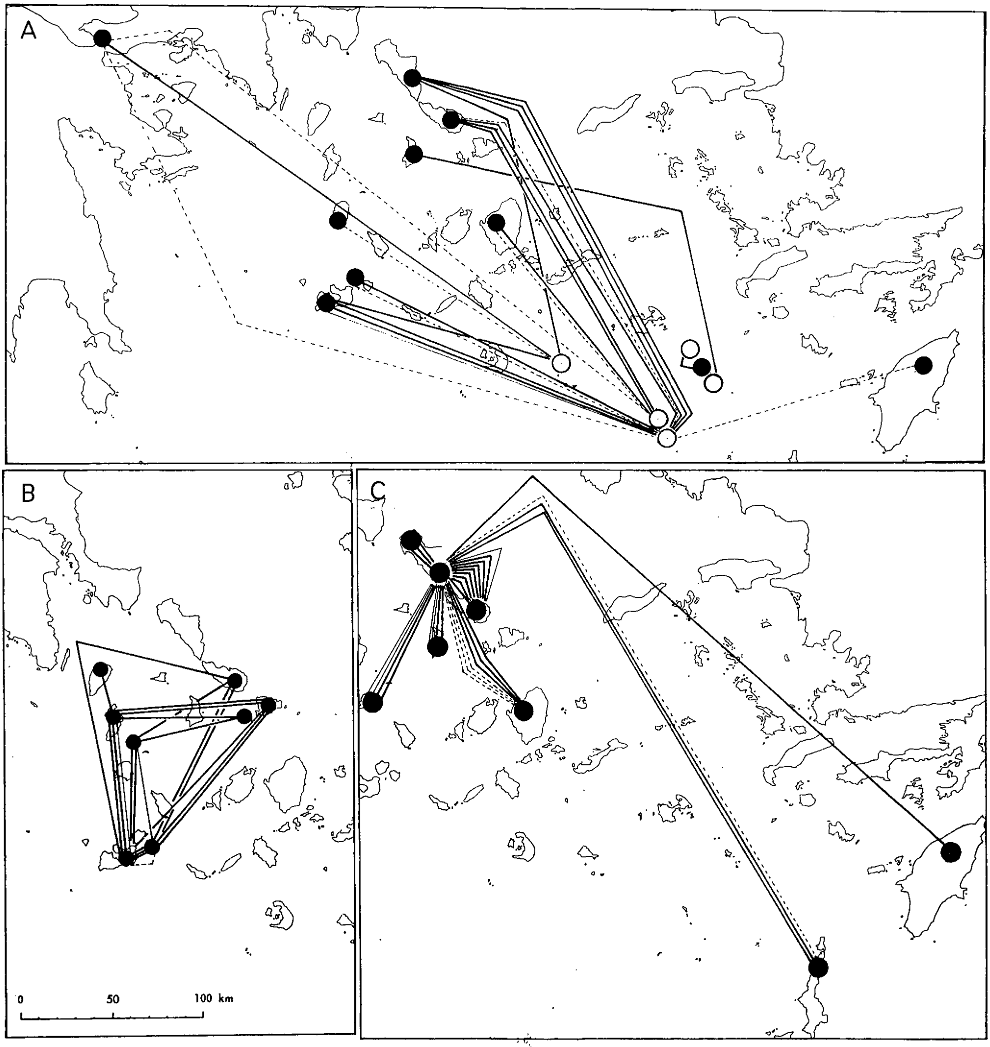


Fig. 27. *Leopoldia.* Crossability within and between different taxa. Heavy lines indicate that crossing attempts have resulted in seeds that germinated to more than 50 %. Fine lines indicate that crossing attempts have resulted in seeds that germinated to less than 50 %. Dotted lines indicate that crossing attempts have failed. Rings and dots do not represent individual populations but groups of populations within a restricted area. — A: Crossability between *L. weissii* (4x) and *L. dionysica* (4x). Dots=*L. weissii.* Rings=*L. dionysica.* — B: Crossability between diploid populations of *L. weissii.* — C: Crossability between *L. weissii* (4x) from Andros and other groups of populations of *L. weissii* (4x).

that the taxa are very old inhabitants, presumably dating back to the Tertiary. It is likely that the distribution of the different taxa was formerly, i.e. in Tertiary to Pleistocene times, wider and more continuous, the present areas of distribution being remnants. *L. comosa* is impossible to incorparate into a phytogeographical scheme since it appears as a weed in the entire Mediterranean region and may well be a comparatively new inhabitant in the Aegean region.

Modes of Differentiation

The evolutionary mechanisms that have contributed to the present morphological diversification of *Leopoldia* are difficult to demonstrate and evaluate in relation to one another. One limiting factor in the discussion is the unknown extent and the significance of proliferation in nature.

A number of ways in which evolution may have acted will be enumerated and their possible importance for the present material will be pointed out.

(1) The migration of founder taxa to the pre-Pleistocene land bridges between Greece and Anatolia and the subsequent hybridization between these taxa. After the break-down of the bridges each of the islands that remained had a characteristic part of the total gene pool. Such an evolutionary outline was proposed by EHRENDORFER (1971) for some *Galium* species in SW Asia.

(2 A) A differentiation of local types at different taxonomic levels is caused by the fixation of alleles that originate from one large polymorphic parental taxon which has been split up into a mosaic of micropopulations (GREUTER 1972).

(2 B) A complex of small populations produces a high degree of stability over long periods of time, while dynamic phases of evolution are concentrated to periods when fluctuations of sea level, and climatic factors, make it possible for isolated populations to establish contact and exchange genes (GREUTER 1972).

(3) Climatic fluctuations may give rise to new ecological possibilities for exploitation. New forms may evolve to colonize the new habitats. A further climatic change may then reduce the new habitat, with resulting strong selection and the concentration of marginal populations. Such concentrations would increase the possibilities for hybridization and further differentiation. Continuous climatic changes would act as an "evolutionary pump" as described by MORTON (1972) to explain the high frequency of endemic taxa in the montane habitats of W Africa. GREUTER (1972) explained endemism on the mountains of Kriti in a similar way.

(4) Comparatively recent hybridization between taxa that have established contact in one way or another. The general effect of hybridization on plant speciation has been stressed by a number of workers, e.g. STEBBINS 1950, 1969, GRANT 1953, GILLET 1966, 1972, KRUCKEBERG 1969, BARBER 1970, LEVIN 1970, etc.

(5) The migration of one single plant or very few from one island to another would imply that a very restricted part of the original gene pool would be isolated from the rest. A new population that establishes itself from these few emigrants would have a reasonable chance to evolve differently from the parental population, i.e. "the founder effect" (MAYR 1954).

(6) A very strong and rapid reduction in population size to only a few plants owing to selection ("catastrophic selection", LEWIS 1962) would restrict the gene pool considerably, and make the population very susceptible to the action of random factors.

(7) Climatic fluctuations during long periods of time will necessarily induce oscillations in population sizes. During large-population periods a population will be in a selective phase of evolution, while during small-population periods it will be in a creative phase mainly due to genetic drift. Genetic drift may give rise to the introduction of genetic factors which may be primarily non-adaptive. It may rapidly fixate genetic changes and break down rigid gene blocks (SNOGERUP 1967 b, RUNEMARK 1970, STRID 1970).

The Significance of the Differentiation Mechanisms

(1) To be able to discuss this hypothesis it is necessary to know the degree of differentiation of *Leopoldia* on the mainlands of Greece and Turkey about which very little is known.

There are certain indications of frequent hybridization on a number of islands, i.e. structural chromosome heterozygosity (Bentzer 1969 and in prep.), but it is often difficult to determine when the hybridization took place. In some cases it is, however, quite clear that the hybridization is a current phenomenon.

The morphological resemblance between *L. weissii* from Rodhos, Karpathos and Attiki may indicate that formerly *L. weissii* was morphologically fairly uniform in the entire Aegean, but that subsequent differentiation has taken place since the geographical isolation of the islands.

(2 A) In this case it is also necessary to know the extent of the variation in *Leopoldia* on the mainlands of Greece and Turkey in order to evaluate the hypothesis.

Evidence from other material does, however, at least partly contradict Greuter's (1972) assumptions. Snogerup (1967 a, b) showed that the morphological variation in *Erysimum corinthium* (Boiss.) Wettstein on Peloponnisos is much less than the variation in *Erysimum senoneri* (Heldr. & Sart.) Wettstein on the islands. Representatives of the *Nigella arvensis* coenospecies are distributed from Peloponnisos over the Greek mainland to Anatolia with comparatively wide bands of intermediate form series between the taxa while in other representatives of the coenospecies there are sharp discontinuities between islands in the archipelago (Strid 1970, 1972). According to Greuter (op. cit.) one would, in the above-mentioned cases, expect a high degree of polymorphism in the large mainland populations as well as distinct differentiation on the islands. This is obviously not currently so.

(2 B) Greuter's hypothesis (1972) in which he stresses the static conditions in small isolated populations and the great evolutionary potential when such small populations meet, can be questioned. If two adjacent islands were originally inhabited each by one small population which primarily originated from the same gene pool, and if after a considerable period of time in isolation the populations met and established one large population, no sudden evolutionary expansion would be expected unless each population during isolation had developed in some specific direction.

(3) The climatic fluctuations causing the repeated opening up and decline of new ecological habitats as a driving force in the evolutionary process, may have been of importance on the islands. There are indications that cliffs may constitute refugia for a number of species which originally had a wider distribution under ecological conditions that no longer exist (Snogerup 1967 b, 1971). *L. cycladica* ssp. *cycladica* and to some extent *L. dionysica* are examples of taxa that may have survived in chasmophytic habitats and to which they have subsequently been adapted.

(4) Hybridization as a factor in evolution seems to be evident in *L. weissii*. Hybridization between *L. weissii* (4x) and *L. comosa* (2x) certainly often takes place when they occur sympatrically. It seems very likely that introgressive hybridization between tetraploid *L. weissii* and *L. comosa* towards *L. weissii* has contributed to the local polymorphism on islands. It is, however, worth noting that aneuploid chromosome numbers have very rarely been found. One would normally expect a certain number of such unbalanced genomes in introgressive swarms between diploid and tetraploid founders. It seems less certain that the differentiation of *L. weissii* between islands has arisen from species hybridization. It has not been pos-

sible to find any cytological proof of hybridization between diploid *L. weissii* and *L. comosa* although they occur sympatrically in several localities, nor was it possible to perform artificial crosses between these two cytotypes. The diploid populations of *L. weissii* show almost as much differentiation as the tetraploid, a fact indicating that the differentiation in both diploids and tetraploids is caused by additional factors.

I cannot see that there is anything to prevent hybridization between *L. comosa* and other polyploid taxa although there is at present no proof of such hybridization. One may, however, suspect that hybridization between *L. weissii* (4x) and *L. cycladica* ssp. *cycladica* as well as ssp. *subsessilis* may be responsible for intermediate populations that are found, e.g. in the Siros area, on the island of Makronisi E of Paros and on Folegandros.

(5, 6, 7) The effect of these factors are bound together and they may have played an important part in local differentiation.

If two large populations are sufficiently isolated from each other to preclude gene exchange, and if they grow in similar habitats, they are likely to evolve along more or less parallel lines. The type of selection in both populations is likely to be more or less similar, i.e. stabilizing in a stable environment and disruptive in a changing one.

If on the other hand one or both of the populations is small owing to: (1) slowly deteriorating climatic factors; (2) catastrophic selection; (3) the migration of a few plants from one population to establish another; (4) rapid decrease in population size due to other factors, then selection is still likely to be parallel. The genetic supply on which selection operates may, however, be different in the two populations since only parts of a presumed common original gene pool are present in each population, and which part is a matter of chance. In each of the small populations similarly adapted but differently balanced types may be established. Genotypic differences between the populations may be reflected in the phenotypes which are not necessarily adapted to the environments (LEWIS & JOHN 1963).

When small-sized populations are successively created, mainly directional selection operates during a long period of time and it is likely to be more or less parallel in similarly adapted populations. The resulting small surviving gene pools of such populations may consequently be more or less similar.

In the case of catastrophic reduction in population size the resulting small gene pools may to a larger extent be due to chance.

To sum up, one may conclude that genotypic differences between two small populations are more likely to occur if the populations are products of catastrophic reduction or "founder effect" than if they are products of climatic fluctuation.

The most deviating populations of *Leopoldia* spp. are those which are composed of a limited number of plants (see pp. 104—105). Such populations are mainly found on small islands. One may presume that many of these small islands have been submerged below sea level owing to climatic conditions — mainly during the Pleistocene. Later recolonization from adjacent large islands is therefore likely to have taken place and the uniqueness of the present populations is probably caused by the "founder effect".

Differentiation on large islands is usually less conspicuous as to apparently nonadaptive characters. One may suspect that climatic fluctuations have entailed occasional gene exchanges between populations on large islands as well as occasional reinforced spatial isolation barriers due to reduction in population sizes.

Catastrophic reduction may have had a certain effect on differentiation on volcanic islands such as Santorin, the Milos-Kimolos-Poliaigos group, etc. although there are no clear indications of it. Similarly, tectonic movements may have played a certain part as a source of catastrophic reduction in population sizes.

The effects of mutations on the variation range is difficult to estimate. If proliferation does not take place, then mutations are more likely to be established in small populations than in larger ones, in spite of a lower number of mutations in the former; see e.g. SNOGERUP 1967 b.

If on the other hand proliferation takes place, then the proliferating mutants minimize the effect of selection in the establishment phase after each cycle of generation and may be maintained unchanged in a population for indefinite periods of time. In this case the size of the population is of no importance for the establishment of the mutant.

Conclusion

Local differentiation in *Leopoldia* taxa is presumably the result of a combination of drift, adaptive radiation, "founder effect", and occasional hybridization between species as well as between temporarily sympatric populations of the same taxon. As a generating factor in the mechanism of evolution, fluctuations in population size, mainly resulting from climatic changes and the creation of small populations by means of colonization, have been of major importance.

The Polyploid Populations

L. WEISSII

In *L. weissii* the different cytotypes (2x, 4x) are geographically separated (Fig. 28). Only on the islands of Milos, Ay. Yeoryios (close to Milos), and Tinos have diploids as well as tetraploids been found. The situation could conveniently be explained by assuming that in Miocene—Pliocene times, when the land bridges existed between Greece and Anatolia over the Kikladhes and Kriti, *L. weissii* occurred as a diploid in one minor area on one of the land bridges, but was tetraploid in its main distribution. The establishment of polyploidy may also have been influenced by the large climatic fluctuations that preceded the collapse of the land bridges (GRANT 1971 p. 261). The distribution of cytotypes on the Pliocene—Pleistocene islands then mainly corresponded with their earlier distribution on the land bridges. Reciprocal migrations between islands with diploid and tetraploid populations may have taken place during glacial periods when land connections existed. Such an assumption is supported by the fact that the islands that are inhabited by diploids as well as tetraploids, are situated close to islands with either diploid or tetraploid populations only, viz. Milos (2x, 4x), Ay. Yeoryios (2x, 4x) — Kimolos (4x, few populations) — Poliaigos (2x, few populations), Tinos (2x, 4x, 6x) — Andros (4x) — Mikonos (2x). There are indications of recent polyploidization in *L. weissii* on Tinos, where one population (no. 325) constituted a mixture of tetraploid and hexaploid plants. This is the only case of hexaploid *L. weissii* that has been recorded.

L. CYCLADICA

In *L. cycladica* ssp. *cycladica* there are also indications of recent polyploidization on Folegandros where tetraploid as well as hexaploid populations were found.

L. DIONYSICA

The species is tetraploid except in two localities, i.e. on Unia Nisia (no. 50) and Astakidha (no. 97), where it is diploid. The chromosome numbers of *L. dionysica* from the islands immediately north of Kriti are not known.

During the Pliocene and Pleistocene a large continuous area of distribution may have been split into a number of smaller isolated areas. If one accepts this hypothesis the distribution of the present polyploidy would best be explained in the same way as for *L. weissii*. One may assume that all populations south of Karavi are remnants of one large distributional area

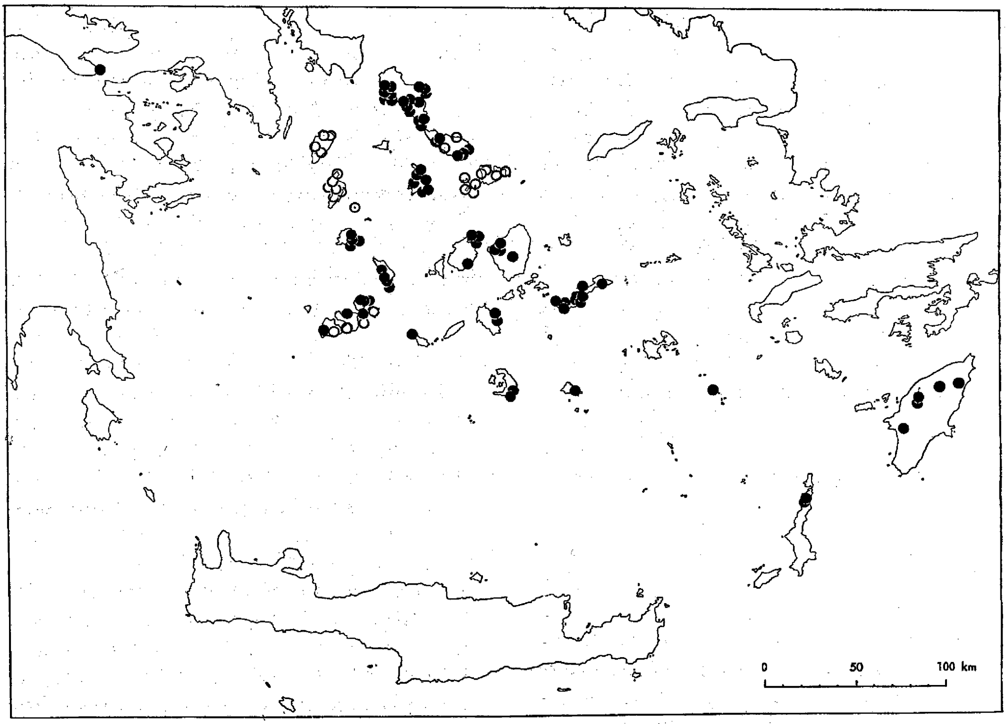


Fig. 28. *Leopoldia weissii* (2x, 4x). Distribution of populations studied cytologically. Dots=diploid populations. Rings=tetraploid populations.

of diploids while those north of Karavi are remnants of a larger area of tetraploids.

L. SPREITZENHOFERI

The species has only been superficially studied. On the southern coast of Kriti, diploid as well as tetraploid populations occur in similar habitats separated from one another by only a few kilometres. It seems at present unwise to support any particular hypothesis as an explanation of the evolution of polyploidy in this taxon.

ACKNOWLEDGEMENTS

The present study has been supported by grants from the Swedish Natural Science Research Council, the Bokelund's Foundation for Natural Science, the Anna and Svante Murbeck Foundation and the Längmanska Foundation for Culture.

LITERATURE CITED

ASCHERSON, P. & GRAEBNER, P. 1905. Synopsis der Mitteleuropäischen Flora, 3. — Leipzig.

BAKER, J. G. 1871. A revision of the genera and species of herbaceous capsular gamophyllous Liliaceae. — Journ. Linn. Soc. 11: 349—436.

BARBER, H. N. 1970. Hybridization and the evolution of plants. — Taxon 19: 154—160.

BARTHOLOMEW, J. 1956 (ed.). The Times atlas of the world, 4. Southern Europe and Africa. — London.

BENTZER, B. 1969. Chromosome morphology in Aegean populations of Leopoldia Parl. (Liliaceae). — Bot. Notiser 122: 457—480.

— 1972 a. Structural chromosome polymorphism in diploid Leopoldia weissii (Freyn) Freyn ex Heldr. (Liliaceae). — Bot. Notiser 125: 180—185.

— 1972 b. The chromosomes of Leopoldia bicolor (Boiss.) Eig & Feinbr. (Liliaceae). — Bot. Notiser 125: 329—330.

— 1972 c. Variation in the chromosome complement of Leopoldia comosa (L.)

Parl. (Liliaceae) in the Aegean (Greece). — Bot. Notiser 125: 406—418.

Boissier, E. 1844. Diagnoses plantarum orientalium novarum I, 5: 62. — Lipsiae.

— 1884. Flora Orientalis, 5. — Genevae et Basileae.

Cain, S. A. 1944. Foundations of plant geography. — New York and London.

Creutzburg, N. 1963. Die palägeographische Entwicklung der Insel Kreta von Miozän bis zur Gegenwart. — Kritika Chronika 15—16: 336—344. Iraklion. (In Greek with a summary in German).

— 1966. Die südägäische Inselbrücke. Bau und geologische Vergangenheit. — Erdkunde 20: 20—30.

Davis, P. H. & Stuart, D. S. 1967. Three new species of Muscari. — The Lily Year Book 30: 123—126.

Desfontaines, R. 1800. Flora atlantica sive historia plantarum, 1. — Parisiis.

Ehrendorfer, F. 1971. Evolution and ecogeographical differentiation in some South-West Asiatic Rubiaceae. — In P. H. Davis et al. (eds.): Plant life of South-West Asia, pp. 195—215. — Aberdeen.

Fiori, A. & Paoletti, G. 1898. Flora analitica d'Italia, 1. — Padova.

Freyn, J. 1878. Muscari (Bellevalia, Leopoldia) Weissii n. sp. — Österr. Bot. Zeitschr. 28: 87—88.

Galil, J. 1958. Physiological studies on the development of contractile roots in geophytes. — Bull. Res. Counc. Israel 6 D: 221—236.

Gandoger, M. 1916. Flora Cretica. — Parisiis.

Garbari, F. 1968 a. Sul rango tassonomico di Leopoldia Parl., Muscarimia Kostel., Muscari Mill. — Giorn. Bot. Ital. 101: 300—301.

— 1968 b. Il genere Muscari (Liliaceae): Contributo alla revisione citotassonomica. — Giorn. Bot. Ital. 102: 87—105.

— 1969. Nuove osservazioni citologiche sui generi Muscari e Leopoldia. — Giorn. Bot. Ital. 103: 1—9.

— & Greuter, W. 1970. On the taxonomy and typification of Muscari Miller (Liliaceae) and allied genera, and on the typification of generic names. — Taxon 19: 329—335.

— & Martino, A. 1972. "Leopoldia gussonei" Parl. (Liliaceae), specie endemica siciliana. — Webbia 27: 289—297.

Gillet, G. W. 1966. Hybridization and its taxonomic implications in the Scaevola gaudichandiana complex of the Hawaiian islands. — Evolution 20: 506—516.

— 1972. The role of hybridization in the evolution of the Hawaiian flora. — In D. H. Valentine (ed.): Taxonomy, phytogeography and evolution, pp. 205—219. — London and New York.

Grant, V. 1953. The role of hybridization in the evolution of the leafy-stemmed Gilias. — Evolution 7: 51—64.

— 1971. Plant speciation. — New York and London.

Greuter, W. 1970. Zur Palägeographie und Florengeschichte der südlichen Ägäis. — Feddes Rep. 81: 233—242.

— 1971. Betrachtungen zur Pflanzengeographie der Südägäis. — In A. Strid (ed.): Evolution in the Aegean, pp. 49—64. — Opera Bot. 30.

— 1972. The relict element of the flora of Crete and its evolutionary significance. — In D. H. Valentine (ed.): Taxonomy, phytogeography and evolution, pp. 161—177. — London and New York.

Halácsy, E. 1904. Conspectus Florae Graecae, 3. — Lipsiae.

Harper, J. L. 1966. The reproductive biology of the British poppies. — In J. G. Hawkes (ed.): Reproductive biology and taxonomy of vascular plants, pp. 26—39. — London.

Hayek, A. 1933. Prodromus Florae peninsulae Balcanicae, 3. — Feddes Rep. Beih. 30: 3.

Heldreich, Th. von 1876. Sertulum plantarum novarum Florae Hellenicae. — In: Atti Congr. Firenze, pp. 4—8. — Florentiae.

— 1878. Über die Liliaceen-Gattung Leopoldia und ihre Arten. — Bull. Soc. Imp. Natural. Moscou, 53: 56—75.

Herbert 1820. Amaryllis reticulata. β. striatifolia. Griffin's netted-veined Amaryllis. — Curtis's Bot. Mag. 47: 2113 (1—6).

Knoll, F. 1921. Insekten und Blumen. Experimentelle Arbeiten zur Vertiefung unserer Kenntnisse über die Wechselbeziehungen zwischen Pflanzen und Tieren. — Abh. Zool.-Bot. Ges. Wien 12 (1): 1—119.

Kosteletzky, V. F. 1844. Index plantarum horti caesarei regii botanici pragensis. — Prag (not seen).

Krause, K. 1930. In A. Engler (ed.), Die Natürlichen Pflanzenfamilien 15 a: 348—349. — Leipzig.

Kruckeberg, A. R. 1969. The implications of ecology for plant systematics. — Taxon 18: 92—120.

Kunth, C. S. 1843. Enumeratio plantarum omnium hucusque cognitarum, 4. — Stutgardiae et Tubingae.

Lanjouw, J. & Stafleu, F. A. 1964. Index Herbariorum, 1. — Regn. Veg. 31.

Levin, D. A. 1970. Hybridization and evolution — a discussion. — Taxon 19: 167—171.

Lewis, D. 1943. Physiology of incompatibility in plants, 3. Autopolyploids. — Journ. Genetics 45: 171—185.

— 1966. The genetic integration of the breeding system. — In J. G. HAWKES (ed.): Reproductive Biology and Taxonomy of vascular plants, pp. 20—25. — London.

LEWIS, H. 1962. Catastrophic selection as a factor in speciation. — Evolution 16: 257—271.

LEWIS, K. R. & JOHN, B. 1963. Chromosome marker. — London.

LINNAEUS, C. 1753. Species plantarum, 1. — Holmiae.

MAYR, E. 1954. Change of genetic environment and evolution. — In HUXLEY et al. (eds.): Evolution as a process, pp. 157—180. — London.

MEULENKAMP, J. E. 1971. The Neogene in the southern Aegean area. — In A. STRID (ed.): Evolution in the Aegean, pp. 5—12. — Opera Bot. 30.

MILLER, PH. 1768. The gardener's dictionary. Ed. 8, no. 2 (not seen). — London.

MORTON, J. K. 1972. Phytogeography of the West African Mountains. — In D. H. VALENTINE (ed.): Taxonomy, phytogeography and evolution, pp. 221—236. — London and New York.

MÜNTZING, A. 1937. The effects of chromosomal variation in Dactylis. — Hereditas 23: 113—235.

NADJI, A. 1892. Fait nouveaux relatifs à la province de Salonique. — Empire Ottoman Géographie Botanique, 42. — Salonique.

NYMAN, C. F. 1882. Conspectus florae Europaeae. — Örebro.

ORNDUFF, R. 1969. Reproductive biology in relation to systematics. — Taxon 18: 121—133.

OSTERMEYER, F. 1890. Beitrag zur Flora von Kreta. — Verh. Zool.-Bot. Ges. Wien, 40: 291—300.

PARLATORE, F. 1845. Flora Palermitana, I. — Firenze.

— 1852. Flora Italiana, II. — Firenze.

PFANNENSTIEL, M. 1954. Die Schwankungen des Mittelmeerspiegels als Folge der Eiszeiten. — Freiburger Universitätsreden, N. F., 18.

RECHINGER, K. H. 1943 a. Flora Aegaea. — Denkschr. Akad. Wiss. Wien, Math.-Nat. Kl. 105 (1).

— 1943 b. Neue Beiträge zur Flora von Kreta. — Ibid. 105 (2).

— 1950. Grundzüge der Pflanzenverbreitung in der Aegäis, I—III. — Vegetatio 2: 55—119, 239—308, 365—386.

— 1951. Phytogeographia Aegaea. — Ibid. 105 (3).

RICHTER, K. 1890. Plantae Europeae, I. — Leipzig.

RUNEMARK, H. 1969. Reproductive drift, a neglected principle in reproductive biology. — Bot. Notiser 122: 90—129.

— 1970. The plant geography of the central Aegean. — Feddes Rep. 81: 229—231.

— 1971. The phytogeography of the central Aegean. — In A. STRID (ed.): Evolution in the Aegean, pp. 20—28. — Opera Bot. 30.

SALISBURY, R. A. 1866. The genera of plants. — London.

SNOGERUP, S. 1967 a. Studies in the Aegean flora. 8. Erysimum sect. Cheiranthus. A. Taxonomy. — Opera Bot. 13.

— 1967 b. Studies in the Aegean flora. 9. Erysimum sect. Cheiranthus. B. Variation and evolution in the small-population system. — Opera Bot. 14.

— 1971. Evolutionary and plant geographical aspects of chasmophytic communities. — In P. H. DAVIS et al. (eds.): Plant life in South-West Asia, pp. 157—170. — Aberdeen.

SONDAAR, P. Y. 1971. Paleozoogeography of the Pleistocene Mammals from the Aegean. — In A. STRID (ed.): Evolution in the Aegean, pp. 65—70. — Opera Bot. 30.

STEBBINS, G. L. 1950. Variation and evolution in plants. — New York and London.

— 1969. The significance of hybridization for plant taxonomy and evolution. — Taxon 18: 26—35.

STEARN, W. T. 1966. Botanical latin. — London and Edinburgh.

STORK, A. L. 1972. Studies in the Aegean flora. 20. Biosystematics of the Malcolmia maritima complex. — Opera Bot. 33.

STRID, A. 1970. Studies in the Aegean flora. 16. Biosystematics of the Nigella arvensis complex. With special reference to the problem of non-adaptive radiation. — Opera Bot. 28.

— 1972. Some evolutionary and phytogeographical problems in the Aegean. — In D. H. VALENTINE (ed.): Taxonomy, phytogeography and evolution, pp. 289—300. — London and New York.

STUART, D. 1965. Muscari and allied genera. A lily group discussion. — The Lily Year Book 29: 125—138.

TÄCKHOLM, V. & DRAR, M. 1954. Flora of Egypt, 3. — Cairo.

TURRILL, W. B. 1932. On the flora of the Nearer East, 13. Miscellaneous new records and extensions of known distributions. — Kew Bull. 1932: 450—454.

VIERHAPPER, F. 1916. Beiträge zur Kenntnis der Flora Kretas. — Österr. Bot. Zeitschr. 66: 166—169.

— 1919. Beiträge zur Kenntnis der Flora Griechenlands, 3. — Verh. Zool.-Bot. Ges. Wien 69: 157—245.

ZAHARIADI, C. 1966. In T. SAVULESCO & E. I. NYÁRÁDY (eds.): Flora Reipublicae Socialisticae Romania, 11. — Academiei Republicii Socialiste Romania.

ZOHARY, D. & NUR, U. 1959. Natural triploids in the orchard grass, Dactylis glomerata L., polyploid complex and their significance for gene flow from diploid to tetraploid levels. — Evolution 13: 311—317.

APPENDIX 1

Code to Collections Grown in Cultivation

Cultivation numbers are in bold type. Chromosome numbers are within parentheses. The origin of cultivated *L. comosa* is given in BENTZER 1972 c.

L. weissii

3 (36): Naxos, 2 km E of Engares, phrygana and cliffs, R & Be, 1967. — **5** (36): Santorin, cliffs near Perissa, H, 1967. — **6** (36): Naxos, NW of Melanes, phrygana, R & Be, 1967. — **8** (36): Kimolos, the island of Ay. Yeoryios, the S part, volcanic soil, R & Be, 1967. — **9** (36): Milos, in the W part, in the valley N of the monastery, 10—20 m alt., R & Be, 1967. — **10** (36): Serifos, the peak N of the town, phrygana, 300 m, R & Be, 1967. — **12** (36): Santorin, S side of Mt Proph. Elias, schist, 50 m, R & Be, 1967. — **19** (36): Amorgos, in the valley SE of Katapola, R & Be, 1967. — **20** (36): Sifnos, S of Kamares, N facing cliffs, 300 m, R & Be, 1967. — **21** (36): Sifnos, the island of Kitriani, phrygana, R & Be, 1967. — **26** (36): Serifos, the island of Vous, 0—70 m, R & Be, 1967. — **28** (36): Amorgos, near Katapola, phrygana, 0—200 m, R & Be, 1967. — **29** (36): Sifnos, the island of Kitriani, phrygana, 50 m, R & Be, 1967. — **32** (36): Rodhos, 1 km SW of Siana, cliffs, 300 m, R & Be, 1967. — **37** (18): Anatolia, 1 km S of Yelcegiz, cliffs near the shore, R & Be, 1967. — **38** (36): Attiki, near Loutraki, fields, c. 300 m, R & Be, 1967. — **41** (36): Kimolos, 2 km W the NE cape, seashore, R & Be, 1967. — **44** (36): Naxos, near the monastery close to the town of Naxos, c. 100 m, R & Be, 1967. — **45** (36): Kimolos, SW of Ormos Vroma, fields, 100 m, R & Be, 1967. — **47** (18): Piperi, (NE of Serifos), schist, 0—160 m, R & Be, 1967. — **49** (18): Poliaigos, SW of the highest peak, volcanic soil, R & Be, 1967. — **51** (36): Attiki, near Loutraki, fields, 300 m, R & Be, 1967. — **53** (36): Naxos, near the monastery E of the town of Naxos, 100 m, R & Be, 1967. — **54** (18): Kimolos, the island of Ay. Yeoryios, the N cape, volcanic soil, R & Be, 1967. — **59** (36): Atimo, (N of Amorgos), phrygana, 50 m, R & Be, 1967. — **61** (36): Kimolos, the island of Prasonisi, R & Be, 1967. — **64** (18): Milos, SSW of Mt. Proph. Elias, 300 m, R & Be, 1967. — **66** (36): Sirna, the NE part, phrygana, R & Be, 1967. — **67** (36, 37): Karpathos, SE of Vurgunda, cliffs, 400 m, R & Be, 1967. — **68** (36): Milos, the island of Kaloyeroi, R & Be, 1967. — **69** (36): Rodhos, S of Salakos, meadow, R & Be, 1967. — **71** (—): Kimolos, 3 km NNW of the town of Kimolos, phrygana, 300 m, R & Be, 1967. — **73** (18): Milos, the S-most part of the harbour bay, sandy soil, R & Be, 1967. — **74** (36): Sirna, the NE part, cliffs, c. 100 m, R & Be, 1967. — **77** (36): Serifos, 1 km SW of Livadhion, cliffs, R & Be, 1967. — **85** (36): Paros, small island NW of Naousa, R & Be, 1967. — **87** (36): Amorgos, the island of Gramvousa, R & Be, 1967. — **94** (36): Ios, 1 km NW of Ak. Louka, phrygana, R & Be, 1967. — **99** (36): Rodhos, 3 km SW of Salakos, 200—450 m, R & Be, 1967. — **300** (36): Tinos, Panormos, saline soil, R & E, 1968. — **301** (36): Naxos, between Moni and Sifones, meadow, cliffs, 500—700 m, R & E, 1968. — **303** (18): Kithnos, Ormos Apokrousis, seashore—phrygana, R & E, 1968. — **304** (36): Siros, between Varvara and Kini, R & E, 1968. — **305** (18): Dhilos, Ekati, R & E, 1968. — **306** (18): Mikonos, the mountain N of Ano Mera, R & E, 1968. — **307** (18): Rhinia, the S part, in sandy soil, R & E, 1968. — **308** (18): Kithnos, Ag. Stefanos, phrygana, R & E, 1968. — **309** (18): Mikonos, the W Ag. Elias, the W peak, cliffs, 200—250 m, R & E, 1968. — **310** (18): Mikonos, Ag. Georgios, R & E, 1968. — **313** (18): Kithnos, 3 km N of Loutra, R & E, 1968. — **314** (18): Dhilos, among the ruins, R & E, 1968. — **315** (18): Kithnos, 2 km N of Mavropouta, fields—phrygana, R & E, 1968. — **316** (—): Mikonos, the S part of the W Ag. Elias, R & E, 1968. — **317** (—): Dhilos, the central part, R & E, 1968. — **318** (18): Rhinia, the N part, R & E, 1968. — **319** (36): Tinos, Tsimenas Oros, 650 m, R & E, 1968. — **321** (36): Rodhos, Proph. Elias, 5 km S of Salakos, near a rivulet, c. 400 m, E, 1968. — **324** (18): Kithnos, E of Merixas, phrygana, R & E, 1968. — **325** (36, 54): Tinos, Exoburgo, c. 400 m, R & E, 1968. — **326** (18): Tinos, near the church S of Kardiani, fields, c. 250 m, R & E, 1968. — **327** (36): Serifos, N of Pirgos, roadside—phrygana, R & E, 1968. — **328** (36): Tinos, N of Isternia, R & E, 1968. — **329** (36): Naxos, 1.5 km E of Moni, cliffs, c. 700 m, R, S, B & E, 1968. — **330** (18): Kithnos, roadside S of Dhriopis, R & E, 1968. — **332** (36): Tinos, Manados, old fields, c. 200 m, R & E, 1968. — **333** (18): Tinos, the islet of Ag. Apomopleto, R & E, 1968. — **334** (18): Hagion Oros

(Athos), W of Kariai, deciduous wood, c. 400 m, E, 1968. — **336** (18): Thasos, 1 km W of Theologos, fields, c. 300 m, E, 1968. — **337** (36): Andros, 1.5 km ESE of Ak. Apothikos, phrygana, cliffs, limestone, c. 80—200 m, S & B, 1968. — **338** (36): Andros, 1 km ESE of Gavrion, sandy seashore, 0—5 m, S & B, 1968. — **339** (36): Andros, the islet of Akomatis S of Gavrion, S & B, 1968. — **340** (36): Andros, 4 km SE of the peak of Mt. Kouvara, rivulet near the road, c. 300 m, S & B, 1968. — **341** (36): Siros, the islet of Strongylo E of Didymi, R & E, 1968. — **342** (36): Siros, in the valley W of Plati Vouri, 150—300 m, R & E, 1968. — **343** (36): Andros, Ori Rakhi, 600—800 m, S & B, 1968. — **344** (27, 36): Andros, 1.5 km S—SSE of the peak of Mt Ag. Saranda, in the valley, 150—200 m, S & B, 1968. — **346** (36): Andros, 0.5 km SW of Opiso Meria, near the rivulet, 300—400 m, S & B, 1968. — **348** (36): Andros, 1.2 km E of Ak. Apothikes, sandy sea shore, phrygana, 0—20 m, S & B, 1968. — **349** (—): Siros, the islet of Varvarousa, limestone, c. 25 m, R & E, 1968. — **350** (18): Kea, N—NE of the monastery of Kastriani, cliffs, limestone, S & B, 1968. — **351** (36): Andros, the islet of Megalo S of Gavrion, S & B, 1968. — **352** (—): Andros, 1.5—2 km WNW of Apoikia, maccia, 430—530 m, S & B, 1968. — **353** (18): Kea, Ormos Poles E of old Skarthea, S & B, 1968. — **354** (36): Andros, E—ESE of Palaioupolis, in the rivulet valley, maccia, 250—350 m, S & B, 1968. — **355** (36): Andros, NW of Apoikia, near the road to Vourkoti, 350—450 m, S & B, 1968. — **357** (36): Andros, the islet of Akramatis S of Gavrion, S & B, 1968. — **358** (36): Andros, the double island of Theotokos, 2 km S of Ak. Gria, the outer islet, c. 20 m, S & B, 1968. — **359** (36): Andros, 1.5 km ENE of Vourkoti, N slopes, schist, 400 m, S & B, 1968. — **360** (36): Siros, the islet of Aspro, limestone, c. 50 m, S & B, 1968. — **361** (36): Siros, the islet of Komeno, c. 20 m, S & B, 1968. — **362** (36): Andros, 3 km S of the peak of Mt Rakhi, cultivations, 100—200 m, S & B, 1968. — **363** (36): Andros, N of the town of Gavrion, meadow, sandy soil, S & B, 1968. — **364** (36): Andros, the double island of Theotokos, 2 km S of Ak. Gria, the inner islet, 0—20 m, S & B, 1968. — **365** (36): Andros, the islet of Gaidharos, S of Gavrion, S & B, 1968. — **366** (—): Andros, the outer part of the valley S Ak. Gria, 0—10 m, S & B, 1968. — **367** (36): Siros, the islet of Ampelos E Vari, c. 5 m, R & E, 1968. — **368** (36): Andros, the outer part of the valley S Ak. Gria, 0—10 m, S & B, 1968. — **369** (18): Kea, 1—2 km NW of Kastriani, c. 150 m, S & B, 1968. — **408 b** (18): Kithnos, S of Merikha bay, 80 m, Be, 1969. — **409 a** (18): Kea, the bay N of Ormos Kalogeros, phrygana, Be, 1969. — **410** (18): Kea, S of the monastery of Kastriani, phrygana, 10—20 m, Be, 1969. — **411** (18): Kea, near Otzia, phrygana, 0—15 m, Be, 1969. — **413** (18): Piperi (NE of Serifos), phrygana, 50—75 m, Be, 1969. — **416 a** (36): Folegandros, S of Ak. Vigla, schist, phrygana, R & G, 1969. — **420** (36): Ios, the islet of Psatho on the E part of Ios, limestone, 0—50 m, Be & G, 1969. — **423** (36): Anafi, Drepanon, phrygana, c. 50 m, R & St, 1969. — **426** (36): Amorgos, near the monastery of Panagia Chotsoviotissa, cliffs, limestone, c. 200 m, Be & G, 1969. — **427** (36): Amorgos, along the road between Chora and the monastery, limestone, phrygana, Be & G, 1969. — **428** (36): Amorgos, 2 km SW of Katapola, phrygana and old fields, 200 m, Be, 1969. — **432** (36): Amorgos, Ormos Akrotiri, phrygana, limestone and schist, 0—200 m, R, St, G & Be, 1969. — **440** (36): Siros, the islet of Komeno, S & B, 1969. — **442 a, b, & c** (—): Sifnos, Taxiarkhis, along the valley, R & G, 1969. — **444** (—): Ios, 1.5 km S of Ak. Aspros Gremnos, old fields, 100 m, G & Be, 1969. — **445** (18): Kea, N of the monastery of Kastriani, phrygana, 75 m, Be & G, 1969. — **446** (18): Kithnos, close NE to Merikha bay, phrygana, fields, 60 m, Be, 1969. — **510** (—): Rodhos, 2 km NE of Laerma, Bt & Hl, 1971. — **511** (36): Rodhos, 2 km NW of Aphandos, Bt & Hl, 1971. — **513** (36): Rodhos, 1 km S of Arphageios, Bt & Hl, 1971. — **526** (—): Andros, the N slope of the valley 1.5—2.5 km NE of Varidion, 100—200 m, S & G, 1971. — **527** (—): Andros, 1—2 km WNW of Gavrion, 50—200 m, S & G, 1971.

L. cycladica ssp. cycladica

2 (54): Folegandros, 1 km W of the harbour village on the E end of the island, cliffs, limestone, 130 m, R & Be, 1967. — **17** (36): Nikouria (N of Amorgos), on the main peak, N facing cliffs, c. 300 m, R & Be, 1967. — **31** (54): Folegandros, W side of the bay on the S side of the island, R & Be, 1967. — **36** (36, 54): Santorin, Mt Proph. Elias, H, 1967. — **60** (54): Santorin, the E peak of Mt Proph. Elias, cliffs, c. 450 m, R & Be, 1967. — **78** (54): Santorin, Kamari, H, 1967. — **83** (—): Sikinos, the E part, S exposed steep slope, R & Be, 1967. — **90** (54): Folegandros, N of the town of Folegandros, cliffs, R & Be, 1967. — **93** (—): Santorin, Mt Proph. Elias, R & Be, 1967. — **414** (54): Folegandros, 1 km W of the harbour village on the E part of the island, cliffs, Be & St, 1969. — **416 b** (36): Folegandros, S of Ak. Vigla, phrygana, schist, R & G, 1969. — **430** (36): Amorgos, Langadhia, limestone cliffs above the village, c. 300 m, R & St, 1969.

L. cycladica ssp. subsessilis

13 (36): Paros, 1 km E of Naousa, serpentine, R & Be, 1967. — **23** (36): Paros, Ak. Makria, islet, R & Be, 1967. — **52** (36): Paros, the islet of Filizi, R & Be, 1967. — **56** (36): Tsimindiri (Between Andiparos and Dhespotiko), R & Be, 1967. — **57** (36): Andiparos, the SW-most part, R & Be, 1967. — **63** (36): Andiparos, small islet N of the island of Kavouras, R & Be, 1967. — **72** (36): Strongilo (W of Andiparos), phrygana, schist, R & Be, 1967. — **75** (36): Makronisi (E of Paros), phrygana, R & Be, 1967. — **80** (36): Andiparos, seashore, R & Be, 1967. — **82** (36): Dhespotiko (W of Andiparos), close to the seashore, volcanic ground, R & Be, 1967. — **89** (36): Tourlos (E of Andiparos), R & Be, 1967. — **96** (36): Dhespotiko (W of Andiparos), seashore, R & Be, 1967. — **100** (36): Gaidhouronisi (N of Paros), R & Be, 1967. — **417** (36): Ios, 0.5 km E the islet of Aryiro, phrygana, fields, Be & G, 1969. — **418** (36): Ios, 2 km N of Aspros Gremnos, phrygana, c. 100 m, Be & G, 1969. — **433** (36): Paros, the SW cape, phrygana, limestone, 0—100 m, R, St, G & Be, 1969. — **434** (36): Andiparos, E side of the central part, phrygana, limestone, 0—50 m, R, St, G & Be, 1969. — **435** (36): Paros, 1.5 km SE of Korifi Karamboli, in a rivulet valley, phrygana, limestone, Be & G, 1969.

L. dionysica

15 (36): Zafora, the N island, limestone, 100 m, R & Be, 1967. — **25** (36): Dio Adelfi, the W island, limestone, R & Be, 1967. — **30** (36): Karavi, R & Be, 1967. — **42** (36): Tria Nisia, the N island, R & Be, 1967. — **48** (36): Anafi, the peak of Ak. Kalamos, the E peak, 430 m, R & Be, 1967. — **50** (18): Unia Nisia, limestone, R & Be, 1967. — **76** (36): Karavi, R & Be, 1967. — **84** (36): Zafora, the S island, cliffs, R & Be, 1967. — **91** (36): Zafora, the S island, cliffs, R & Be, 1967. — **97** (18): Astakidha, the N peak, limestone, R & Be, 1967. — **421** (36): Anafi, the peak of Kalamos, limestone, Be & G, 1969. — **439** (36): Skiropoula (W of Skiros), N side, 50—150 m, S & B, 1969.

L. spreitzenhoferi

402 (36): Kriti, Sfakion, 0.5 km N of the village of Khora, phrygana, Be, 1969. — **404** (36): Kriti, Sfakion, near the road between Anopolis and Khora, phrygana, c. 400 m, Be, 1969. — **405** (18): Kriti, Sfakion, 1 km W of Frankokastello, phrygana, Be, 1969. — **406** (18): Kriti, Sfakion, Frankokastello, on sand dunes, Be, 1969. — **503** (36): Kriti, Sitias, 4 km NE Ag. Fotia, c. 30 m, Bt & Hl, 1971. — **505** (36): Kriti, Sitias, 2 km WNW Pele Kastron, c. 40 m, Bt & Hl, 1971.

Hybrid Populations

422 (27, 36) Anafi, near the monastery on the E part of the island, Be & G, 1969. — **425** (27, 36): Amorgos, along the road between Katapola and Chora, c. 200 m, Be & G, 1969. — **429** (18, 27, 36): Amorgos, 2 km SW of Katapola, old fields, 200 m, Be, 1969. (Population no. 429 constitutes pure **L. comosa,** pure **L. weissii** as well as hybrids.)

APPENDIX 2

Failing Crosses

Per cent failing crosses. The number of failing crossings is given in parentheses.

Female parent	Male parent: *L. cycladica* ssp. *cycladica* (6x)	*L. cycladica* ssp. *cycladica* (4x)	*L. cycladica* ssp. *subsessilis* (4x)	*L. dionysica* (4x)	*L. dionysica* (2x)	*L. weissii* (4x)	*L. weissii* (2x)	*L. spreitzenhoferi* (4x)	*L. spreitzenhoferi* (2x)	*L. comosa* (2x)
L. cycladica ssp. *cycladica* (6x)	50 (1)	.	.	.	.	.	.	.	.	.
L. cycladica ssp. *cycladica* (4x)	100 (1)	.	.	100 (1)	.	.	.	.	.	.
L. cycladica ssp. *subsessilis* (4x)	.	.	.	.	.	.	.	.	.	.
L. dionysica (4x)	.	.	67 (2)	60 (3)	.	33 (1)	.	.	.	.
L. dionysica (2x)	.	.	.	.	.	.	.	.	.	.
L. weissii (4x)	.	75 (3)	36 (5)	33 (7)	67 (2)	23 (17)	33 (3)	.	50 (1)	67 (6)
L. weissii (2x)	.	50 (1)	.	33 (1)	.	30 (3)	4 (1)	.	.	20 (1)
L. spreitzenhoferi (4x)	.	.	.	.	100 (1)	.	.	.	.	.
L. spreitzenhoferi (2x)	.	.	.	.	.	.	100 (1)	.	.	.
L. comosa (2x)	.	.	.	.	.	.	100 (2)	.	.	67 (8)

APPENDIX 3

Successful Crosses

Crossing no.	Female parent	Male parent	Seeds obtained	Per cent germination
L. cycladica ssp. **cycladica**×**L. cycladica** ssp. **cycladica,** 6x×6x				
1	31-6 Folegandros	60-2 Santorin	28	92
L. cycladica ssp. **cycladica**×**L. cycladica** ssp. **cycladica,** 6x×4x				
2	60-10 Santorin	17-2 Nikouria	22	32
L. cycladica ssp. **cycladica**×**L. cycladica** ssp. **subsessilis,** 4x×4x				
3	17-4 Nikouria	75-19 Makronisi	10	50
4	17-4 Nikouria	75-19 Makronisi	20	40
L. cycladica ssp. **cycladica**×**L. cycladica** ssp. **subsessilis,** 6x×4x				
5	60-8 Santorin	80-6 Andiparos	17	65

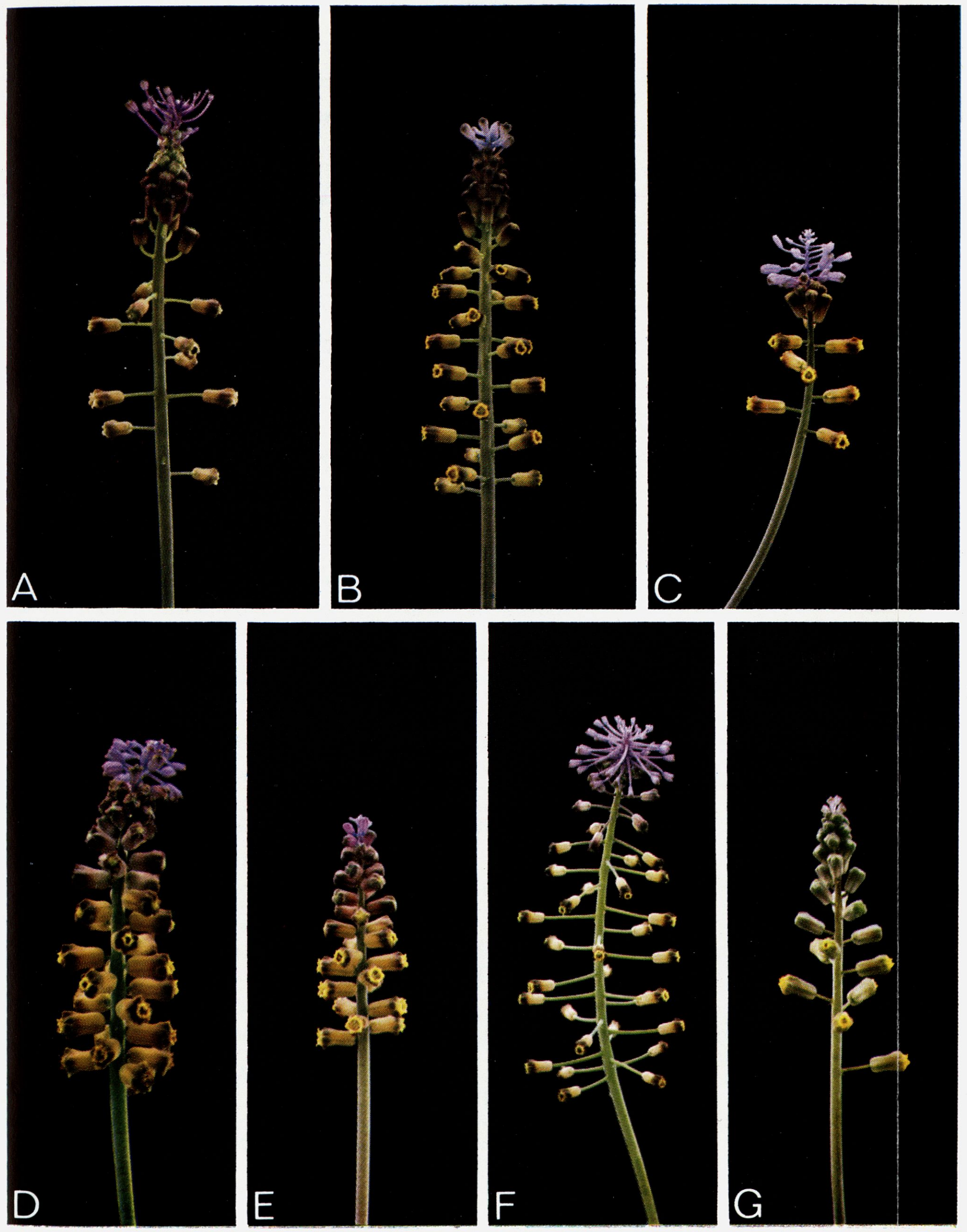


Fig. 29. Inflorescences of *Leopoldia*. — A: *L. comosa* (no. 517), ×c. 0.5. — B: *L. weissii* (no. 340), ×c. 0.5. — C: *L. weissii* (no. 3), ×c. 0.6. — D: *L. cycladica* ssp. *cycladica* (no. 60), ×c. 0.6. — E: *L. cycladica* ssp. *subsessilis* (no. 82), ×c. 0.7. — F: *L. dionysica* (no. 76), ×c. 0.2. — G: *L. spreitzenhoferi* (no. 404), ×c. 0.6.

Fig. 30. Map of the central and southern Aegean. The broken lines indicate RECHINGER's phytogeographical subdivision of the area. Map and text: STRID 1970.

Crossing no.	Female parent	Male parent	Seeds obtained	Per cent germination
L. cycladica ssp. **cycladica** × **L. weissii,** 6x × 4x				
6	60-8 Santorin	67-12 Karpathos	20	100
7	60-10 Santorin	361-1 Siros	28	75
L. cycladica ssp. **subsessilis** × **L. cycladica** ssp. **subsessilis,** 4x × 4x				
8	80-6 Andiparos	56-1 Tsimindiri	10	60
9	75-2 Makronisi	96-2 Dhespotiko	17	82
10	75-3 Makronisi	96-2 Dhespotiko	4	75
11	13-11 Paros	75-19 Makronisi	3	100
12	72-4 Strongilo	96-2 Dhespotiko	21	43
L. cycladica ssp. **subsessilis** × **L. cycladica** ssp. **cycladica,** 4x × 4x				
13	417-2 Ios	416b-1 Folegandros	1	100
14	75-9 Makronisi	17-7 Nikouria	2	50
15	75-12 Makronisi	17-7 Nikouria	5	40
L. cycladica ssp. **subsessilis** × **L. dionysica,** 4x × 4x				
16	75-5 Makronisi	48-1 Anafi	6	100
17	75-1 Makronisi	76-3 Karavi	14	100
18	13-6 Paros	48-4 Anafi	8	88
19	72-3 Strongilo	84-5 Zafora	3	33
L. cycladica ssp. **subsessilis** × **L. weissii,** 4x × 4x				
20	80-4 Andiparos	67-3 Karpathos	6	83
21	80-3 Andiparos	327-6 Serifos	2	100
22	80-3 Andiparos	10-2 Serifos	2	100
23	75-3 Makronisi	10-2 Serifos	5	80
24	75-12 Makronisi	362-1 Andros	34	91
25	75-20 Makronisi	69-3 Rodhos	3	0
26	96-1 Dhespotiko	361-1 Siros	4	75
L. dionysica × **L. dionysica,** 4x × 4x				
27	25-6 Dio Adelfi	76-3 Karavi	16	100
28	42-9 Tria Nisia	25-7 Dio Adelfi	25	76
L. dionysica × **L. cycladica** ssp. **subsessilis,** 4x × 4x				
29	48-4 Anafi	80-5 Andiparos	11	100
L. dionysica × **L. weissii,** 4x × 4x				
30	42-9 Tria Nisia	361-1 Siros	1	100
31	30-6 Karavi	68-13 Milos	11	9
L. dionysica × **L. weissii,** 2x × 2x				
32	50-2 Unia Nisia	324-1 Kithnos	5	0
L. weissii × **L. weissii,** 2x × 2x				
33	314-6 Dhilos	324-1 Kithnos	4	75
34	317-2 Dhilos	47-7 Piperi	19	100
35	334-7 Hagion Oros	49-12 Poliaigos	36	44
36	409a-1 Kea	330-1 Kithnos	4	100
37	54-3 Ay. Yeoryios	49-20 Poliaigos	12	100
38	54-6 Ay. Yeoryios	47-7 Piperi	8	50
39	54-9 Ay. Yeoryios	310-6 Mikonos	28	75
40	54-10 Ay. Yeoryios	330-1 Kithnos	33	42
41	54-11 Ay. Yeoryios	308-1 Kithnos	34	97
42	303-1 Kithnos	306-1 Mikonos	16	88
43	308-1 Kithnos	310-6 Mikonos	13	100
44	310-9 Mikonos	49-21 Poliaigos	16	100
45	73-4 Milos	330-1 Kithnos	17	76

Crossing no.	Female parent	Male parent	Seeds obtained	Per cent germination
46	73-9 Milos	333-1 Tinos	13	100
47	73-10 Milos	49-20 Poliaigos	5	80
48	73-12 Milos	49-12 Poliaigos	3	100
49	73-16 Milos	47-3 Piperi	9	100
50	49-19 Poliaigos	47-7 Piperi	19	42
51	49-22 Poliaigos	310-6 Mikonos	16	75
52	326-1 Tinos	49-20 Poliaigos	34	97
53	333-4 Tinos	49-21 Poliaigos	19	100
54	333-5 Tinos	47-3 Piperi	9	100
L. weissii×L. weissii, 4x×4x				
55	338-2 Andros	327-6 Serifos	34	50
56	338-3 Andros	361-1 Siros	43	44
57	339-2 Andros	361-1 Siros	34	100
58	344-1 Andros	339-1 Andros	18	56
59	344-6 Andros	364-2 Andros	27	81
60	346-4 Andros	338-1 Andros	4	50
61	351-1 Andros	325-3 Tinos (6x)	15	33
62	351-3 Andros	319-3 Tinos	47	53
63	351-7 Andros	329-4 Naxos	24	92
64	354-1 Andros	3-2 Naxos	9	67
65	354-2 Andros	10-5 Serifos	43	56
66	357-5 Andros	319-4 Tinos	3	100
67	359-2 Andros	319-4 Tinos	19	68
68	362-3 Andros	10-5 Serifos	5	20
69	363-1 Andros	341-1 Siros	4	100
70	363-2 Andros	329-4 Naxos	2	50
71	363-3 Andros	325-2 Tinos	39	85
72	364-1 Andros	67-3 Karpathos	13	92
73	365-3 Andros	325-2 Tinos	49	59
74	365-7 Andros	69-11 Rodhos	12	92
75	365-9 Andros	67-3 Karpathos	26	69
76	59-2 Atimo	69-11 Rodhos	11	27
77	51-2 Loutraki, Attiki	10-4 Serifos	3	0
78	51-3 Loutraki, Attiki	327-6 Serifos	30	0
79	67-11 Karpathos	10-2 Serifos	6	83
80	45-8 Kimolos	3-2 Naxos	8	100
81	61-16 Kimolos	12-3 Santorin	7	86
82	68-9 Milos	67-11 Karpathos	4	100
83	68-12 Milos	10-5 Serifos	5	100
84	3-1 Naxos	10-4 Serifos	5	80
85	3-7 Naxos	67-12 Karpathos	11	64
86	44-2 Naxos	12-3 Santorin	11	82
87	32-1 Rodhos	10-2 Serifos	12	75
88	69-4 Rodhos	325-3 Tinos (6x)	16	100
89	69-5 Rodhos	325-3 Tinos (6x)	15	93
90	69-6 Rodhos	67-3 Karpathos	16	81
91	99-2 Rodhos	319-3 Tinos	16	94
92	99-4 Rodhos	325-3 Tinos (6x)	40	90
93	321-1 Rodhos	325-3 Tinos (6x)	14	86
94	321-2 Rodhos	67-3 Karpathos	12	100
95	12-4 Santorin	10-5 Serifos	18	100
96	327-8 Serifos	340-6 Andros	7	42
97	66-4 Sirna	67-3 Karpathos	21	100
98	74-6 Sirna	325-2 Tinos	34	100
99	74-11 Sirna	67-3 Karpathos	11	100
100	74-13 Sirna	67-3 Karpathos	5	100

Crossing no.	Female parent	Male parent	Seeds obtained	Per cent germination
101	304-4 Siros	365-8 Andros	1	0
102	342-1 Siros	332-3 Tinos	27	89
103	342-2 Siros	67-12 Karpathos	1	100
104	367-2 Siros	300-4 Tinos	1	100
105	300-7 Tinos	327-6 Serifos	29	79
106	319-1 Tinos	366-1 Andros	5	60
107	319-1 Tinos	366-1 Andros	21	95
108	319-4 Tinos	366-1 Andros	20	35
109	332-5 Tinos	68-13 Milos	6	100
110	332-6 Tinos	362-1 Andros	3	66
111	26-11 Vous	325-2 Tinos	17	94
L. weissii × **L. weissii**, 2x × 4x				
112	314-1 Dhilos	51-6 Loutraki, Attiki	2	100
113	445-5 Kea	69-11 Rodhos	3	33
114	303-2 Kithnos	67-12 Karpathos	1	0
115	315-1 Kithnos	68-13 Milos	1	0
116	408b-2 Kithnos	10-5 Serifos	1	0
117	326-5 Tinos	329-4 Naxos	5	0
118	333-2 Tinos	366-1 Andros	3	33
L. weissii × **L. weissii**, 4x × 2x				
119	357-1 Andros	310-6 Mikonos	9	22
120	363-2 Andros	310-6 Mikonos	7	0
121	44-7 Naxos	324-1 Kithnos	6	100
122	321-2 Rodhos	47-7 Piperi	3	33
123	20-2 Sifnos	324-1 Kithnos	9	0
124	300-3 Tinos	324-1 Kithnos	5	100
L. weissii × **L. cycladica** ssp. **cycladica**, 2x × 4x				
125	308-3 Kithnos	17-7 Nikouria	13	31
L. weissii × **L. cycladica** ssp. **cycladica**, 4x × 4x				
126	361-1 Siros	17-7 Nikouria	4	75
L. weissii × **L. cycladica** ssp. **subsessilis**, 2x × 4x				
127	64-1 Milos	80-6 Andiparos	3	0
L. weissii × **L. cycladica** ssp. **subsessilis**, 4x × 4x				
128	19-7 Amorgos	80-6 Andiparos	20	95
129	51-3 Loutraki, Attiki	75-19 Makronisi	3	0
130	41-2 Kimolos	75-2 Makronisi	13	100
131	3-14 Naxos	96-2 Dhespotiko	21	67
132	301-1 Naxos	75-19 Makronisi	21	76
133	301-1 Naxos	96-2 Dhespotiko	28	71
134	329-1 Naxos	96-2 Dhespotiko	8	25
135	85-2 Paros	75-19 Makronisi	3	0
136	85-2 Paros	75-19 Makronisi	11	91
L. weissii × **L. dionysica**, 4x × 4x				
137	343-1 Andros	76-3 Karavi	31	90
138	344-3 Andros	30-2 Karavi	1	100
139	355-1 Andros	30-2 Karavi	8	88
140	339-3 Andros	48-4 Anafi	5	100
141	45-14 Kimolos	30-2 Karavi	6	83
142	38-3 Loutraki, Attiki	48-1 Anafi	6	100
143	9-1 Milos	30-2 Karavi	16	94
144	9-1 Milos	48-4 Anafi	34	97
145	68-9 Milos	30-2 Karavi	4	75

Crossing no.	Female parent		Male parent		Seeds obtained	Per cent germination
146	44-7	Naxos	84-3	Zafora	5	100
147	66-2	Sirna	25-7	Dio Adelfi	25	100
148	300-8	Tinos	84-3	Zafora	3	100
149	328-2	Tinos	84-3	Zafora	3	100
150	328-3	Tinos	76-3	Karavi	13	92
L. weissii × L. dionysica, 2x × 2x						
151	326-5	Tinos	50-3	Unia Nisia	4	75
152	309-6	Mikonos	50-3	Unia Nisia	1	0
L. weissii × L. dionysica, 2x × 4x						
153	409a-3	Kea	25-7	Dio Adelfi	10	50
154	326-1	Tinos	48-1	Anafi	9	67
L. weissii × L. dionysica, 4x × 2x						
155	344-2	Andros	50-3	Unia Nisia	2	0
L. weissii × L. spreitzenhoferi, 2x × 2x						
156	303-2	Kithnos	405-9	Kriti	14	57
L. weissii × L. spreitzenhoferi, 4x × 2x						
157	41-2	Kimolos	405-9	Kriti	1	100
L. weissii × L. comosa, 2x × 2x						
158	54-11	Kimolos	92-11	Tria Nisia	4	0
159	54-13	Kimolos	347-2	Siros	10	0
160	47-3	Piperi	28-1[1]	Amorgos	3	0
161	49-20	Poliaigos	16-5	Naxos	3	0
L. weissii × L. comosa, 4x × 2x						
162	344-3	Andros	347-2	Siros	13	69
163	3-8	Naxos	451-2	Mt Parnon	14	36
164	74-9	Sirna	347-1	Siros	23	74
L. comosa × L. comosa, 2x × 2x						
165	330-4	Kithnos	451-2	Mt Parnon	14	100
166	16-6	Naxos	347-2	Siros	5	60
167	452-3	Peloponnisos	347-1	Siros	11	27
168	347-3	Siros	451-2	Mt Parnon	6	17

---

[1] The locality for this collection is missing in BENTZER 1972 c.: **28** (18): Amorgos, near Katapola, phrygana, 0—200 m, R & Be, 1967.

Botanical Literature

DAHL, E. & KROG, H.: Macrolichens of Denmark, Finland, Norway and Sweden. — Universitetsforlaget, Oslo 1973 (printed at Odense). 185 pp., 61 line drawings in the text. Price N. Cr. 46.00 (bound).

Since TH. M. FRIES, Lichenographia Scandinavica (2 volumes, 1871—1874, not completed) no comprehensive work on the Scandinavian lichens has been published. The well-known Swedish floras by KROK & ALMQUIST (1962) and URSING (1967) and the Danish counterpart ROSTRUP (1925) contain chapters on lichens, but they mention only a selected number of species. Some floras have dealt with foliose and fruticose lichens ("macrolichens") only, e.g., LYNGE (1909) and MAGNUSSON (1929), PAASIO (1950), RÄSÄNEN (1951), HAKULINEN (1963), the three last-mentioned works written in Finnish. The present volume by Professor EILIF DAHL and Dr HILDUR KROG (both Oslo) is a successor to MAGNUSSON's work, which was an excellent guide to the Scandinavian macrolichens. The latter has been out of print, however, for many years.

Brief introductory chapters treat "Morphology", "Distribution of Lichens" and "Lichen Chemistry". The chemical compounds known from all species treated are presented in a separate list.

The bulk of the work consists of "Analytical keys to genera and species". A total of 45 genera have been accepted. MAGNUSSON (1929) dealt with 29 genera. The difference is partly due to the inclusion of some genera, *Pannaria, Parmeliella* (both compiled by P. W. JAMES) and *Lichina,* which MAGNUSSON counted as "crustose lichens", partly to the use of a somewhat narrower generic concept. Some examples: *Heterodermia* has been segregated from *Anaptychia, Pycnothelia* from *Cladonia, Hypogymnia, Pseudevernia, Menegazzia* and *Cetrelia* from *Parmelia, Asahinea* and *Platismatia* from *Cetraria, Pseudocyphellaria* from *Sticta, Leprocaulon* from *Stereocaulon.* In other cases the authors have taken a more conservative attitude: *Physcia* has been treated in a broad sense (including *Physciopsis* and *Physconia*) as well as *Umbilicaria* (including the 5 genera proposed by the Norwegian lichenologist SCHOLANDER in 1934, which have been accepted by several lichenologists).

In the main chapter "Keys to the species", the genera have been arranged in alphabetical order. This is certainly the best solution in a volume of this scope. A "natural system" (in fact not very much differing from the one used by MAGNUSSON, after ZAHLBRUCKNER) has been outlined on pp. 160—161. Under most genera we find useful references to recent taxonomic revisions.

The species are described briefly, often in 2—5 lines (in addition to the characters met with at the higher stages of the key). Some chemical characters are mentioned. Ecology and distribution of each species are sketched in very few words. In many cases, the concise text is elucidated essentially by line drawings. Some of these are originals, others have been taken from other sources, e.g., POELT (1969) and OZENDA & CLAUZADE (1970). Cf. reviews in Botaniska Notiser 1971 p. 521 and 1972 p. 128.

A total of 396 species are treated. MAGNUSSON, more than 40 years ago, dealt with 284 species. To some extent the difference is due to the fact that MAGNUSSON did not include Finland in his Flora. There are some 10 species which, according to DAHL & KROG, are restricted to Finland only within our area. The authors quote one macrolichen (viz. *Ramalina duriaei*) from Denmark only. *Parmelia* *quercina,* recorded from several Danish localities during the 19th century, has evidently been omitted.

The species concept used is fairly broad. "Chemical species", where the chemical difference is not correlated to a morphological one, have not been accepted. "*Parmelia discordans*" has been treated as a variety of *P. omphalodes.* The two chemical strains within *Thamnolia vermicularis* have also been quoted as varieties. The species recently described by CULBERSON within *Ramalina siliquosa* are not accepted "at present". The *Cladonia chlorophaea* complex has been treated as a "very variable species".

It is evident that the striking increase of the number of species recorded from Scandinavia, compared with MAGNUSSON, has been due to an increasing knowledge of our macrolichen flora during the past four decades. Many interesting novelties, in some cases quite unexpected, have been published during this period, e.g., *Asahinea chrysantha, Cavernularia hultenii, Dactylina muricata, Erioderma boreale, Leptogium burgessii, L. hibernicum, Lobaria hallii,* and *Sticta dufourii.* It can be presumed that further research will reveal more lichenological secrets, not the least from the western and central parts of Norway.

There are lists of synonyms, of abbreviated authors' names and a glossary at the end of the book. Especially as we meet many species names previously little known, the reviewer would have preferred a choice of the most frequent synonyms in brackets under the epithet in the keys instead of in a separate list.

This well-organized and attractive book is warmly recommended both to students and to amateur botanists. It will certainly promote a wider knowledge of the macrolichens of our area. It is to be hoped that this century will see a complete Lichen Flora of Northern Europe also treating the crustose lichens which amount to some 1500—1800 species including several very neglected groups.

OVE ALMBORN

MEYLAN, B. A. & BUTTERFIELD, B. G. 1972. Three-dimensional Structure of Wood. — Chapman & Hall Ltd., London. 80 pp. £ 2.

TROUGHTON, J. & DONALDSON, L. A. 1972. Probing Plant Structure. — Chapman & Hall Ltd., London. 116 pp. £ 1.75.

The two books well illustrate the brilliant power of Scanning Electron Microscopy in descriptive botany.

The former book focusses on rather "pure" anatomy, the latter on functional anatomy with physiological aspects. The reader is, however, also frequently reminded of the taxonomic significance of the structures illustrated.

Both volumes are very pleasantly designed. The reproductions of the micrographs are of high quality. The authors of "Probing Plant Structure" could have mentioned that some of the pollen grains illustrated are collapsed. I should also prefer the achenes of *Felicia* and *Galinsoga* not to be called seeds.

In both volumes only short accounts of the microscopic technique are given. A good deal of their value lies in the pictures; which indeed require fairly little commentary.

GUNNAR WEIMARCK

OPERA BOTANICA

Vol. 1. N. HYLANDER, I. JØRSTAD and J. A. NANNFELDT: Enumeratio Uredinearum Scandinavicarum. 1953. 102 pp. — H. HORN AF RANTZIEN: Middle Triassic Charophyta of South Sweden. 1954. 83 pp. — H. HJELMQVIST: Die älteste Geschichte der Kulturpflanzen in Schweden. 1955. 186 pp. — Price Sw. Kr. 30 (15).

Vol. 2. H. RUNEMARK: Studies in Rhizocarpon. I. Taxonomy of the Yellow Species in Europe. 1956. 152 pp. — H. RUNEMARK: Studies in Rhizocarpon. II. Distribution and Ecology of the Yellow Species in Europe. 1956. 150 pp. — G. KNABEN: On the Evolution of the Radicatum-Group of the Scapiflora Papavers as Studied in 70 and 56 Chromosome Species. A. Cytotaxonomical Aspects. 1959. 76 pp. — Price Sw. Kr. 30 (15).

Vol. 3. A. GUSTAVSSON: Studies on Nordic Peronosporas. I. Taxonomic Revision. 1959. 271 pp. — A. GUSTAVSSON: Studies on Nordic Peronosporas. II. General Account. 1959. 61 pp. — G. KNABEN: On the Evolution of the Radicatum-Group of the Scapiflora Papavers as Studied in 70 and 56 Chromosome Species. B. Experimental Studies. 1959. 96 pp. — Price Sw. Kr. 30 (15).

Vol. 4. R. DAHLGREN: Revision of the Genus Aspalathus. I. The Species with Flat Leaflets. 1960. 393 pp. — Price Sw. Kr. 30 (15).

Vol. 5. Á. LÖVE and D. LÖVE: Chromosome Numbers of Central and Northwest European Plant Species. 1961. 581 pp. — Price Sw. Kr. 40 (20), bound Sw. Kr. 48 (28).

Vol. 6. Å. PERSSON: Mire and Spring Vegetation in an Area North of Lake Torneträsk, Torne Lappmark, Sweden. I. Description of the Vegetation. 1961. 187 pp. — R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 1—2. 1961. 120 pp. — Å. PERSSON: Mire and Spring Vegetation in an Area North of Lake Torneträsk, Torne Lappmark, Sweden. II. Habitat Conditions. 1962. 100 pp. — Price Sw. Kr. 40 (20).

Vol. 7. N. MALMER: Studies on Mire Vegetation in the Archaean Area of Southwestern Götaland (South Sweden). I. Vegetation and Habitat Conditions on the Åkhult Mire. 1962. 322 pp. — II. Distribution and Seasonal Variation in Elementary Constituents on Some Mire Sites. 1962. 67 pp. — Price Sw. Kr. 40 (20).

Vol. 8. R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 3. 1963. 183 pp. — N. SYLVÉN: Det skandinaviska floraområdets Carices Distigmaticae. The Carices Distigmaticae of the Scandinavian Flora District. 1963. 161 pp. — C. BLIDING: A Critical Survey of European Taxa in Ulvales. I. Capsosiphon, Percursaria, Blidingia, Enteromorpha. 1963. 160 pp. — Price Sw. Kr. 40 (20).

Vol. 9. R. DAHLGREN: Studies on Aspalathus and Some Related Genera in South Africa. 1963. 301 pp. — S. O. STRANDHEDE: Chromosome Studies in Eleocharis, subser. Palustres. III. Observations on Western European Taxa. 1965. 86 pp. — Price Sw. Kr. 40 (20).

Vol. 10. R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 4. 1965. 231 pp. — S. O. STRANDHEDE: Morphologic Variation and Taxonomy in European Eleocharis, subser. Palustres. 1966. 187 pp. — Price Sw. Kr. 40 (20).

Vol. 11. R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 5. 1966. 266 pp. — G. NORDBORG: Sanguisorba L., Sarcopoterium Spach, and Bencomia Webb et Berth. Delimitation and Subdivision of the Genera. 1966. 103 pp. — Price Sw. Kr. 50 (30).

Vol. 12. B. E. BERGLUND: Late-Quaternary Vegetation in Eastern Blekinge, Southeastern Sweden. A Pollen-analytical Study. I. Late-Glacial Time. 1966. 180 pp. — II. Post-Glacial Time. 1966. 190 pp. — Price Sw. Kr. 70 (42).

No. 13. S. SNOGERUP: Studies in the Aegean Flora. VIII. Erysimum Sect. Cheiranthus. A. Taxonomy. 1967. 70 pp. — Price Sw. Kr. 15 (9).

No. 14. S. SNOGERUP: Studies in the Aegean Flora. IX. Erysimum Sect. Cheiranthus. B. Variation and Evolution in the Small-Population System. 1967. 86 pp. — Price Sw. Kr. 16 (9.40).

No. 15. R. DAHLGREN: Studies on Penaeaceae. I. Systematics and Gross Morphology of the Genus Stylapterus A. Juss. 1967. 40 pp. — Price Sw. Kr. 8 (4.80).

No. 16. G. NORDBORG: The Genus Sanguisorba Section Poterium. Experimental Studies and Taxonomy. 1967. 166 pp. — Price Sw. Kr. 27 (16.20).

No. 17. I. BJÖRKQVIST: Studies in Alisma L. I. Distribution, Variation and Germination. 1967. 128 pp. — Price Sw. Kr. 25 (15).

No. 18. R. DAHLGREN: Studies on Penaeaceae. II. The Genera Brachysiphon, Sonderothamnus and Saltera. 1968. 72 pp. — Price Sw. Kr. 13 (7.80).

No. 19. I. BJÖRKQVIST: Studies in Alisma L. II. Chromosome Studies, Crossing Experiments and Taxonomy. 1968. 138 pp. — Price Sw. Kr. 25 (15).

No. 20. B. NORDENSTAM: The Genus Euryops. I. Taxonomy. 1968. 409 pp. — Price Sw. Kr. 55 (33).

No. 21. R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 6. 1968. 309 pp. — Price Sw. Kr. 75 (45).

No. 22. R. DAHLGREN: Revision of the Genus Aspalathus. III. The Species with Flat and Simple Leaves. 1968. 126 pp. — Price Sw. Kr. 30 (18).

No. 23. B. NORDENSTAM: Phytogeography of the Genus Euryops (Compositae). A Contribution to the Phytogeography of Southern Africa. 1969. 77 pp. — Price Sw. Kr. 20 (12).

No. 24. T. MÖRNSJÖ: Studies on Vegetation and Development of a Peatland in Scania, South Sweden. 1969. 187 pp. — Price Sw. Kr. 50 (30).

No. 25. G. TYLER: Studies in the Ecology of Baltic Sea-Shore Meadows. II. Flora and Vegetation. 1969. 101 pp. — Price Sw. Kr. 25 (15).

No. 26. M. SONESSON: Studies on Mire Vegetation in the Torneträsk Area, Northern Sweden. III. Communities of the Poor Mires. 1970. 120 pp. — Price Sw. Kr. 30 (18).

No. 27. F. ANDERSSON: Ecological Studies in a Scanian Woodland and Meadow Area, Southern Sweden. I. Vegetational and Environmental structure. 1970. 190 pp. — Price Sw. Kr. 50 (30).

No. 28. A. STRID: Studies in the Aegean Flora. XVI. Biosystematics of the Nigella arvensis Complex. With Special Reference to the Problem of Non-adaptive Radiation. 1970. 169 pp. — Price Sw. Kr. 50 (30).

No. 29. R. DAHLGREN: Studies on Penaeaceae. VI. The Genus Penaea. 1971. 58 pp. — Price Sw. Kr. 30 (18).

No. 30. A. STRID (ed.): Evolution in the Aegean. Proceedings of a Symposium held at the Department of Plant Taxonomy, Lund, Sweden on January 22—24, 1971. 1971. 83 pp. — Price Sw. Kr. 35 (21).

No. 31. J. LUNDGREN: Revision of the Genus Anaxeton Gaertn. (Compositae). 1972. 59 pp. — Price Sw. Kr. 25 (15).

No. 32. A. K. STRID: Revision of the Genus Adenandra (Rutaceae). 1972. 112 pp. — Price Sw. Kr. 40 (24).

No. 33. A. L. STORK: Studies in the Aegean Flora. XX. Biosystematics of the Malcolmia maritima Complex. 1972. 118 pp. — Price Sw. Kr. 50 (30).

OPERA BOTANICA SER. B: FLORA OF ECUADOR

No. 1. G. HARLING: 216. Cyclanthaceae. 1973. 48 pp. — Price Sw. Kr. 35 (21).

Volumes in preparation. B. SPARRE: 89. Tropaeolaceae. — PH. A. MUNZ: 141. Onagraceae. — MILDRED MATHIAS and L. CONSTANCE: 145. Umbelliferae. — K. RAHN: 184. Plantaginaceae.

BOTANISKA NOTISER SUPPLEMENT

Vol. 1. S. WALDHEIM: Kleinmoosgesellschaften und Bodenverhältnisse in Schonen. 1947. 203 pp. — O. ALMBORN: Distribution and Ecology of some South Scandinavian Lichens. 1948. 254 pp. — Price Sw. Kr. 15 (10).

Vol. 2. H. HJELMQVIST: Studies on the Floral Morphology and Phylogeny of the Amentiferae. 1948. 171 pp. — O. ANDERSSON: Larger Fungi on Sandy Grass Heaths and Sand Dunes in Scandinavia. 1950. 89 pp. — A. ALMESTRAND and A. LUNDH: Studies on the Vegetation and Hydrochemistry of Scanian Lakes. I—II. 1951. 174 pp. — Price Sw. Kr. 15 (10).

Vol. 3. A. LUNDH: Studies on the Vegetation and Hydrochemistry of Scanian Lakes. III. 1951. 138 pp. — O. HEDBERG, O. MÅRTENSSON, and S. RUDBERG: Botanical Investigations in the Pältsa Region of Northernmost Sweden. 1952. 209 pp. — K. H. RECHINGER FIL.: Monograph of the Genus Rumex in Africa. 1954. 114 pp. — Price Sw. Kr. 15 (10).