Drawings of Scandinavian Plants 37–40
Rubus L. Subgen. Rubus

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Rubus vestitus Weihe & Nees 1825

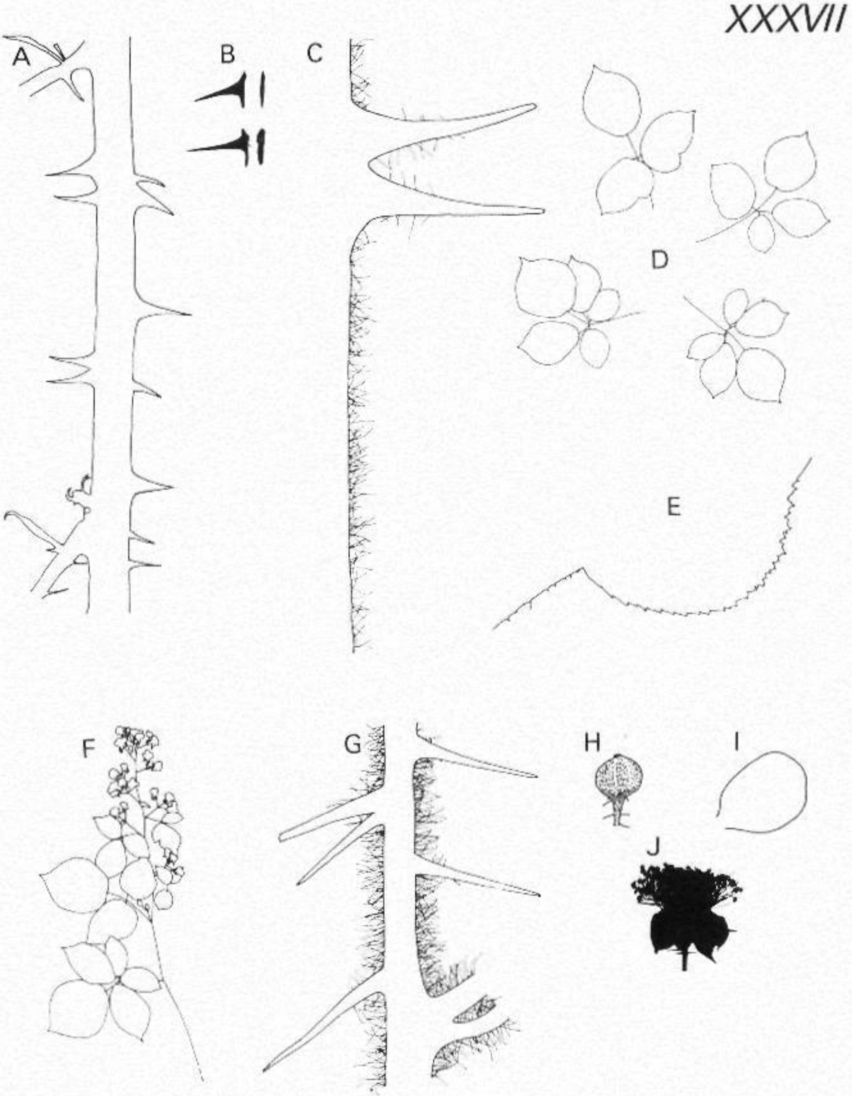
(*Rubus leucostachys* Schleicher 1824)

Stem arching, densely hairy, glands few or none; *prickles* 6—9 mm long, patent, subulate, base 6—10 mm long, narrow; *leaves* (3—)5-foliolate, rather hairy above, shiny below from dense, rigid hairs, often also white-tomentose; *terminal leaflet* broadly obovate—orbiculate with a broad, rather short tip; *inflorescence* long, leafy below, hardly narrowed to a rather dense, abrupt apex, glandular; *flowers* about 2.5 cm across; *sepals* grey-tomentose, glandular, sometimes equipped with scattered prickles; *petals* pink—white, broadly obovate—orbicular; *filaments* about 5 mm long.

Normally, the stem is terete—angled, rather strong, purple—brown, and almost bristleless; the leaves are dark green; the terminal leaflet, except the tip, is twice as long as the petiolule; the petiolules of the upper pair of leaflets are about 1 cm long, while the petiolules of the lower pair are 0.25—0.5 cm; the prickles in the apex of the inflorescence are long and subulate, slightly recurved; the sepals are deflexed. *R. vestitus* is one of the relatively few European blackberries that probably prefer calcareous ground. The species occurs in Sweden on the southern slope of Söderåsen in north-western Skåne; in Denmark the species is rather common in the south and also occurs in one locality (Bangsbo) in northern-most Jylland.

Rubus radula Weihe 1824

Stem arching, sparsely hairy, glandular; *prickles* of two kinds, one bristle-like with a rather strong base, the other 6—9 mm long, falcate or patent, flat with a 3—7 mm long base; *leaves* 5-foliolate, glabrescent

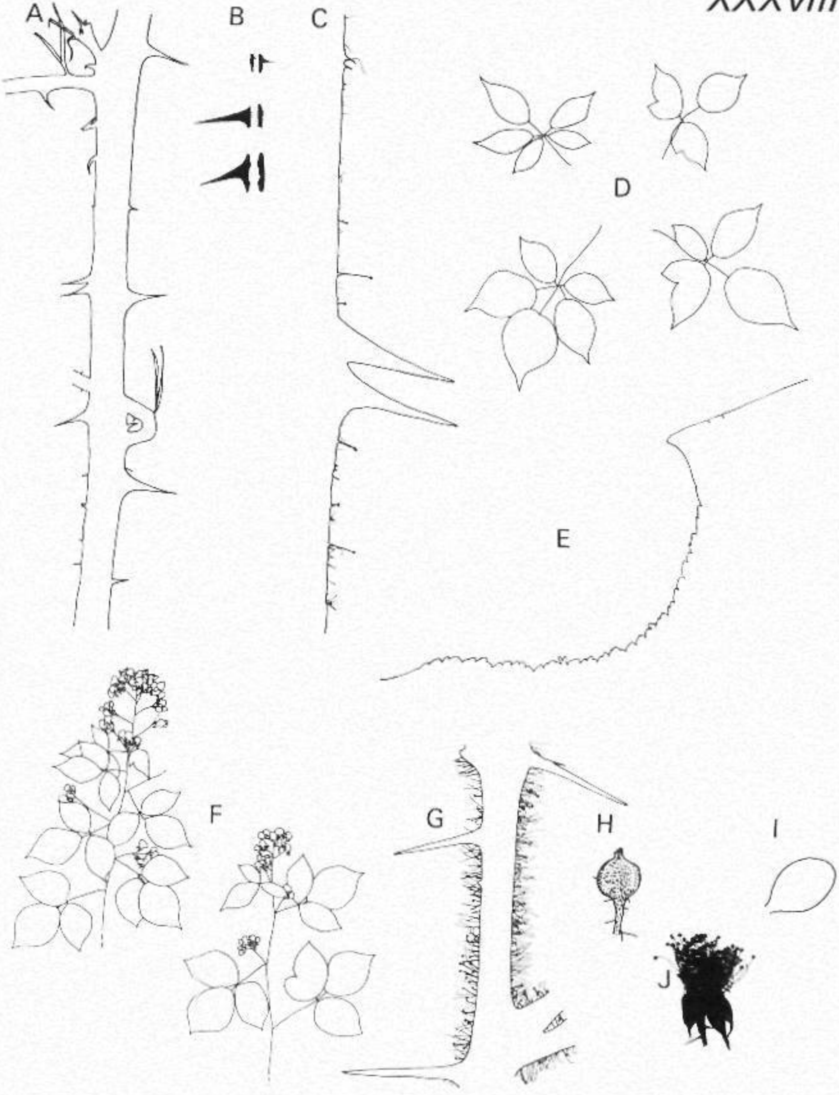


Pl. XXXVII. *Rubus vestitus* WEIHE & NEES. — Remark: E refers to a 5-foliolate leaf.

GENERAL LEGEND FOR THE PLATES

First-year growth (*primocane*): A. Stem with prickles. 1: 1. — B. Prickles, drawn from the side and from above. 1: 1. — C. Stem with prickles, glands, and hairs. 4: 1. — D. Leaves (without serration and petiole diameter shown). 1: 8. — E. Margin of a terminal leaflet with a petiolule. 1: 2. — *Second-year*

XXXVIII



Pl. XXXVIII. *Rubus radula* WEIHE. — Remarks: D. The leaves of the primocane are normally 5-foliolate. — E refers to a 5-foliolate leaf.

growth (floricane): F. Inflorescences (without prickles, serration of the leaves, and axis diameters shown). 1: 8. — G. Rachis with prickles, glands, and hairs. 4: 1. — H. Floral bud with prickles. 1: 1. — I. Petal (without hairs). 1: 1. — J. Flower (without petals, glands, and hairs). 1: 1.

above, pale green—grey-white felted beneath; *terminal leaflet* ovate, or elliptic—rhombic, gradually acuminate; *inflorescence* pyramidal, large and leafy or short, dense, and leafless, glandular; *flowers* 2—2.5 cm across; *sepals* grey-tomentose, glandular, acuminate; *petals* pink—white, broadly elliptic; *filaments* about 5 mm long.

Normally, the stem is low-arching with a creeping tip, angled, rather strong, dark red; the prickles at the apex of the inflorescence are long, straight, patent, or slightly recurved; the sepals are deflexed and devoid of prickles. *R. radula* seems to prefer dry pasturelands on rather fertile soils. The species occurs in Norway along the south-eastern coast only; in Sweden it is rare in Bohuslän, Halland, and Småland, but rather common in some parts of Skåne and Blekinge; in Denmark the species occurs over most of the country.

Rubus taeniarum LINDEBERG 1858

(*Rubus infestus* auct. mult. non WEIHE 1824)

Stem arching, hairy, glands few; *prickles* of two kinds, one fragile, up to 5 mm long, the other stronger, 5—8 mm long, falcate or straight and recurved, flat with 5—8 mm long base; *leaves* 5-foliolate, glabrescent above, green, hairy or greyish green, softly pubescent below; *terminal leaflet* elliptic—obovate, acuminate; *inflorescence* relatively small, leafy, branches widely spreading, glands present; *flowers* about 2 cm across; *sepals* greyish green, tomentose, with a white-felted border, glands and prickles present; *petals* pink—white, broadly elliptic; *filaments* about 5 mm long.

Normally, the stem is angled—furrowed, dark red; both kinds of prickles are rather numerous, the stronger ones (always present), except the pale tip, are dark red and hairy; the leaves are small and have sharply biserrate margins; the apex of the terminal leaflet is long and oblique; the petiolule of the terminal leaflet is three times longer, or more, than the petiolules of the upper pair of leaflets, while the petiolules of the lower pair are 0.1—0.2 cm long; the armament of the inflorescence is rather well developed, consisting partly of rather strong, flat, falcate, or hooked prickles, and partly of straight, smaller bristle-like prickles; the sepals are spreading. *R. taeniarum* is known from several localities in the Bohuslän archipelago south-west of Uddevalla on the Swedish west coast.

FRIDERICHSEN (1922) reports *R. infestus* WEIHE from four localities

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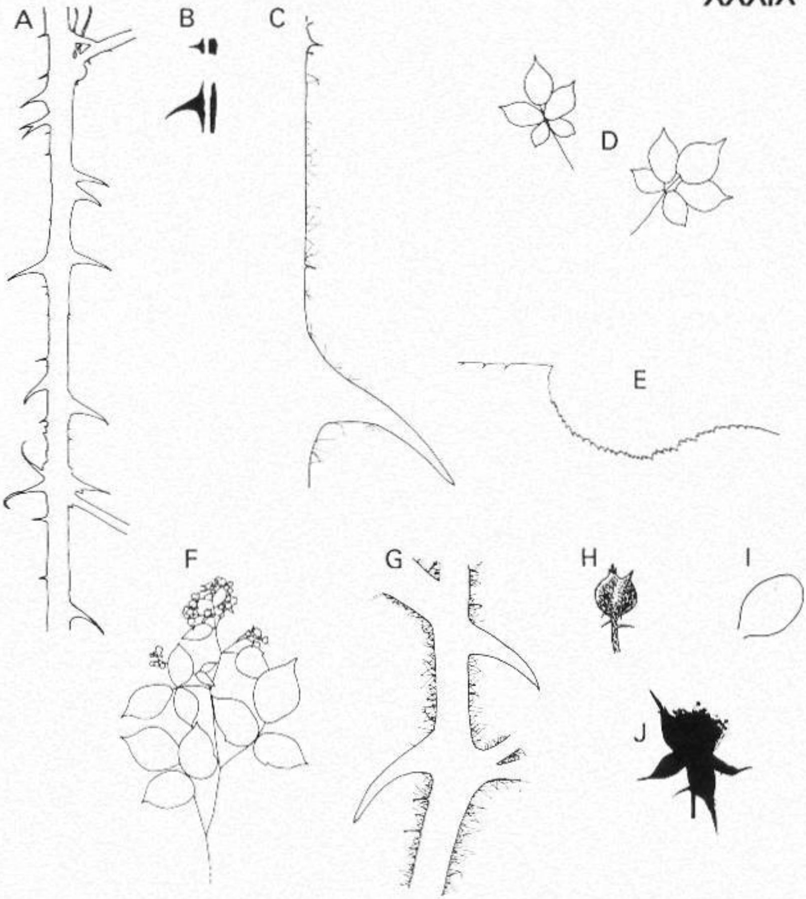
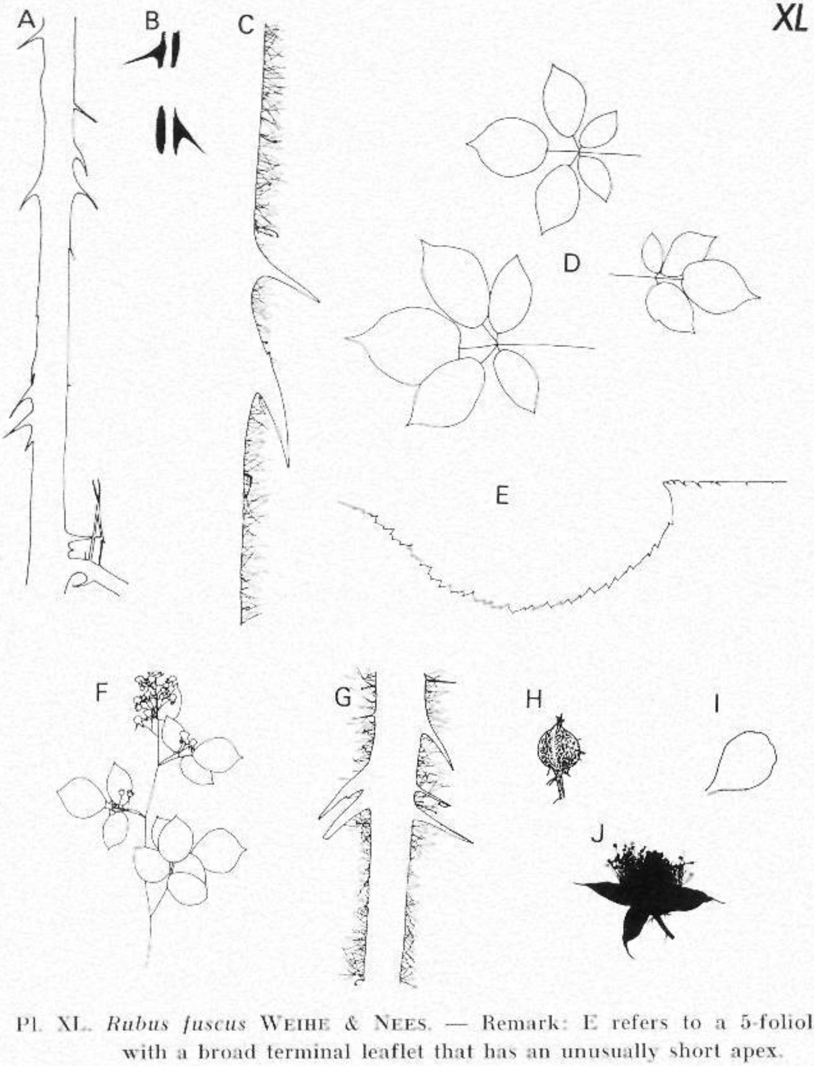


Pl. XXXIX. *Rubus taeniarum* Lindeberg. — Remarks: B. The base of the upper prickle is too large, especially as seen from above. — J. The apices of the sepals are unusually prolonged.

in Denmark, but he does not mention *R. taeniarum*. Watson (1958), as well as Heslop-Harrison (1968), reports both species as Danish, while Focke (1914) treats them as a single taxon. Hylander (1955) seems to share the view of Friderichsen (1914, 1922). I, myself, have not been able to reach a decision.

Rubus fuscus Weihe & Nees 1825

Stem arching, densely hairy, glands scattered; *prickles* 5—7 mm long, recurved and straight, hooked, or reflexed, from a 3—5 mm long,



Pl. XL. *Rubus fuscus* WEIHE & NEES. — Remark: E refers to a 5-foliolate leaf with a broad terminal leaflet that has an unusually short apex.

flat base, abruptly subulate; *leaves* (3—)5-foliolate, glabrescent above, provided with sparse, stiff hairs below; *terminal leaflet* broadly elliptic, acuminate; *inflorescence*, except a few axillary branches below, leafless, relatively short, with one or a few flowers on each branch, pedicels long, glands rather numerous; *flowers* about 2.5 cm across; *sepals* grey-tomentose, glandular, prickles numerous; *petals* white.

cuneate—broadly elliptic with an elongate, narrow base; *filaments* 5—6 mm long.

Normally, the stem is low-arching or procumbent, terete—angled, greyish green or purple—brown; the prickles are pale yellow, scattered, bristle-like prickles few or none; the leaves are large, dark green, with coarsely serrate leaflets; the petiolule of the terminal leaflet is twice as long as the petiolules of the upper pair of leaflets, while those of the lower pair are about 0.4 cm long; the prickles of the inflorescence are recurved—reflexed and straight; the hairs, as well as the stalks of the glands, are rather long both on the stem and in the inflorescence; the sepals are long-acuminate, spreading or deflexed. *R. fuscus* seems to prefer boggy areas associated with forests. The species is known from two small areas in Scandinavia; namely, in north-eastern Småland, between the towns of Valdemarsvik and Västervik, where it grows near the Baltic inlets and connecting lakes, and on the Danish island of Als, south of "The Little Belt".

The species was formerly named *R. pallidus* W. & N. in Sweden. In Denmark, this species is known from Fyen and eastern Sønderjylland.

In the next two papers, I intend to terminate my current contribution to "Drawings of Scandinavian Plants" with four taxa — namely, *R. hartmanii*, *R. bellardii*, *R. caesius*, and the *Corylifolii* group, a key for the treated taxa, and a brief discussion.

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Observations on the Taxonomy and Ecology of the Epilithic Crustaceous Brown Algae in the SW Archipelago of Finland (Seili Islands)

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ABSTRACT

RAVANKO, O.: Observations on the Taxonomy and Ecology of the Epilithic Crustaceous Brown Algae in the SW Archipelago of Finland (Seili Islands). — Bot. Notiser 123: 220—230, Lund.

The epilithic brown-algal crusts that generally were referred to *Lithoderma fatiscens* ARESCHOUG in the inner part of the Baltic, but after WAERN's (1949, 1952) studies were treated as three different species — viz., *Petroderma maculiforme*, *Lithoderma subextensum*, and *L. rosenvingii* — have been studied.

According to the observations on the development of the crusts *Petroderma maculiforme* (WOLLNY) KUCKUCK seems to be a juvenile stage of *Lithoderma subextensum* WAERN. The morphological features considered to separate *L. subextensum* from *L. fatiscens* ARESCHOUG and *L. fatiscens* ARESCHOUG in the sense of KUCKUCK are unstable and probably change readily under different environmental conditions. The characteristics of *Lithoderma rosenvingii* WAERN are believed to represent abnormal development; thus, *L. rosenvingii* is conspecific with *L. fatiscens* ARESCHOUG.

Also the resemblance of a number of other taxa to *Lithoderma fatiscens* ARESCHOUG has been discussed.

INTRODUCTION

In 1949, WAERN published a preliminary report on the crustaceous brown algae that occur north of the Baltic proper (Öregrund Archipelago). Three species were reported that were new to Sweden. Two of them — *Lithoderma rosenvingii* and *L. subextensum* — were described as new species. The third one, *Petroderma maculiforme*, was previously described, but its distribution was not known. Further details of the brown-algal crusts were treated later by WAERN (1952).

Although more records now exist for *Petroderma maculiforme*, its distribution (EDELSTEIN & MCLACHLAN 1969) is still poorly known. Apparently, it has a wide distribution, having been reported, besides in Europe, from the Atlantic Coast of North America, from South Georgia and the Antarctic (EDELSTEIN & MCLACHLAN 1969), and as well from the Pacific Coast (WYNNE 1969). Both *Lithoderma subextensum* and *L. rosenvingii* have been reported from the same areas according to WAERN's publications (see, e.g., LUND 1959 p. 84; RAVANKO 1968 pp. 24—25).

During the floristic studies from 1961 to 1966 (RAVANKO 1968), attention was given to the epilithic brown-algal crusts that occur on the southwest coast of Finland. My studies were limited in some cases in that I did not have an opportunity to study the crusts in a living state nor to follow the development of other crusts throughout the year. The studies were carried out generally between June and September. During the summer of 1966, more attention was directed to the brown-algal crusts from May until the end of August. At this time *Petroderma maculiforme* was observed to be fairly common in the Seili Islands — seeming to favor shores with relatively high nutrition (i.e., somewhat polluted shores). This species was especially abundant on pebbles near landings and on the shores facing the shipping lanes. On other shores it was rare, while *Lithoderma subextensum* was the dominating member in the epilithic crustaceous vegetation. No new records of *L. rosenvingii* could be made in 1966.

MATERIALS AND METHODS

During 1968—1969 a detailed study was made of the brown-algal crusts. They were examined in the living state and their development was followed through the entire year.

Material was collected from the same pebbles at different times during the summer months for morphological and developmental studies. Young crusts were also taken into culture and their development was followed in the laboratory.

Erdschreiber's solution (prepared with brackish water from the Seili Islands) was used in the cultures. Relatively poor illumination and temperatures of 10° to 13° C seemed to be the most favorable for growth. Accordingly, growth of blue-green algae could be controlled. About twenty pebbles with very young crusts were taken into culture from May to September and the crusts' development were followed. The collections of epilithic crustaceous brown algae from the southwestern archipelago of Finland (mainly the Seili Islands), and reported on in this paper, are preserved in formaldehyde in the herbarium of the University of Turku (TUR) (box 4, jar 53; box 8, jars 100, 101, 104; box 17, jar 237; box 18, jars 239—241, 244—248; box 20, jars 267—269; box 24, jar 326; box 25, jars 339, 340).

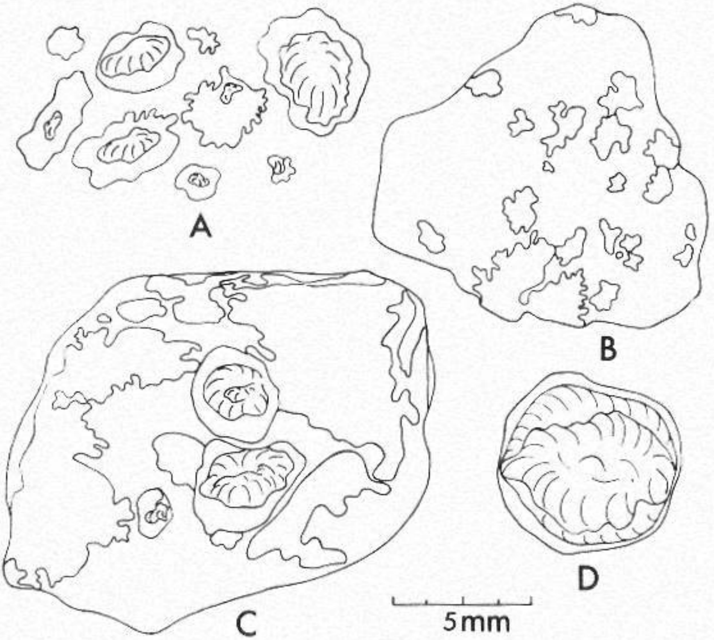

Fig. 1. — A: Young crustaceous brown algae that are either monostromatic or distromatic. — B: Young monostromatic crusts on a pebble. — C: Crusts of various developmental stages on the same pebble. — D: A threelayered (tristromatic) crust. (All crusts were collected on 20.7.1968 in the SW side of Seili Island.)

OBSERVATIONS ON THE MORPHOLOGY AND DEVELOPMENT

The Development of the Young Crusts

The algae under consideration were usually observed in shallow water (20—50 cm), where they formed irregular, reddish-brown monostromatic crusts. The diameter of the crusts was usually a few millimetres (Fig. 1), whereas the filaments of the young crusts could easily be separated. The cells in the filaments of the center of the crust soon started to divide and the thallus became distromatic (Fig. 1 A). The second layer consisted of loosely joined filaments that sometimes terminated in reproductive organs (Fig. 2 L—N). The space between the filaments was mucilaginous. The cells of the centermost filaments divided more rapidly than the others, and thus some of the older crusts were multilayered (Fig. 1 A, C—D).

Development proceeds in a similar way both in nature and in culture.

The cells of the young monostromatic basal part have one large chloroplast, which often is more or less cup-shaped (Fig. 2 B); moreover, the chloroplasts in the cells of the erect filaments have a similar form (Fig. 2 A). This type of chloroplast characterizes the cells of the young crusts both in nature and in culture.

In young crusts with developing unilocular reproductive organs, the uppermost cells of the erect threads are often observed to have several chloroplasts before the eyespots appear. Thus, most cells of the crust, when seen in surface view, appear to contain two to eight chloroplasts (Fig. 2 G, P).

The filaments usually have a single terminal unilocular sporangium (Fig. 2 L—M). Rarely the filaments terminate in two sporangia (Fig. 2 O), and the walls of the old sporangium can be observed as husks on the side of the new (Fig. 2 M, O). This type of sporangium may develop repeatedly in series — resulting in some of the filaments appearing to be clothed with hairs (Fig. 2 M, O). New cells may also arise in the old sporangium prior to the initiation of the new sporangium.

In young cultures the sporangia do not differ from the sporangia that are observed in the natural habitats.

Further Development of the Thallus

The individual crusts "coalesce" in nature and may cover the entire surface of the pebble. The mucilaginous spaces between the erect filaments fill up with other substances (become encrusted) with the result that it is not easy to separate the filaments as in younger plants.

When young crusts were kept in culture for six to eight weeks, some cells in the erect filaments of the middle of the thalli gave rise to very long and slender unbranched filaments (Fig. 2 F). The filaments were completely free, unlike the shorter erect filaments of the young crusts, which were joined with a mucilaginous substance. In old cultures the cells in the upper part of the short, loosely joined filaments divided vertically (Fig. 2 Q, S). Sometimes, cell divisions took place in all directions, with the tops of the filaments becoming crowded and occasionally branched. Terminal hairs were observed occasionally. Short branches occurred on some of the long branches in the middle of the thallus.

In old crusts the chloroplast may divide, but this division is not accompanied by cell division. Consequently, several chloroplasts may be observed in the cells. Often the basal part may have several chloroplasts, while the upper part of the thallus may have only one or two in each cell (see also WAERN 1952 p. 142, Fig. 2 H).

During a short period of culturing (2—3 weeks), the chloroplasts did not change in appearance; and in most instances, each cell retained a single chloroplast over an extended period of time.

In old cultures (6 weeks or more), the chloroplasts became very large and irregularly lobed—filling the cell (Fig. 2 D). In other cells, the cloroplasts divided and two or three bands were observed (Fig. 2 C).

In approximately two-month-old cultures, the cells of the crust gave rise to a few long, initially unbranched filaments. The cells of these filaments had either one or two cup-shaped chloroplasts (Fig. 2 E), or more seldom irregularly divided ones.

In old cultures the sporangia could be intercalary, with several sporangia even occurring in tandem. The sporangia were then somewhat globoid in form (Fig. 2 U—Z). Sporangia were also occasionally disposed laterally (Fig. 2 Z); and sometimes they occurred in crowded masses (Fig. 2 R, T) resembling the so-called sori of some brown-algal

Fig. 2. — A: Erect filaments of young crusts from nature (20.7. 1968, SW side of Seili Island). — B: Cells of the basal parts of the crust in A (20.7. 1968). — C: Cells of the crust in A (4.9. 1968) after being grown in culture for one month. — D—F: Cells of long unbranched filaments of the crust in A (4.9. 1968). — G: Parts of a young crust from nature (5.5. 1969, SW side of Seili Island) showing developing unilocular sporangia (surface view of the crust). — H: A crust from nature (29.8. 1968) with basal cells containing several chloroplasts and cells of the erect filaments with only one chloroplast. — I: Part of a crust from nature (10.9. 1968, E side of Seili Island) showing variation in the number of chloroplasts. The central cells have several chloroplasts and the marginal cells have only one chloroplast. — J: Marginal part of a crust from nature (31.7. 1968, SW side of Seili Island). — K: A part of the crust in J (31.7. 1968). The cells are closer to the center than in J. — L: Unilocular sporangium on an erect filament of the crust in A. — M: Unilocular sporangium on a crust collected in Bromarv, Bromholmen, N side (24.5. 1968). — N: Two terminal unilocular sporangia on the erect filaments of crusts from the SW side of Seili Island (29.9. 1968). — O: Cells of the crust in N showing great numbers of sporangial husks on the sides of an erect filament. — P: Cells of a crust from nature (29.9. 1968, SW side of Seili Island) showing developing unilocular sporangia, of which two are tripartite (surface view of the crust). — Q: Erect filaments of the crust in A after culturing for more than two months. — R—Z: Erect filaments of the crust in A after culturing for more than one month. Terminal, intercalary, and lateral sporangia are present, as well as peculiar sorus-like structures (R).

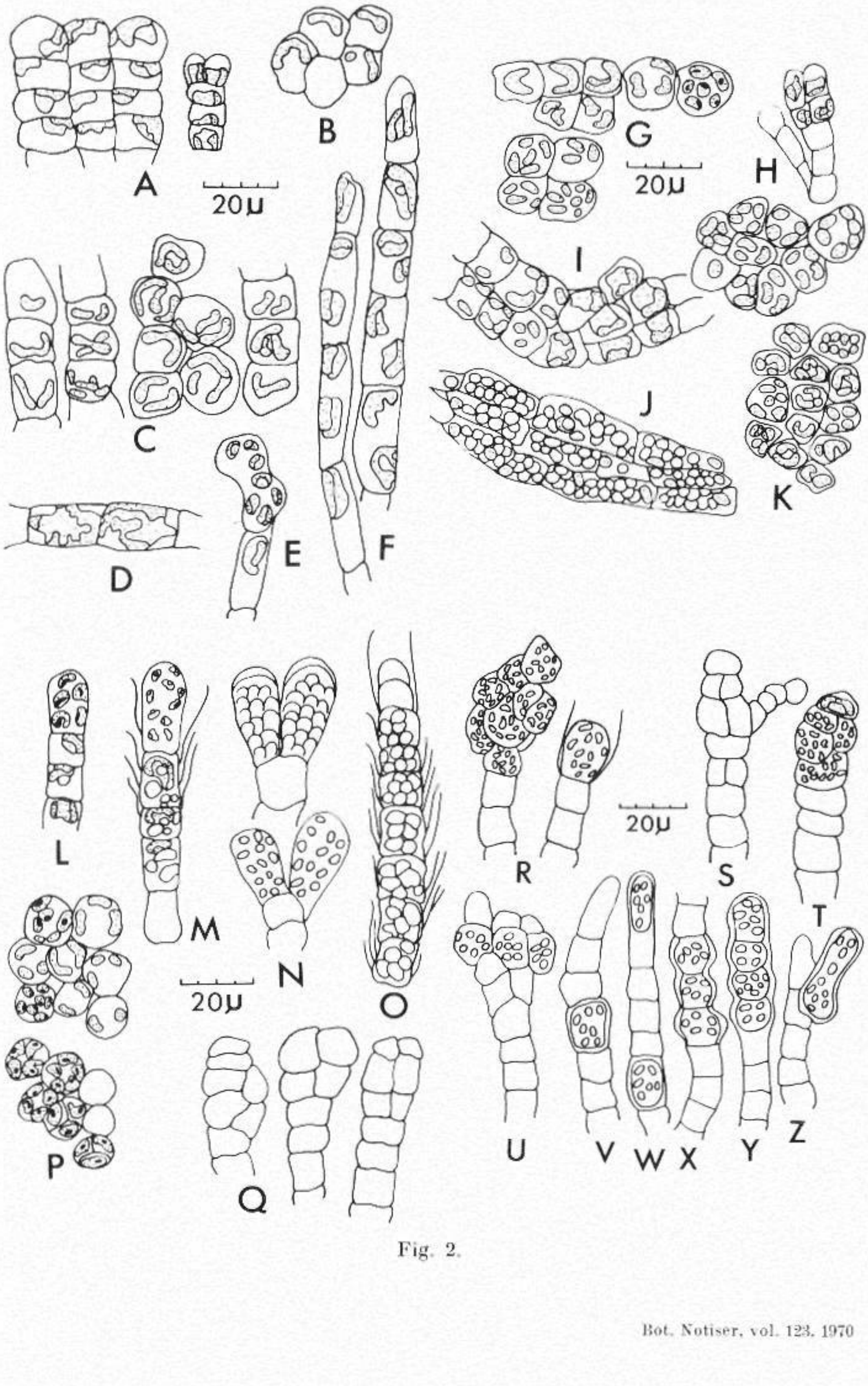

Fig. 2.

species—arising as a result of cell divisions, which in old cultures occurred in several directions.

TAXONOMIC ASPECTS

A detailed study of brown-algal crusts of various sizes, forms, and ages — both in nature and in culture — has shown that the young monostromatic crusts can be referred to *Petroderma maculiforme*. The young thalli become fertile very early and both the cells and the chloroplasts divide very quickly; and as a result of this, each cell, consequently, rarely has more than one chloroplast.

A thorough study of the young crusts has confirmed that *Sorapion simulans* KUCKUCK, *S. kjellmani* (WILLE) ROSENVINGE, and *Ralfsia ovata* ROSENVINGE are very close to *Petroderma maculiforme*: at least they cannot be separated on morphological grounds. Such characters as the form and the disposition of the unilocular reproductive organs, and the number of free filaments between them, which have been considered taxonomically important when separating the above-mentioned taxa, have been found to be highly variable both in the natural habitats of the plants and under cultural conditions.

When the "*Petroderma*" crusts age, they can be referred to *Lithoderma subextensum*, or to *L. rosenvingii* if they have quadripartite unilocular reproductive organs. The form of these organs has been considered to be the basic difference distinguishing *L. subextensum* and *L. rosenvingii*.

My studies have, however, shown that the quadripartite organs are very rare and that they can be present on plants that also possess the usual type of unilocular sporangia, as *L. subextensum*. Bipartite and tripartite sporangia (Fig. 2 P) have been observed more often than quadripartite sporangia.

In culture experiments the unilocular sporangia have been found to be easily modifiable. The generally terminal sporangia may become intercalary or lateral (Fig. 2 U—Z). Chains of intercalary sporangia may also occur (Fig. 2 U—Y) either in the vertical (Fig. 2 X—Y) or in the transverse (Fig. 2 U) direction. Cell divisions may take place in several directions, and as a result peculiar sori are formed (Fig. 2 R, T).

It is a known fact that cultures, and especially old ones, have a tendency to give rise to morphological anomalies, but stable morphological characters tend also to be fairly stable in cultures. Therefore, it is believed that the easily modifiable unilocular sporangia might also become modified under natural conditions, and thus it is quite likely that the quadripartite sporangia only are exceptions or abnormalities. Consequently, on this basis, *Lithoderma rosenvingii* cannot be retained as an independent species.

The fact that two terminal sporangia (Fig. 2 N) have been observed many times in nature on the same filament, as well as the occurrence of branches in the upper parts of the erect filaments brings *Lithoderma fatiscens* ARESCHOUG close to *L. subextensum*. The lateral plurilocular sporangia that have been considered to characterize *L. fatiscens* ARESCHOUG are equivalent to the lateral branches that have been observed in *L. subextensum*, and which easily can be transformed to plurilocular sporangia, which always develop from normal vegetative cells. It was also possible to induce *L. subextensum* to form lateral unilocular sporangia in culture (Fig. 2 Z). On the basis of LUND (1938), the lateral plurilocular sporangia was the only character that kept *L. fatiscens* ARESCHOUG separate from *L. fatiscens* ARESCHOUG emend. KUCKUCK. On the basis of the present studies, there is nothing that maintains *L. subextensum*, *L. fatiscens* ARESCHOUG, and *L. fatiscens* ARESCHOUG emend. KUCKUCK distinct.

In the present study, *Petroderma* has been observed to change into *Lithoderma* during the course of development, but in nature also single crusts can be seen that have both the characteristics of *Petroderma* and *Lithoderma* (Fig. 2 I). The central part of the basal crust may have several small chloroplasts in each cell. Also LUND (1959 p. 83) noticed a variation in the number of chloroplasts in the cells of *L. fatiscens* ARESCHOUG.

Petroderma maculiforme has usually been reported to have only unilocular sporangia, but plurilocular sporangia were reported to occur occasionally by EDELSTEIN and MCLACHLAN (1969).

My observations have definitely established that the morphological characters, such as the form and disposition of the reproductive organs and the number of chloroplasts, that have been considered to separate the above-discussed taxa do not have taxonomic value for such a separation. Because no other characters exist for separating the taxa discussed, I am inclined to believe that *Lithoderma fatiscens* ARESCHOUG, *L. rosenvingii* WAERN, *L. fatiscens* ARESCHOUG emend. KUCKUCK, *L. subextensum* WAERN, *Sorapion kjellmani* (WILLE) ROSENVINGE, *S. simulans* KUCKUCK, *Ralfsia ovata* ROSENVINGE, and *Petroderma maculiforme* (WOLLNY) KUCKUCK belong to the same species, and will, until further deviating observations have been made other than on a morphological basis, call them *Lithoderma fatiscens* ARESCHOUG, which is the first combination used. In case the brown-algal crusts would represent prostages or reduced stages of larger algae, they cannot be identified on a morphological basis.

I also believe that *Heribaudiella fluviatilis* (ARESCHOUG) SVEDELIUS is a form of *L. fatiscens* ARESCHOUG that inhabits fresh water. On the basis of the present observations, *L. fatiscens* ARESCHOUG is quite indifferent to fluctuations in salinity. It occurs often in abundance near landings and grows high up in the geolittoral belt of the shore. *L. fatiscens* ARESCHOUG (as *L. subextensum*) has also been reported from the northern part of the Gulf of Bothnia, where the salinity is relatively low (JULIN & PEKKARI 1965).

It is very likely that *L. fatiscens* ARESCHOUG is able to survive in fresh water, especially if the nutrient supply meets its requirements. The description of *Heribaudiella fluviatilis* in SVEDELIUS (1930) indicate that its morphology is very similar to the morphology of the *Lithoderma* crusts that have grown in culture. The chloroplasts tended to divide several times in the cells (Fig. 2 C, E), tall and sometimes branched filaments developed, and the unilocular sporangia had a tendency to become intercalary (Fig. 2 U—Z); see also WYNNE (1969 pl. 3). Similar sporangia were described by SVEDELIUS (1930 p. 906), but he called them plurilocular organs, paying, however, attention to their peculiar form and to their resemblance to unilocular sporangia. *Ralfsia lucida* LUND (1967) from a heavily polluted area of the Danish waters also has characteristics that are similar to the features of *Lithoderma* that I have had in culture especially in the development of the unilocular sporangia. It is also probable that brown-algal crusts with still other described taxa might belong to the same complex.

ECOLOGICAL ASPECTS

Young crusts are found early in the spring growing frequently in the lower geolittoral and the hydrolittoral belts of the shore. They form light to dark brown, small spots (a few millimetres in diameter) on the surface of pebbles.

Often the crusts in the geolittoral belt are destroyed in the spring during the low-water periods, but the crusts that grow lower in the hydrolittoral belt increase in breadth and coalesce forming few-centimetre-wide spots on stones under *Cladophora glomerata*. The crusts also become thicker, and many of them assume a nodulated appearance. Old crusts have also been observed during the winter (January—February) on stones in the hydrolittoral belt under *Monostroma*, *Pilayella*, and *Ceramium* (see RAVANKO 1969 p. 229, Fig. 1).

Epilithic brown algal crusts also occur in the upper part of the sublittoral belt on stones under *Fucus vesiculosus* and often also in deeper water on stones and pebbles in the lower sublittoral belt, where they sometimes form their own vegetation zone (observed by diving).

At the end of summer and in the autumn, and at certain times of the year when the water level is high, young brown-algal crusts colonize stone surfaces near the water surface. When the filamentous brown algae have disappeared from the shores in late autumn, the number of young crustaceous brown algae increase here.

Throughout the year, young brown-algal crusts are common in somewhat polluted waters near landings, where they may cover pebbles and pieces of glass, but they may also grow on objects constructed of cement or wood, though less often than on pebbles and glass.

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Spontaneous and Induced Variation in some Chemical Leaf Constituents in Hierochloë (Gramineae)

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ABSTRACT

WEIMARCK, G.: Spontaneous and Induced Variation in some Chemical Leaf Constituents in Hierochloë (Gramineae). — Bot. Notiser 123: 231—268, Lund.

The results of a chromatographic study of non-identified leaf substances in *Hierochloë australis*, in tetra-, hexa- and octoploid *H. odorata*, and in *H. occidentalis*, *H. pauciflora*, *H. alpina*, and *H. monticola* were subjected to a modified analysis of variance and an analysis of correlation between spots. The indices traditionally used in so-called "numerical chemotaxonomy" were avoided.

The effects of sampling season and different treatments during cultivation were elucidated by a modification test. Some deviations could also be ascribed to differences in sampling and storing techniques. The analysis further permitted an estimation of the role played by chance, technical aberrations, co-occurrence of spots etc., thus facilitating the evaluation of obtained results.

The method used gave indications on breeding systems and population structures otherwise difficult to obtain.

Some collections of the tufted perennials *H. australis* and *H. alpina* were found to be heterogeneous as to spot patterns. Collections of the rhizomatous perennial *H. odorata* were homogeneous in all studied cases, the plants being likely to form clones in each locality.

Tetraploid and hexaploid *H. odorata* could not be distinguished by spot patterns, nor could with reasonable certainty *H. alpina* and *H. monticola*. Diagnostic spots or spot groups in other taxa nearly always permitted a correct grouping in spite of the observed variability between collections within each taxon.

The obtained knowledge on population structures and pattern affinities is to be used in the current taxonomic work on the genus.

INTRODUCTION

In my current taxonomic study of the grass genus *Hierochloë* R. Br. in the Northern hemisphere the following taxa are treated:
H. australis (Schrader) Roemer & Schultes, 2n=14
H. odorata (L.) Wahlenb., 2n=28, 42, 56
H. occidentalis Buckl., 2n=42
H. pauciflora R. Br., 2n=28
H. alpina (Swartz) Roemer & Schultes, 2n=56, 66
H. monticola (Bigelow) Löve & Löve, 2n=63.

Within this study some embryological problems are already treated (Weimarck 1967 a, b, and unpubl.). Studied plants of *H. odorata* 2n=28 set seed sexually. *H. australis*, *H. odorata* 2n=42 and 56, *H. alpina* and *H. monticola* set seed by means of facultative or obligate apospory. One of the remaining problems is the taxonomic rank of the different cytotypes of *H. odorata*, which are only partly distinguishable by morphologic characters (Weimarck unpubl.). The interrelationships between the morphologically rather similar *H. alpina* and *H. monticola* are to be elucidated. The affinities of *H. australis*, *H. occidentalis* and *H. pauciflora* are also to be explained.

In the present paper an approach to the problems is made on the basis of a two-dimensional thin-layer chromatographic analysis of miscellaneous substances extractable in HCl-methanol, giving additive characters. As yet I have made no attempt to identify the substances (probably mainly phenolic compounds) corresponding to the spots obtained on the chromatograms, which were dealt with only as patterns. This and similar methods using identified or non-identified substances separated by paper-, thin-layer- or gas chromatography have been widely used to throw light upon problems involving polyploidy and hybridity in plants.

AIMS

The aims of my present investigation were

1. to choose a suitable chromatographic technique
2. to obtain a method of presenting and treating data
3. to estimate the degree of repeatability and consistency of results
4. to study and obtain an estimate of the possible modification of patterns due to different light, temperature, artificial manuring, season of the year, sampling technique and storing of samples
5. to study and obtain an estimate of the variation within collections of the taxa concerned
6. to study and obtain an estimate of the variation between different collections of each single taxon
7. to study differences and similarities between chromatographic patterns of taxa mentioned and search for spots or spot groups of diagnostic value.

PLANT MATERIAL

The material studied is mainly plants cultivated in the Botanical Garden, Lund, and grown up from rhizomes collected in original sites. Each locality is designated by three capital letters and an individual plant of a collection by an arabic figure. Clone individuals of a single plant are designated by a small letter. For more detailed information on localities, see separate list (WEIMARCK unpubl.). Voucher specimens are preserved at the Institute of Systematic Botany, Lund (LD).

The experimental part is reported on in Tables 2—6. For purposes 4 and 5 (cf. p. 232), a few collections of *Hierochloë australis* and *H. odorata* were chosen. The following variations were made (the number of plants available did not permit all possible combinations to be tested):

1. plant in the experimental garden, in shadow under trees (original treatment before start of experiment)
2. as *1*, but with weekly addition of Superba fertilizer in water (17 % K as K_2O; 14 % N, equal parts as nitrate and ammonium; 7.1 % P as P_2O_5; 6.5 % S; 0.6 % Mg; and micro nutritients)
3. plant in the experimental garden, in full day-light
4. plant in greenhouse, in deep shadow under table, fertilizer as in *2*
5. plant in greenhouse, in full day-light upon table, fertilizer as in *2*
6. plant from the locality AKP in the original site (a pasture in Norra Nöbbelöv some kilometres N of the centre of Lund).

Samples were dried during 1967 in the traditional way between papers at room temperature (*a*) May 2, (*b*) June 14, (*c*) July 5, and (*d*) August 9. The plants were moved from the original treatment *1* to the test stations after the May sampling.

In addition, parallel samples of chosen plants (treatment *1*, occasion *b*) were dried as above and in a thermoconstant cabinet in 50°C for 2 hours. The results were compared to each other and to results from corresponding herbarium material.

Plants from the collections involved in culture experiments are also represented in the comparison.

An account of the regional part is given in Tables 7—14. Tables 7—10 contain results from selected collections of material in culture, treatment *1*, sampled in June 1967 and dried between papers. One plant (in *H. australis* in some cases more) from each locality was chosen. Tables 11 and 12 contain data from small samples taken from herbarium sheets. Tables 13 and 14 consist of samples partly collected directly in the field, and partly collected in culture in the Arctic Greenhouse in Copenhagen in summer 1968.

Regional subdivision within Fennoscandia and Denmark and abbreviations given in Tables 6—14 are made according to HYLANDER (1953, map towards p. 392). Other abbreviations of territories within Europe are in accordance with TUTIN et al. (1964, map towards p. 464).

CHROMATOGRAPHIC METHOD AND TABULAR ARRANGEMENT

50 mg dry leaf tissue of each sample were ground for 2 min. in a small glass homogenizer and extracted for at least 24 hours in 1 ml methanol, one drop of hydrochloric acid added. The extracts were stored overnight or a few days at +4°C before separation.

By a spreading device according to NYBOM (1963), having a c. 350 μ high slot, clean glass plates 12×16 cm were prepared 14—16 at a time with a suspension of 20 g cellulose powder (Merck Avicel) in 120 ml distilled water. Two grooves in the cellulose layer restricted the run length to 90 mm in direction I and 130 mm in direction II. 10 μliter of the extract were applied at the starting-point. When in a few cases a smaller amount than 50 mg tissue had been available, a correspondingly larger amount of extract was applied, apparently giving a comparable result.

A "multiple sandwich chamber" technique was developed for the running of chromatograms. 12 plates were stacked with small plastic pellets (c. 1.7 mm thick) between and a blank plate on top as in the "chromatostack" technique of NYBOM (1964). The stack was surrounded on three sides by a frame padded with foam plastic and placed with the fourth side downwards in an open jar with 2 % formic acid in distilled water for the short run (I). No time was thus needed for equilibration, each space between two plates being a separate sandwich chamber with a constant and very small volume.

The plates were dried after the first run and checked in UV light. Approved plates were restacked and run in a mixture of amyl alcohol, glacial acetic acid and distilled water 22: 13: 11 (II). Each extract was run on at least two plates. Running was performed at room temperature.

The plates were dried and examined in UV light (Fluotest, 360 nm) (a) before spraying (b) after spraying with 1 % $AlCl_3$ in methanol and (c) after subsequent spraying with 1 % NaOH in methanol. Each spot was thus characterized by position and colour at three stages. Spot intensity was roughly stated as follows: not visible, less clearly visible, and more clearly visible. Maximum estimates obtained from two or more plates represented by the symbols ·, — and +, respectively, are combined in Tables 2—14. Typical colours and R_F values from representative plates are given in Table 1. Representative spot sizes and forms are indicated in Figs. 1 and 2.

The order of tabulated spots is made regardless of colour. 13 spots, widespread in the material and occurring in 90 % or more of the plants accounted for in Tables 7—14, are grouped together. Spots 14—26 are less frequent but spread in most of the material (absence of some less frequent spots in one or more of the taxa *Hierochloë occidentalis*, *H. pauciflora*, *H. alpina*, and *H. monticola* has been disregarded because of the small material studied). Spots 27 and 28, in most cases occurring together, form a group of their own. The following groups are regarded as more or less diagnostic to one or a few of the taxa. Some spots with obviously sporadic occurrence and being impossible to identify from one plate to another have been omitted. A cluster of blue spots in approximate position R_F .65—.90×.60—.90 constitutes the main part of such excluded spots.

STATISTICAL TREATMENT

I have subjected the Tables 2—14 to a modified analysis of variance in order to clarify trends otherwise difficult to point out more exactly. Instead of only counting the presence or absence of a spot, I have used the following scale: not visible: 0, less clearly visible: 2, more clearly visible: 3. A quantity gradient, in all likelihood continuous, is thus translated into three stages.

The squared deviations from the mean were calculated for each spot. The obtained values for all spots of each plant were summed, divided by degrees of freedom or otherwise corrected to give unbiased estimates, E, of the total variance of the respective means. These corrections were $n/n-1$ if the plant in question was included in the mean, $n/n+1$ if not; n being the number of plants in the mean. E values are given without decimals. They correspond to variance, s^2, summed for all spots.

The total deviation can in Tables 3 and 5 be apportioned to different causes of variation. $E_{\text{collection}}$ gives the variation caused by differences between the two collections involved of each taxon. $E_{\text{treatment}}$ gives the variation due to the different test conditions *1—5*. E_{time} gives the variation between different sampling periods *a—d*. $E_{\text{time} \times \text{treatment}}$ measures whether the different treatments vary differently with time. $E_{\text{collection} \times \text{time}}$ measures whether different collections react differently with time. $E_{\text{collection} \times \text{treatment}}$ (considering the fact that an individual plant was subjected to only one of the treatments) measures whether plants from different collections subjected to the same treatment react differently and can therefore be designated E_{plants}. $E_{\text{collection} \times \text{time} \times \text{treatment}}$ reflects variation not referrable to any cause mentioned above and is treated as an estimate of variation due to chance and to e.g. possible small differences in plant treatment, inconsistency in defining the intensity of spots, difficulties in registering spots at the perception threshold, etc. It is designated $E_{\text{other sources}}$.

Tables 2, 4 and 6 have been subjected to a more limited treatment. In Tables 7—14 the same type of E values as in Tables 2—6 have been calculated. The values give an estimate of the deviation of each plant from the mean.

Tables 7—10 have been subjected to an analysis of correlation between spots regardless of intensity.

RESULTS

Hierochloë australis. Table 2. The table as a whole could not be treated statistically, being too fragmentary. The plant A K B 3 was killed by treatment *4* after occasion *b*. Differences, especially within the groups 27—28 and 29—34, between plants within collection B A B are directly observable. E between B A B plants in May is 34, more than twice the assumed value for $E_{\text{other sources}}$. (Since some variation must be ascribed to other sources than real differences between plants, a part of it should be subtracted from the total deviation; from Tables 3 and 5 a rough estimate of 9—16 units may be inferred.)

Table 1. Characteristics of registered spots. — Colour is given at three stages (cf. p. 234). Frequencies are taken from Tables 7—14. Names of taxa treated (cf. p. 232) are abbreviated.

No.	Colour			R_F		Frequency in % (number of plants in brackets)									No.
	a	b	c	I	II	aus (18)	o28 (68)	o42 (41)	o56 (54)	occ (2)	pau (3)	alp (4)	mon (5)	Tot (195)	
1	blue	blue	blue	.60	.63	100	100	100	100	100	100	100	100	100	1
2	yellow	yellow	brick red	.61	.56	89	100	100	100	100	67	75	100	98	2
3	invis. or black	yellow	orange	.08	.50	94	97	100	100	100	100	75	100	98	3
4	black	yellow	green	.46	.54	100	94	100	100	0	67	100	100	96	4
5	blue	blue	green	.04	.35	67	100	100	100	100	67	100	100	96	5
6	black	yellow	orange	.35	.46	100	100	100	100	0	33	0	100	96	6
7	invis. or undef.	yellow	undef. or orange	.04	.23	94	99	100	94	100	67	50	100	96	7
8	invis.	yellow	orange	.05	.73	61	100	100	96	50	100	100	100	95	8
9	invis.	yellow	orange	.03	.42	83	88	88	100	100	100	100	100	92	9
10	invis.	yellow	orange	.16	.62	83	84	98	96	100	100	100	100	91	10
11	blue	blue	green	.03	.46	28	97	100	100	100	0	75	100	90	11
12	blue	blue or undef.	undef.	.09	.23	22	96	100	100	100	33	100	100	90	12
13	invis. or blue	invis. or blue	blue	.17	.84	83	90	88	96	100	100	75	60	90	13
14	invis. or blue	invis. or blue	blue	.35	.94	78	60	83	67	100	100	75	100	71	14
15	blue	blue	blue	.52	.62	28	78	20	100	50	0	50	100	66	15
16	blue	blue	blue	.67	.59	44	46	71	93	0	0	50	0	62	16
17	invis. or blue	invis. or blue	blue	.12	.78	6	40	24	94	0	0	50	60	48	17
18	invis. or black	invis. or undef.	dull brown	.39	.80	17	40	78	43	100	0	0	60	46	18
19	blue	blue	blue	.79	.52	78	51	37	44	0	0	0	20	46	19
20	invis.	undef. or yellow	undef.	.03	.81	39	44	27	52	0	100	100	100	45	20
21	invis. or blue	invis. or blue	blue	.03	.93	6	32	51	56	50	0	0	40	39	21
22	invis. or black	yellow	orange	.05	.56	6	7	5	94	0	100	50	100	35	22
23	blue	blue	blue	.66	.53	17	56	22	9	100	0	25	40	31	23
24	invis.	invis. or blue	blue	.45	.91	17	10	49	9	0	0	0	0	18	24
25	invis.	invis. or undef.	dull red	.47	.96	6	3	2	6	0	0	0	0	4	25
26	invis.	yellow	green	.43	.62	0	6	0	4	0	0	0	0	3	26
27	black	yellow	green	.52	.58	83	85	100	98	100	0	0	0	·	27
28	black	yellow	orange	.40	.51	83	85	100	96	0	0	0	0	·	28
29	black	yellow	orange	.43	.39	11	0	0	28	0	0	0	0	·	29
30	black	yellow	green	.51	.49	6	0	0	26	0	0	0	0	·	30
31	black	yellow	green	.73	.62	39	0	0	26	0	0	0	0	·	31
32	black	yellow	orange	.70	.56	50	0	0	26	0	0	0	0	·	32
33	black	yellow	orange	.66	.51	61	0	0	28	0	0	0	0	·	33
34	black	yellow	orange	.68	.47	39	0	0	28	100	0	0	0	·	34
35	invis. or undef.	yellow	invis. or undef.	.04	.35	83	0	0	0	0	0	0	0	·	35
36	yellow	yellow	yellow	.06	.92	11	0	0	0	0	0	0	0	·	36

Table 1. Continued

No	Colour			R_F		Frequency in % (number of plants in brackets)									No.
	a	b	c	I	II	aus (18)	o28 (68)	o42 (41)	o56 (54)	occ (2)	pau (3)	alp (4)	mon (5)	Tot (195)	
37	invis. or blue	invis. or blue	blue	.71	.95	44	71	85	59	0	0	0	0	·	37
38	invis. or black	yellow	orange	.16	.40	0	0	2	81	0	0	0	0	·	38
39	invis. or black	yellow	orange	.17	.32	0	0	2	83	0	0	0	0	·	39
40	invis. or black	yellow	orange	.13	.25	0	0	2	94	0	0	0	0	·	40
41	invis. or black	yellow	orange	.10	.18	0	0	2	93	0	0	0	0	·	41
42	invis.	yellow	green	.03	.60	0	0	0	0	100	0	0	0	·	42
43	invis. or black	yellow	green	.08	.57	0	0	0	0	100	0	0	0	·	43
44	invis. or black	yellow	green	.04	.50	0	0	0	0	100	0	0	0	·	44
45	invis. or black	yellow	orange	.51	.53	0	0	0	0	100	67	0	0	·	45
46	invis.	yellow	orange	.42	.43	0	0	0	0	100	100	0	0	·	46
47	black	yellow	green	.29	.48	0	0	0	0	100	100	100	100	·	47
48	invis. or black	yellow	orange-green	.20	.43	0	0	0	0	100	100	100	100	·	48
49	black	yellow	orange-red	.17	.33	0	0	0	0	100	100	100	100	·	49
50	black	yellow	red	.45	.40	0	0	0	0	0	33	100	100	·	50
51	blue	yellow-green	green	.26	.57	0	0	0	0	0	67	75	40	·	51
52	invis.	yellow	green	.22	.53	0	0	0	0	0	0	50	60	·	52
53	invis.	yellow	orange-green	.18	.38	0	0	0	0	0	0	75	0	·	53

Table 7. Some of the localities are represented by more than one plant, this in contrast to Tables 8—12 and 14.

Differences in the same spot groups occur between plants studied in collections BAD, AXL, AHT, and AXT, are less pronounced in AKB, and none occurs in APR. *E* between collections is 36. *E* within collections is 35. Evidently heterogeneity within collections causes almost all the deviation. *E* values are generally high when compared to those of other taxa (Tables 8—14). The mean *E* value in Table 7 is 36.

Hierochloë odorata 2n=28. Table 3. Values concerning treatment *4* are omitted from statistical treatment in Table 3 B because of the fact

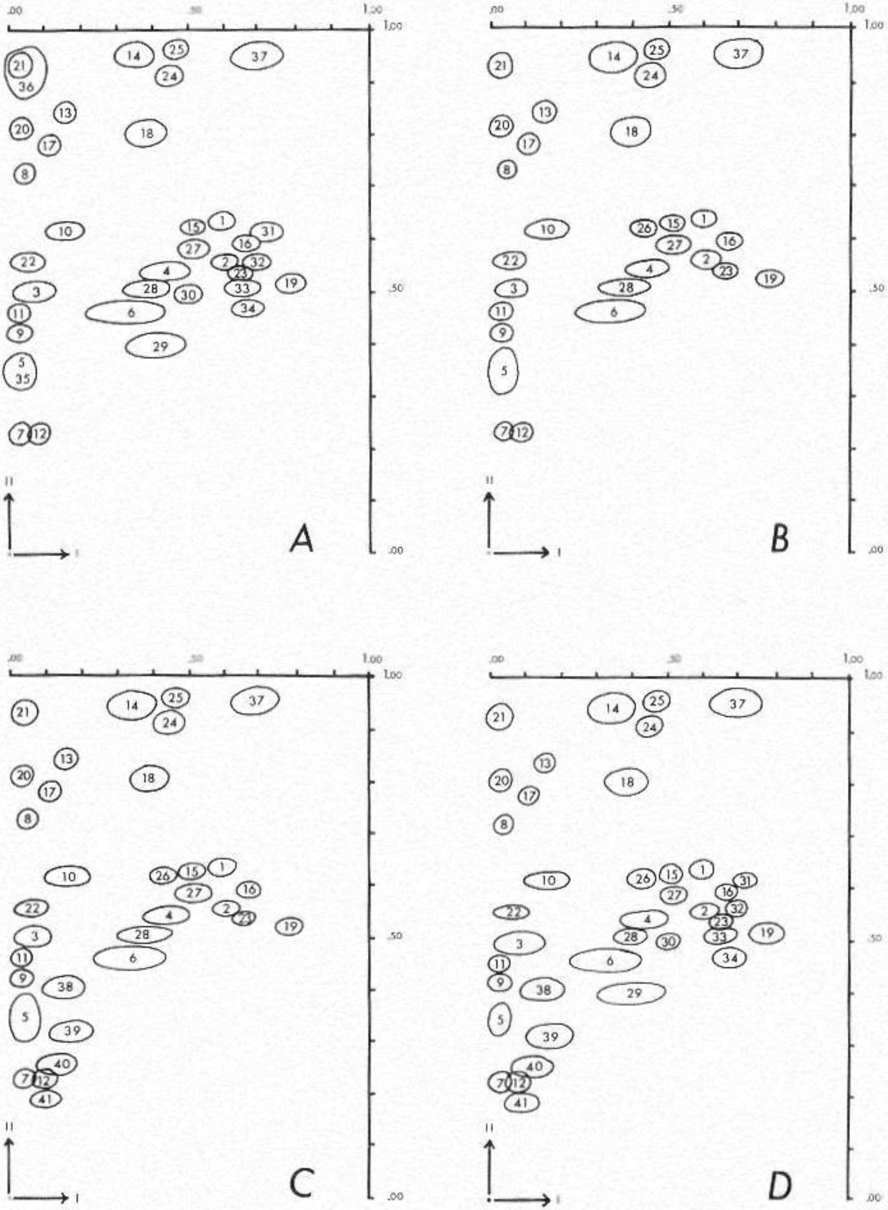

Fig. 1. Spot diagrams. — A: *Hierochloë australis*. — B: *H. odorata* 2n=28. — C: *H. odorata* 2n=42. — D: *H. odorata* 2n=56.

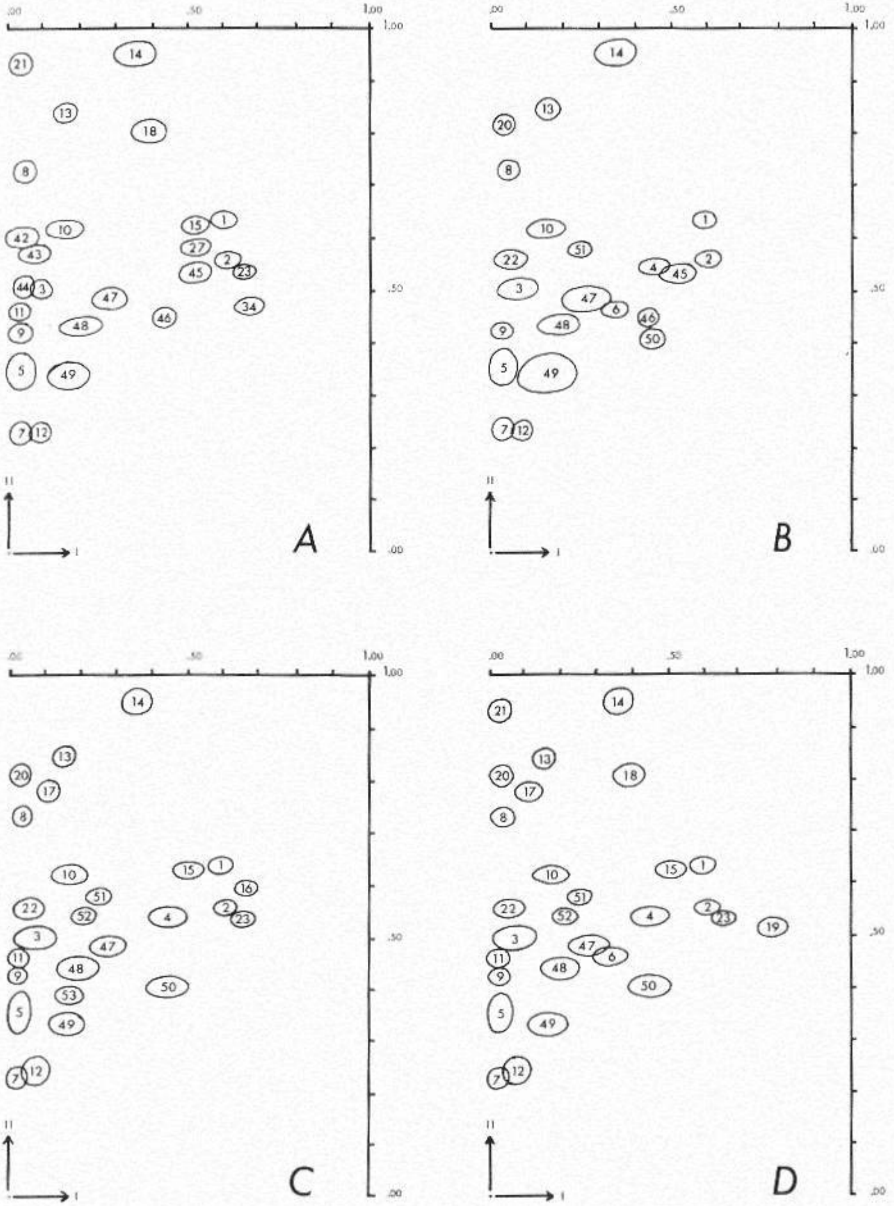

Fig. 2. Spot diagrams. — A: *Hierochloë occidentalis*. — B: *H. pauciflora*. — C: *H. alpina*. — D: *H. monticola*.

Table 2. Culture experiments. *Hierochloë australis*. — Explanations of treatments *1*—*5* and sampling occasions *a*—*d* cf. p. 233.

	A K B 4	A K B 3	B A B 2	B A B 3	B A B 1	B A B 4	
	1	*4*	*1*	*2*	*3*	*5*	
	a b c d	*a b*	*a b c d*	*a b c d*	*a b c d*	*a b c d*	
1	+ + + +	− +	+ + − +	+ + + +	+ + + +	+ + + +	1
2	+ + + +	+ +	+ + + +	+ + + +	+ + · −	+ + · +	2
3	− − − ·	− ·	+ + + +	− − − −	− + − ·	+ · · ·	3
4	+ + + +	+ ·	· + + +	+ + + +	+ + + +	· + · ·	4
5	+ · + −	+ ·	· · · ·	· · · −	· · − ·	· · · −	5
6	+ + + +	+ +	+ + + +	+ + + +	+ + + +	+ + + +	6
7	+ + − −	+ −	− + − +	− − − −	− + − −	− − − −	7
8	− − − ·	− ·	+ − − +	+ − − ·	− − − ·	+ − − ·	8
9	− − − −	− ·	+ − − −	− − − −	− − − ·	− − · ·	9
10	− − · ·	− ·	− + − −	− − · ·	− + − ·	− · · ·	10
11	− · · ·	· ·	· · · −	· · · ·	· · · ·	· · · ·	11
12	· · · ·	· ·	· · · ·	· · · ·	· · · ·	· · · ·	12
13	− + − −	− +	− + − +	+ − − −	+ + − −	− + · ·	13
14	+ + + −	+ +	· − + −	− − · −	− − + −	+ + + +	14
15	· · · ·	· ·	· · · ·	· · · −	· + · ·	− · · ·	15
16	· + + ·	· ·	· · · ·	· + + +	+ · + −	· · − +	16
17	· · · ·	· −	· + · +	· · · ·	· − · ·	· · · ·	17
18	· − · ·	− +	· · · +	· · · −	· · · ·	− − · +	18
19	· − − −	· ·	· + + ·	· · · ·	+ + · ·	· · − ·	19
20	· − · ·	· ·	· · · −	· − · ·	· · · ·	· · · ·	20
21	· · · ·	· ·	· · · ·	· · · ·	· · · ·	· · · ·	21
22	· · · ·	· ·	· · · ·	· · · ·	· · · ·	· · · ·	22
23	· · · +	· ·	· · · ·	− + · ·	· + · ·	· + · ·	23
24	· · · ·	· −	− · · +	· − · −	+ − · ·	· + · +	24
25	· · · ·	· ·	· · · ·	· · · ·	· · + ·	· + · ·	25
26	· · · ·	· ·	· · · ·	· · · ·	· · · ·	· · · ·	26
27	+ + + +	+ +	+ + + +	+ + · ·	· − · ·	+ + − +	27
28	+ + + +	+ +	+ + + +	· · · ·	· · · ·	+ · + +	28
29	· · · ·	· ·	· · · ·	+ − + +	· · · ·	· − · −	29
30	· · · ·	· ·	· · · ·	+ + + −	· · · ·	· · · −	30
31	+ · · ·	· ·	+ − + +	+ − · ·	· · · ·	+ + + −	31
32	· · · ·	· ·	+ + + +	· · · ·	· · · ·	· · · +	32
33	+ − − −	· +	+ + + +	+ + − −	· · · ·	+ − − ·	33
34	+ − · ·	− +	+ · · ·	+ + − −	· · · ·	+ · · ·	34
35	+ − + −	+ −	− − − −	− − − −	− + − −	− − · −	35
36	· + + ·	· +	· · · ·	· · · +	· · · −	· · · ·	36
37	+ + + +	+ ·	+ − + +	+ + + +	+ + + +	+ + − +	37

that plant A E G 6 was killed by treatment *4* after occasion *c* (cf. p. 233) and A K P 2 b was so weak that no sample could be taken on occasion *d*. Plants A E G 2, A E G 4, A K P 2 a, 3 a and 4 a and values of treatment *6* were also omitted in order to facilitate comparisons to Table 5.

The greatest source of variation is time (Table 3 B). Treatment also gives a good deal of variation. Collection, collection × time and time ×

treatment have less influence. Differences between plants are so small that they cannot be separated from other sources of deviation.

Plants A K P 1 a and 1 b are clone individuals of the same rhizome. The same is the case as to A K P 2 a—b, 3 a—b and 4 a—b. Clone individuals a were all kept in treatment *1*, b placed out in other treatments after the May sampling. In Table 3 C—H a special statistical study of collection A K P is performed.

Variation due to sampling time is great in the comparison between A K P 1 a, 2 a, 3 a and 4 a, treatment *1* (Table 3 C). The different plants contribute less to variation than other factors. Also in the comparisons between clone individuals 1 a—1 b, 3 a—3 b and 4 a—4 b (Table 3 D—F) the greatest source of variation is the time during which the plants were subjected to the treatments.

On three of the sampling occasions material was also collected at the original locality. The *E* value of the four samples of May (A K P *6 a*) is 9, within the limits of that normally ascribed to other sources. *E* between the mean of *6 a* and the mean of other A K P in May is 25, indicating a difference, not very great but in all likelihood real, between plants in culture and in natural habitat.

The values for occasions *c* and *d* in comparisons between material from the original locality and material in culture (Table 3 G) suggest that treatments *1* and *3* imitated natural conditions best. Treatments *4* and *5*, and also *2*, gave high differences, treatment *4* making sampling impossible in August.

The *E* value in May between clone individuals a and b of A K P 1—4 (Table 3 H) is of about the same size as that between the different plants 1—4, both values being small. Thus nothing indicates that the originally collected plants 1—4 should be more different from each other than are the experimentally produced clone individuals.

Table 8. *E* between each plant and the mean exceeds in only few cases twice the assumed *E* value to be ascribed to other sources of variance. Most different are collections from Sweden: Lule Lappmark, Holland, Romania, and Canada. To some extent they contribute to raise the values for all other collections. An aberration in the pattern, very conspicuous on chromatograms but not so clearly registered by the statistical treatment, is the lack of group 27—28 in some collections. The mean *E* value in Table 8 is 24.

Hierochloë odorata 2n=42. Table 4. Because of shortage of experimental material the table is not treated statistically as a whole. The

Table 3. A: Culture experiments. *Hierochloë odorata* 2n=28. — B: Variation in A. Exclusions see text. — C: Variation between A K P 1a, 2a, 3a, 4a. — D: Variation between A K P 4a and 4b (treatment *2*). — E: Variation between A K P 1a and 1b (treatment *3*). — F: Variation between A K P 3a and 3b (treatment *5*). — G: Variation

3A.	A E G 1				A E G 2			A E G 7				A E G 3				A E G 4				A E G 6			A E G 5				A K P 1 a			
	1				*1*			*2*				*3*				*3*				*4*			*5*				*1*			
	a	*b*	*c*	*d*	*a*	*b*	*c*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*
1	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+
2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+
3	+	−	−	−	+	+	+	+	−	·	−	−	+	+	+	+	+	−	+	+	−	−	+	·	·	·	+	−	−	−
4	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
5	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
7	+	−	+	+	+	−	+	+	+	−	+	+	+	+	+	+	+	+	+	+	−	+	+	+	·	−	+	+	+	+
8	+	+	+	−	+	+	+	+	−	+	−	+	+	−	−	+	−	−	−	+	+	−	+	+	−	−	+	−	−	−
9	·	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	·	·	·	−	−	−	·
10	·	−	·	·	·	−	·	·	−	·	·	·	−	·	·	·	−	·	·	·	·	·	·	−	·	−	·	·	·	·
11	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
12	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+
13	−	−	·	−	−	+	−	−	+	−	·	−	+	−	−	−	+	−	−	−	−	−	−	+	−	−	−	−	−	−
14	+	+	·	·	−	−	·	·	−	+	·	+	+	·	−	·	+	−	·	+	+	·	−	+	+	·	+	−	·	−
15	·	·	−	+	·	−	−	+	−	·	+	·	·	−	+	−	−	−	+	−	−	−	·	−	+	−	−	+	+	+
16	·	·	−	+	·	+	+	+	−	·	+	−	+	+	+	·	+	+	+	+	+	−	·	+	+	+	·	+	+	·
17	+	−	·	−	−	−	−	·	−	−	−	·	·	−	−	·	·	−	−	·	−	·	·	+	−	−	−	−	−	−
18	+	+	+	−	+	·	+	+	+	−	+	+	+	·	−	+	·	−	−	+	+	·	+	+	+	+	+	−	−	−
19	·	·	·	·	·	+	·	·	·	·	·	·	+	+	+	·	+	−	·	·	·	·	·	·	·	·	·	·	·	−
20	·	−	·	·	·	−	·	·	−	·	·	·	−	·	·	·	−	·	·	·	·	·	·	−	·	−	·	·	·	·
21	·	+	+	·	−	+	−	·	+	−	−	·	−	−	·	+	·	·	·	·	−	−	·	+	+	+	·	+	·	−
22	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
23	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	−	+
24	−	·	·	·	−	·	·	·	−	·	·	·	·	·	·	·	·	·	·	·	+	·	·	+	·	+	·	·	·	−
25	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
26	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
27	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+
28	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
29	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
30	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
31	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
32	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
33	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
34	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
35	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
36	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
37	·	−	+	+	−	+	+	+	−	+	+	+	+	+	+	−	+	+	+	−	−	+	·	−	+	+	−	+	+	+

plant in treatment *4* was very weak in August and could not be used. Between the A F B plants, *E* in May is 7, between the B A F plants 8, well within the limit of variation due to other sources. The dependence of spots on different treatments seems to be of about the same character as in *H. odorata* 2n=28.

between A K P treatment *6 c, d* and other A K P on the same sampling occasions. — H: Variation in May between clone individuals a, b of the plants A K P 1—4 and between plants 1—4. — Explanations of treatments *1*—*6* and sampling occasions *a*—*d* cf. p. 233. (Table 3 B—H see next page.)

A K P 2 a				A K P 3 a				A K P 4 a				A K P 4 b				A K P 1 b				A K P 2 b			A K P 3 b				A K P						
1				*1*				*1*				*2*				*3*				*4*			*5*				*6*						
a	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*a*	*b*	*c*	*d*	*a*	*a*	*a*	*a*	*c*	*d*	
+	+	+	−	+	+	+	−	+	+	+	+	+	+	+	−	+	+	+	+	+	+	·	+	+	+	−	+	+	+	+	+	+	1
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	2
+	−	−	−	+	+	−	−	+	−	−	−	+	−	−	·	+	+	+	+	+	−	·	+	−	·	·	+	+	+	+	−	−	3
+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	−	+	4
+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	5
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	6
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	−	·	·	+	+	+	+	+	+	7
+	+	−	−	+	+	−	−	+	+	−	+	+	+	−	+	+	−	−	−	+	+	−	+	+	·	·	−	+	−	−	−	−	8
−	−	−	−	−	−	−	−	−	−	−	−	−	−	−	·	−	−	−	+	−	−	·	−	−	−	·	−	−	−	−	−	−	9
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	−	10
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	−	+	+	+	−	+	+	−	+	+	+	+	+	−	+	11
−	+	+	+	−	+	+	+	+	−	+	+	+	−	+	+	−	+	+	−	−	+	+	+	+	+	+	+	−	−	−	+	−	12
−	·	−	−	−	−	·	−	−	·	−	+	+	+	−	+	−	−	−	−	−	−	−	+	·	·	+	−	+	−	−	−	−	13
+	−	·	·	+	+	−	·	+	−	·	+	−	−	+	−	−	−	−	·	+	+	+	·	+	−	·	−	−	·	−	·	−	14
−	−	+	+	−	−	−	−	−	−	+	−	+	+	−	·	−	−	+	+	−	·	·	+	−	−	−	−	+	+	+	+	+	15
·	·	·	·	·	+	·	·	·	·	−	·	+	·	−	+	·	+	+	·	·	−	·	·	+	+	·	·	·	·	·	+	·	16
−	·	−	−	−	−	·	−	−	·	−	+	−	+	−	+	−	·	−	−	−	−	+	·	+	−	−	−	−	−	−	−	−	17
+	−	·	+	+	+	−	−	+	−	·	−	+	·	+	−	+	−	·	−	+	+	+	+	+	+	+	·	·	·	+	·	−	18
−	·	−	·	+	+	·	·	·	+	·	·	·	−	·	·	·	+	+	·	·	·	·	·	·	·	·	−	−	+	·	+	+	19
·	·	·	·	·	·	·	−	·	·	·	−	·	·	·	−	·	·	·	·	·	·	·	·	−	−	·	·	·	·	·	·	·	20
·	·	·	−	·	−	·	+	·	−	·	+	·	+	−	+	·	·	·	+	·	−	·	·	−	+	+	·	+	+	·	−	−	21
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	22
·	−	+	+	·	·	+	+	·	·	·	+	−	−	·	·	·	·	·	+	−	·	·	−	·	·	+	·	·	·	·	·	−	23
·	·	·	−	·	−	·	−	·	·	·	−	−	·	·	+	·	·	·	·	·	·	−	·	−	·	+	·	·	·	·	·	·	24
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	25
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	26
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	27
+	+	+	+	−	+	+	−	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	−	+	+	28
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	29
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	30
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	31
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	32
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	33
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·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	35
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	36
−	−	+	+	−	−	+	−	−	−	+	+	·	+	−	−	−	−	+	−	−	·	·	−	·	+	−	+	+	+	+	+	+	37

Table 9. One collection, from Switzerland, differs greatly from the mean and also adds somewhat to the values of other collections. Their *E* values, however, hardly reach twice the variance ascribed to other factors, in many cases as low as the last-mentioned one. No variation occurs in the group 27—28. The mean *E* value in the table is 17.

3 B.

source	*E*	df
collection	23	1
treatment	29	3
time	42	3
time × treatment	19	9
collection × time	21	3
plant	10	3
other	12	9

	3 C.		3 D.		3 E.		3 F.	
source	*E*	df	*E*	df	*E*	df	*E*	df
time	36	3	23	3	19	3	32	3
plant	7	3	–	–	–	–	–	–
treatment	–	–	13	1	8	1	23	1
other	9	9	15	3	10	3	16	3

3 G.

treatment	*1*	*2*	*3*	*4*	*5*
plant / sampling occasion	*E* mean 1 a–4 a	*E* 4 b	*E* 1 b	*E* 2 b	*E* 3 b
c	15	15	5	46	27
d	15	32	11	–	27

3 H.

source	*E*	df
clone individuals	8	4
plants	6	3

Hierochloë odorata 2n=56. Table 5 B. A K U 6 omitted from statistical treatment. Table 5 C. Also values from treatment *4* omitted, although the plants survived this treatment, in order to permit direct comparisons to Table 3. The presence or absence of this treatment does not change the general conclusions.

The greatest source of deviation is treatment, time coming next. The effect of these two factors is much higher than in *H. odorata*

Table 4. Culture experiments. *Hierochloë odorata* 2n=42. — Explanations of treatments *1*—*5* and sampling occasions *a*—*d* cf. p. 233.

	A F B 3				A F B 4			A F B 5				B A F 4				B A F 1				B A F 6			B A F 2				B A F 3			B A F 5				
	1				*2*			*3*				*1*				*1*				*2*			*3*				*4*			*5*				
	a	*b*	*c*	*d*	*a*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*b*	*c*	*d*	*a*	*b*	*c*	*d*	*a*	*b*	*c*	*a*	*b*	*c*	*d*	
1	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	+	+	+	1
2	+	+	+	+	+	+	+	+	+	−	+	+	+	−	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	2
3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	−	·	−	3
4	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	4
5	+	+	+	+	+	+	+	+	+	+	+	+	−	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	5
6	+	+	+	+	+	+	+	+	+	+	+	+	−	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	6
7	+	+	−	−	+	−	−	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	−	+	·	7
8	−	+	−	−	+	−	−	−	−	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	−	+	+	−	−	8
9	−	−	·	·	−	·	−	−	−	−	−	+	−	−	−	−	−	·	−	+	−	−	−	+	−	−	−	−	·	−	−	·	−	9
10	−	+	+	−	+	−	−	+	+	+	−	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	·	+	−	·	−	10
11	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	11
12	−	−	−	−	−	−	+	+	−	−	−	+	+	+	+	+	+	+	+	+	−	+	−	+	+	+	+	+	−	+	+	+	+	12
13	·	−	−	−	+	+	−	−	−	+	−	−	−	−	·	−	·	−	−	−	·	−	+	+	+	·	−	·	−	+	−	·	−	13
14	+	+	−	−	+	+	−	+	−	+	−	·	+	+	−	+	+	+	−	+	+	+	−	+	+	−	+	−	+	·	+	+	−	14
15	−	−	−	+	+	−	+	+	−	−	+	−	·	−	+	−	−	·	−	·	·	·	−	−	−	−	·	−	·	−	·	·	·	15
16	+	+	·	+	+	·	+	+	+	·	+	+	−	·	+	+	·	·	+	·	·	+	+	·	·	+	+	+	+	+	·	·	+	16
17	·	−	−	−	+	+	−	−	·	+	−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	−	−	−	17
18	+	+	·	−	+	−	−	+	+	+	−	+	+	+	−	+	+	+	·	+	−	+	+	+	·	·	+	+	−	−	−	+	−	18
19	·	·	+	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	−	·	−	·	19
20	·	·	·	−	·	·	−	·	·	·	−	·	·	·	·	·	·	−	·	−	−	−	·	·	−	−	·	·	·	·	·	−	−	20
21	−	+	+	·	−	+	+	−	·	−	·	·	−	·	·	·	+	·	+	·	+	+	·	·	·	−	·	·	−	·	−	+	+	21
22	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	22
23	·	·	+	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	23
24	·	·	−	−	·	·	−	−	·	+	−	·	·	·	−	·	·	−	·	·	·	−	·	·	·	·	·	+	+	·	·	·	·	24
25	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	−	·	−	·	·	·	−	·	−	·	·	·	·	·	·	·	25
26	·	·	·	−	·	·	−	·	·	·	·	−	·	·	·	+	·	·	·	·	·	+	·	·	·	−	·	·	·	·	·	+	+	26
27	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	27
28	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	28
29	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	29
30	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	30
31	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	31
32	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	32
33	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	33
34	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	34
35	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	35
36	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	36
37	·	−	−	−	·	−	·	·	+	−	−	·	+	−	+	·	−	−	+	−	−	−	−	+	+	+	·	·	·	−	−	−	+	37

2n=28, possibly due to the greater number of spots involved. Other sources are doubtful or cannot be discriminated from the level of other factors.

E in May between A G O plants is 9, between A K U plants 8.

Table 10. The collections can be classified into two groups, one

Table 5. A: Culture experiments. *Hierochloë odorata* 2n=56. — B: Variation in A, treatment *4* included. Exclusion see text. — C: Variation in A, treatment *4* excluded. — Explanations of treatments *1*—*5* and sampling occasions *a*—*d* cf. p. 233.

5 A.	A G O 1	A G O 6	A G O 2	A G O 3	A G O 4	A K U 1	A K U 6	A K U 5	A K U 2	A K U 4	A K U 3	
	1 *a b c d*	*2* *a b c d*	*3* *a b c d*	*4* *a b c d*	*5* *a b c d*	*1* *a b c d*	*1* *a b d*	*2* *a b c d*	*3* *a b c d*	*4* *a b c d*	*5* *a b c d*	
1	+ + + +	+ + – +	+ + + +	+ · – –	+ + + –	+ + + +	+ + +	+ + + +	+ + + +	+ – – ·	+ + – +	1
2	+ + + +	+ + + +	+ + + +	+ + + +	+ + + +	+ + + +	+ + +	+ + + +	+ + + +	+ + + +	+ + + +	2
3	+ + + +	+ + – –	+ + – –	+ – – –	+ – – –	+ + – +	+ + +	+ + – +	+ + + +	+ + + –	+ – – –	3
4	+ + + +	+ + + +	+ + + +	+ · + –	+ · · ·	+ + + +	+ + +	+ + + +	+ + + +	+ + + –	+ – – –	4
5	+ + + +	+ + – +	+ + + +	– + – –	+ + + +	+ + + +	+ + +	+ + + +	+ + + +	+ + + +	+ + – +	5
6	+ + + +	+ + + +	+ + + +	+ – + +	+ · – ·	+ + + +	+ + +	+ + + +	+ + + +	+ + + +	+ – – –	6
7	+ + + +	+ + – –	+ + + +	+ – – –	+ + – –	+ + + +	+ + +	+ + – +	+ + + +	+ + – +	+ – · +	7
8	– + + –	– – – –	– – – –	· – – –	– – – –	– + – –	· – –	– – · –	– – – –	– + · –	– – – –	8
9	+ + – –	+ + – –	+ – – –	– · · ·	– – · ·	+ + – –	– – –	– + – –	+ – – –	– – · ·	– · · ·	9
10	– + – –	– + · –	+ – – –	– – · ·	– · · –	+ · · ·	– – –	– – – –	– – – –	– · – ·	– · · –	10
11	– + + –	– + · –	+ + – –	– – – ·	+ – – –	– – – –	+ + –	– – – –	+ – – –	+ + – –	+ – – –	11
12	– + – +	+ – – +	+ – – +	– – – –	– – – –	– + + +	+ + +	+ + – +	– + + +	+ + – –	– + – +	12
13	+ – + –	+ – – –	– + – –	– – – –	– · · –	+ – – –	+ – –	+ + – –	+ + – –	+ – · –	– – – –	13
14	· – + ·	– – + –	– + · ·	+ + + –	+ + + ·	– · + ·	– · ·	+ – – –	– · · ·	· – – –	– – – –	14
15	+ – – +	+ + – +	+ – – +	– · – ·	+ – · ·	+ + – +	+ + +	+ + – –	+ + – +	+ · – ·	+ · · –	15
16	– · · +	+ + – +	+ · · +	– – – +	+ + – +	· – – +	+ – ·	– + · ·	+ + + +	– + · –	+ · + +	16
17	– – + –	– – – –	· + – –	– – – –	– – – –	– – – –	– – –	+ – – –	– + – –	– – – –	– – · –	17
18	+ + + –	+ + + –	+ + + ·	+ + + +	+ + + +	+ + + ·	+ + ·	+ – + +	+ + – ·	+ + + –	+ + + –	18
19	· · · ·	· · · ·	· · · ·	· · · ·	· · · ·	· · · ·	· · ·	· · · ·	· · · ·	· · · ·	· · · ·	19
20	· · · –	· · · –	· · · ·	· · · ·	· · · –	· · · ·	· · ·	· · – ·	· · · ·	· · · ·	· · · –	20
21	+ – – –	– + + +	+ – · ·	– – + +	· – + +	+ + + –	· + –	– + – –	– – · –	– · – –	· – – –	21
22	+ + – +	+ + – –	+ + – –	+ · – –	+ · – –	+ + – –	+ – –	+ + – +	+ + – –	+ + + –	+ · – ·	22
23	· · · ·	· · · ·	· · · ·	· · · ·	· · · ·	· · · ·	· · ·	· · · ·	· · · ·	· · · ·	· · · ·	23
24	· · · ·	· – · +	· · · ·	· + – +	· · · +	· · · ·	· · ·	· · · ·	· · · ·	· – – +	· – · +	24
25	· · – ·	· · · ·	· – · ·	· · · ·	· · · ·	· – · ·	· – ·	· – · ·	· – – ·	· · · ·	· · · ·	25
26	· – – –	· · · ·	· – · ·	· · · ·	· – · ·	· · · ·	· · ·	· – – ·	· · · ·	· · – ·	· · · ·	26
27	+ + – +	+ + – –	+ + – +	+ – + –	+ – – ·	+ + – +	+ – +	+ – – –	+ – – ·	+ + – –	+ – – –	27
28	+ + – –	+ + + +	+ + – –	+ · + –	+ · – ·	+ + – –	+ – –	+ – – –	+ – – –	+ + – –	+ · · –	28
29	+ + + +	+ + + +	+ + + +	+ – + –	+ · – ·	+ + + +	+ + +	+ + + +	+ + + +	+ + + +	+ – · –	29
30	+ + – –	+ + – –	+ + – –	+ · – ·	+ · · ·	– – – +	+ – –	+ – – –	– – – +	+ – – –	+ – · ·	30
31	+ + + +	+ + + +	+ + + +	+ · – ·	+ · + –	+ + + +	+ + –	+ + + +	+ + + –	+ + + –	+ + – –	31
32	+ + + +	+ + + +	+ + + +	+ · · ·	+ · · ·	+ + + +	+ + +	+ + + +	+ + + +	+ + + ·	+ + · ·	32
33	+ + + +	+ + + +	+ + + +	+ – + –	+ – – ·	+ + + +	+ + +	+ + + +	+ + + +	+ + + +	+ – – –	33
34	+ + + +	+ + + +	+ + + +	+ – + –	+ – – –	+ + + +	+ + +	+ + + +	+ + + +	+ + + +	+ – – –	34
35	· · · ·	· · · ·	· · · ·	· · · ·	· · · ·	· · · ·	· · ·	· · · ·	· · · ·	· · · ·	· · · ·	35
36	· · · ·	· · · ·	· · · ·	· · · ·	· · · ·	· · · ·	· · ·	· · · ·	· · · ·	· · · ·	· · · ·	36
37	+ + – –	– + · –	· + + –	· · · ·	+ – – ·	· + + ·	– + –	– + – +	· + + –	– – · ·	– – – –	37
38	+ + + +	+ + + –	+ + + +	+ – – –	+ – – –	+ + + –	+ + –	+ + + +	+ + + +	+ + – –	+ – – –	38

source	5 B.		5 C.	
	E	df	*E*	df
collection	19	1	10	1
treatment	78	4	77	3
time	59	3	47	3
time × treatment	21	12	21	9
collection × time	16	3	16	3
plant	20	3	13	3
other	13	12	12	9

having spots 29—34 or at least some of them and one lacking all these spots. This heterogeneity causes a rise in the *E* values. They are highest in collections from Canada and USA and are generally high in collections having spots 29—34, these collections being in minority and therefore more deviating from the mean. As a complement the calculation is made also without the group 29—34. The remaining deviation is in some collections still two to three times the one ascribed to other sources. The mean *E* value is 30 (19, if the group 29—34 is excluded).

Hierochloë occidentalis, H. pauciflora, H. alpina and **H. monticola.** Tables 11—14. *E* between plants are 12, 20, 26 and 14, respectively. Since the material is small and inconsistently sampled, the figures are of restricted value.

The two BDR plants of *H. alpina* show marked differences from each other. The chromosome number of this collection is 2n=66. Other *H. alpina* collections studied have the number 2n=56 (cf. WEIMARCK 1970).

Test of Sampling and Storing Techniques. Table 6. The *E* values in Table 6 B exemplify the magnitude of deviation in paired comparisons due to sampling, storing and other factors together. In a few cases this deviation is about twice the one expected to be due to other factors.

As to *H. odorata* the herbarium material is from the same locality and can be presumed to represent the same genotype (see below, p. 263). Such material was not obtainable as to *H. australis*, which is represented by herbarium material chosen to have the same basic type of pattern. Herbarium material of *H. australis* is therefore excluded from statistical treatment.

Table 6. A: Sampling and storing experiments. *Hierochloë australis, H. odorata* 2n=28, 42, 56. — A: Ab, Vihti 3.6. 1898 G. Lång (S). — B: Ta, Lammi 14.6. 1908 A. Renvall (S). — C: STrd, Opdal 15.6. 1936 J. E. Haugen (O). — D: Srm, Nacka 18.6. 1913 M. Engstedt (S). — E: Dlr, Gagnef 27.6. 1936 J. B. Bengtsson (LD). — Abbreviations: a: conv. dried; b: heat dried; c: herb. mtrl. — B (next page): Variation between techniques. — Regional subdivision cf. p. 233.

	H. australis						*H. odorata* 2n=28							*H. odorata* 2n=42							*H. odorata* 2n=56							
6A.	BAB2	BAB2	A	BAB3	BAB3	B	AEG2	AEG2	AKP1a	AKP1a	ARL2	ARL6	C	AFB3	AFB3	BAF1	BAF1	AFM5	AFM4	D	AGO1	AGO1	AKU1	AKU1	ALE3	ALE3	E	
	a	b	c	a	b	c	a	b	a	b	a	b	c	a	b	a	b	a	b	c	a	b	a	b	a	b	c	
1	+	+	−	+	+	−	+	+	+	+	+	+	+	+	+	+	+	−	+	−	+	+	+	+	+	+	−	1
2	+	−	·	+	+	·	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	2
3	+	−	−	−	−	−	+	−	−	−	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	3
4	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	4
5	·	·	+	·	·	·	+	+	+	−	+	+	+	+	+	+	−	−	+	+	+	−	+	+	+	+	+	5
6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	6
7	+	−	−	−	−	−	−	−	+	+	+	+	+	+	−	+	+	−	+	+	+	+	+	+	+	+	+	7
8	−	−	−	−	−	·	+	−	−	+	+	+	+	−	−	+	+	+	+	−	+	−	+	−	+	−	−	8
9	−	−	−	−	−	−	−	−	−	−	+	−	+	−	−	−	−	·	−	−	+	−	+	−	+	−	−	9
10	+	−	·	−	−	−	−	·	·	·	+	+	−	+	−	+	+	+	+	−	+	−	·	−	+	−	−	10
11	·	·	·	·	·	·	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	−	−	−	+	−	−	11
12	·	·	·	·	·	·	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	−	−	12
13	+	+	−	−	+	−	+	−	−	+	+	−	−	−	+	−	−	+	−	−	−	−	−	+	+	−	−	13
14	−	·	−	−	·	+	−	−	−	·	−	−	+	+	−	+	−	+	−	+	−	·	·	·	−	·	+	14
15	·	·	·	·	·	·	−	−	+	+	+	·	·	−	·	·	·	·	·	·	−	−	+	+	+	+	−	15
16	·	·	·	+	·	·	+	·	+	+	+	·	·	+	−	−	−	+	·	·	·	−	−	−	+	·	−	16
17	+	−	−	·	·	−	−	−	−	−	+	−	−	−	−	·	·	·	·	·	−	−	−	−	+	+	−	17
18	·	·	·	·	·	·	·	−	−	·	·	−	+	+	−	+	·	−	−	+	+	·	+	·	−	−	−	18
19	+	−	·	·	−	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	19
20	·	·	·	−	·	·	−	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	·	·	·	·	20
21	·	·	·	·	·	·	+	+	+	+	−	−	·	+	+	−	·	+	·	·	−	·	+	−	−	·	−	21
22	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	−	+	+	+	+	−	22
23	·	·	·	+	−	·	·	+	·	+	+	+	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	23
24	·	·	·	−	·	·	·	·	·	·	−	·	−	·	·	·	·	+	−	·	·	·	·	·	·	·	+	24
25	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	−	·	·	·	·	25
26	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	26
27	+	+	+	+	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	−	+	+	+	27
28	+	+	+	·	·	·	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	−	+	−	+	28
29	·	·	·	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	+	29
30	·	·	·	+	+	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	−	−	−	+	−	−	30
31	+	+	·	−	−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	−	31
32	+	+	−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	−	32
33	+	+	−	+	−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	+	33
34	·	·	−	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	+	34
35	−	−	−	−	−	−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	35
36	·	·	+	·	−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	36
37	−	+	·	+	−	·	+	+	+	+	−	−	·	−	−	+	·	+	−	·	+	·	+	·	·	−	·	37
38	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	+	+	+	+	+	+	+	38
39	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	+	+	+	+	+	+	+	39
40	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	+	40
41	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	+	+	+	41

6 B.

	BAB 2	BAB 3	AEG	AKP	ARL	AFB	BAF	AFM	AGO	AKU	ALE
	E	*E*	*E*	*E*	*E*	*E*	*E*	*E*	*E*	*E*	*E*
conv. dried — heat dried	6	22	21	10	17	8	14	18	22	16	14
conv. dried — herb. mtrl	·	·	·	·	24	·	·	28	·	·	12
heat dried — herb. mtrl	·	·	·	·	11	·	·	16	·	·	19

In chromatograms from herbarium material I have sometimes observed sporadic spots besides the ordinary patterns, possibly due to decomposition of some compound involved. Such extra spots are very often weak. They are not accounted for in the table, and the deviation given in comparisons to herbarium material is therefore a little lower than it should be in reality.

Comparisons Between Taxa. *Hierochloë australis* has great pattern affinities to *H. odorata*, especially to the 2n=56 cytotype, with which it shares the occurrence of spots 29—34. The spot group 35—36 has not been found in the other taxa.

Almost all the *H. odorata* 2n=56 plants have spots 38—41. These are found very rarely in *H. odorata* 2n=42.

Spots 27 and 28 are common to *H. australis* and all cytotypes of *H. odorata,* spot 27 also to *H. occidentalis*. The *H. occidentalis* material exhibits a pattern distinct from the rest of the taxa treated. It has one spot group, 42—44, of its own and the groups 45—46 and 47—49 in common with *H. pauciflora*. The last-mentioned group occurs also in *H. alpina* and *H. monticola*. The spots 50—52 and 53 are not represented in the *H. occidentalis* plants. The occurrence of spots 27 and 34 distinguishes them from *H. pauciflora, H. alpina* and *H. monticola*. These three taxa have no spots of their own in the present material besides spot 53 in *H. alpina*. *H. pauciflora* exhibits a pattern most affined to *H. alpina* and *H. monticola*.

As to spots common to two or more taxa great frequency differences are often found.

Correlation Between Spots in Tables 7—10. A number of positive and negative correlations were found in each table, the most significant ones illustrated in Figs. 3 and 4. In addition, spots with 100 % frequency were marked with heavy outlines in Fig. 3. Only few correlations were the same in all tables.

Table 7. Regional study. *Hierochloë australis.* — Regional subdivision cf. p. 233.

	Ta							Ab						Nyl			It	Rm	
	BAD 2	BAD 3	AXL 1	AXL 2	AXL 5	AHT 3	AHT 5	BAB 2	AKB 2	AKB 4	APR 1	APR 4	ADG 3	AXS 1	AXT 5	AXT 6	BBA 4	BBC 1	
1	+	+	+	+	+	+	–	+	+	+	+	+	+	+	+	+	+	+	1
2	+	+	+	+	+	+	+	+	+	+	+	·	+	+	+	·	+	–	2
3	+	–	+	–	–	–	·	+	–	–	+	+	–	+	+	+	–	–	3
4	+	+	+	+	+	+	+	+	+	+	+	+	+	–	+	+	+	+	4
5	–	–	–	–	–	–	·	·	+	·	·	–	+	·	·	–	–	–	5
6	+	+	–	+	+	+	+	+	–	–	+	+	+	+	+	+	–	+	6
7	–	–	–	+	+	–	·	–	–	+	–	+	–	–	–	+	–	–	7
8	·	–	–	–	·	·	·	–	–	–	–	–	·	–	·	–	–	·	8
9	–	–	–	–	–	–	·	–	+	–	–	–	·	–	–	–	–	·	9
10	–	–	–	–	–	–	·	+	–	–	–	–	·	–	+	–	–	·	10
11	·	·	·	–	·	·	·	·	·	·	·	–	–	·	·	–	·	–	11
12	·	·	·	–	·	·	·	·	·	·	·	–	·	·	·	–	–	·	12
13	–	–	–	+	–	–	–	+	–	+	·	+	–	+	+	–	·	·	13
14	+	–	+	+	+	·	·	–	+	+	·	+	–	–	·	+	–	–	14
15	–	·	·	·	·	–	–	·	·	·	·	·	–	·	·	+	·	·	15
16	·	+	+	+	–	·	·	·	+	+	·	·	·	·	+	–	·	·	16
17	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	17
18	·	·	·	·	·	·	+	·	·	–	·	·	·	·	·	·	–	·	18
19	–	+	·	+	–	–	+	+	–	–	·	·	–	+	+	+	·	–	19
20	–	·	–	·	·	·	·	·	–	–	–	·	–	·	·	–	·	·	20
21	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	–	·	21
22	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	22
23	·	+	·	·	·	·	·	·	·	·	·	·	–	·	+	·	·	·	23
24	·	–	·	·	·	·	–	·	·	·	·	·	·	·	–	·	·	·	24
25	·	·	·	·	·	–	·	·	·	·	·	·	·	·	·	·	·	·	25
26	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	26
27	+	·	+	+	·	+	+	+	+	+	+	+	+	+	·	+	–	+	27
28	+	·	+	+	·	+	+	+	+	+	+	+	+	+	·	+	–	+	28
29	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	·	·	29
30	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	30
31	·	·	+	·	·	·	+	+	·	·	+	+	·	+	·	·	+	·	31
32	–	·	+	·	–	·	–	+	·	·	+	+	·	+	·	·	+	·	32
33	·	·	+	+	–	–	+	+	·	–	+	+	·	+	·	·	+	·	33
34	·	+	·	+	·	·	+	·	·	–	·	·	·	+	+	·	+	·	34
35	·	–	–	–	–	–	–	–	·	–	–	·	–	–	–	–	–	–	35
36	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	36
37	·	+	·	+	·	·	+	–	·	+	+	·	·	+	+	·	·	·	37
E	22	44	26	28	25	23	59	31	34	31	31	39	32	34	54	60	37	29	*E*

SUMMARY AND DISCUSSION

1. The chromatographic method has turned out to give acceptable separation of spots and to permit work on a large scale due to rather rapid extraction and running procedures.

Since a major aim was to study variation at a low taxonomic level, I have chosen not to hydrolyze extracts. Glycosylation takes place late in the biosynthesis (cf. HARBORNE 1967 p. 271), and glycosides can therefore be expected to give a more detailed information on minor differences than aglycones. In addition, non-hydrolyzed extracts give a greater number of spots. Unfortunately, non-hydrolyzed compounds are more difficult to identify with certainty. A provisional identification of at least some substances may, however, be possible on the basis of R_F values and colour reactions (cf. HARBORNE 1959).

The cellulose layer used gave better results than other brands tested. I have avoided the use of silica gel recommended by GRANT and WHETTER (1966) who found cellulose to give only about 25 % of the spot number obtained on silica gel in *Lotus* material. Silica gel has, however, lower mechanical resistance and the somewhat "bad reputation" of easily causing artifacts.

Calculations of means ± standard errors of R_F values as made by some authors, e.g. BJÖRKQVIST (1968 p. 90), are somewhat questionable according to my experience. Since the plates are checked with respect to false run and other technical faults before using, the values are already subjectively selected and should not be treated statistically. Moreover no attempt to apply a correction formula (BATE-SMITH 1956 p. 166) and thereby afterwards try to diminish the effects of false run has been made. Instead I have accepted a variation in spot site of 0.02—0.03 R_F units in either direction, leading to no difficulties in identifying spots.

2. The modified analysis of variance used gives valuable estimates of deviations due to technique and chance and of experimentally induced and intrinsic deviations in plants. The correlation analysis indicates that most substances are in themselves independent of each other.

Many attempts have been published to make use of indices to demonstrate in figures the similarities and differences between taxa, e.g. by ELLISON, ALSTON and TURNER (1962), LORENZ and SCHULZ-SCHAEFFER (1964), HARNEY and GRANT (1965), MATTHEWS (1966), JAWORSKA and NYBOM (1967), OLSSON (1967), DASS and NYBOM (1967), GRANT and ZANDSTRA (1968), LAROI and DUGLE (1968), OLDÉN and NYBOM (1968), DEDIO et al. (1969 a, b), ISING and FRÖST (1969), and THIELGES (1969). Among the more wide-spread ones, the matching coefficient, the coefficient of similarity, the correlation coefficient and the biochemical distance as tools in connexion with chromatography have been criticized by RUNEMARK (1968), the two last-mentioned ones also by COLLESS (1967 pp. 24, 25).

In the present study none of the indices mentioned would work well because of the difficulty of estimating variation within and between collections, technical irregularities etc. The analysis of variance, although modified in a somewhat unorthodox manner, gives the taxonomist valuable facts to judge from, but leaves the very judging to him. The taxonomic treatment still has to be a matter of personal subjective discernment, whereby many facts other than chromatographic ones have to be considered.

In the statistical treatment all spots have been weighted alike. From the

Table 8. Regional study. *Hierochloë odorata*

	Fnm	Trs				Nrd										NTrd				STrd			MöRo	Hdm	Opl		Akh		Östf		LL	LyL	Jmt	
	AUB 3	ATH 2	AST 2	ASU 2	ASR 4	ASP 4	ASO 1	ASM 5	ASK 5	ASI 3	ASG 3	ASF 1	ASD 2	ASC 3	ASA 4	ARX 3	ARU 3	ART 2	ARS 4	ARO 3	ARN 1	ARL 2	ARK 6	ARC 2	ARD 6	ARE 5	ARA 5	APX 3	APU 3	APT 4	ANA 2	AMP 1	AML 6	AMH 1
1	+	+	+	+	+	+	+	+	+	+	+	+	+	−	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
4	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	−	+	+	+	−	+	+	+	·	·	+	+	+	+	+
5	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	−	+	+	+
6	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
7	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+
8	+	+	+	+	−	+	+	+	+	+	+	+	+	+	−	+	+	+	−	+	−	+	+	+	+	+	+	+	+	−	+	+	+	+
9	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	·	−	−	+	+	+	+	−	+	−	−	−	+	+	+	+	−	+
10	+	+	+	+	+	+	+	·	+	+	+	+	+	−	·	+	+	−	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+
11	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	+	+
12	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	+	+
13	−	·	−	·	−	+	+	+	+	+	−	−	+	−	−	+	−	−	−	+	−	+	·	−	+	+	−	−	+	−	−	−	+	·
14	·	·	·	+	−	−	−	+	−	−	·	−	+	·	−	−	−	+	·	·	·	−	·	·	·	−	−	·	−	+	−	−	−	·
15	−	·	·	−	·	+	−	·	−	+	−	+	−	+	−	−	−	−	+	+	+	+	·	−	−	−	·	−	−	·	+	−	−	+
16	+	−	·	−	·	·	·	·	·	·	·	+	·	+	+	+	+	−	+	+	·	+	+	·	+	+	·	+	·	·	+	+	+	·
17	·	·	−	·	·	−	·	·	·	−	·	−	·	−	·	·	−	·	−	+	·	+	·	·	−	·	−	−	·	·	−	−	+	·
18	·	·	+	+	·	·	+	·	·	·	·	−	+	+	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	+	+	+	+	−
19	+	·	−	−	·	+	·	·	+	−	−	·	·	−	·	·	·	·	·	·	−	·	·	−	·	·	·	−	−	−	+	−	·	·
20	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	+	·	−	−	−	−	·	·	·	·	·	·	·	·	·	·	−
21	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	·	·	·
22	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
23	·	·	·	·	·	+	·	·	+	+	+	−	·	·	+	+	·	−	·	·	·	+	·	+	+	·	+	·	+	·	·	·	·	·
24	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	·	·	−
25	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−
26	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
27	+	+	+	+	+	+	·	·	+	+	·	+	·	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	+	·
28	+	+	+	+	+	+	·	·	+	+	·	+	·	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	+	·
29	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
30	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
31	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
32	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
33	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
34	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
35	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
36	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
37	+	·	−	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	·	−	·	+	+	+	+	+	+	+	−	+	·	+
E	17	24	19	20	17	15	29	37	14	13	26	12	31	19	19	14	29	17	17	21	17	22	27	12	16	14	17	23	20	21	19	29	23	40

method used follows, however, that a different value in a spot can give a higher weight if this value is rare in the material. The effects is rather desirable in the present study, because as a rule it stresses a deviation more if it occurs in an otherwise homogeneous material.

2n=28. — Regional subdivision cf. p. 233.

Hrj	Bh								Vg					Hl		Sk							Jl			Sj	Mön	Hb	Ho		Rm	Canada		
ALU 5	AGU 2	AHA 3	AHB 3	AEO 7	AEP 3	AOC 1	AER 7	AEN 4	AHK 5	AHG 3	AHC 2	AHD 3	AES 5	AEM 8	AEL 9	AAT 1	AEG 1	AAS 2	AEF 10	AEE 1	APS 2	AKP 1a	BCO 5	BCU 5	BDD 5	BDL 2	BDI 5	AHP 1a	AOB 1	ADC 1	BCC 9	ADE 1a	AKG 1	
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	1
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	2
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	−	+	+	+	·	+	+	−	−	·	+	−	3
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	·	+	+	4
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	5
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	6
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	−	−	+	−	+	·	−	+	−	+	−	7
−	+	+	−	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	−	−	−	−	−	+	−	−	−	−	−	−	8
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	−	−	−	−	·	−	·	·	·	·	·	·	9
+	+	·	+	+	−	+	+	+	−	−	·	+	−	·	+	−	−	−	−	+	+	·	−	−	−	·	·	−	·	·	·	−	−	10
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	+	+	11
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	·	+	+	12
−	−	−	−	−	−	+	+	−	+	−	+	+	−	−	+	+	−	+	+	−	−	−	+	+	+	−	+	−	·	−	−	·	·	13
+	·	·	·	−	·	·	·	·	+	−	−	·	+	·	·	+	+	−	·	·	−	−	−	−	+	+	+	·	−	+	+	·	−	14
+	+	−	+	+	·	+	·	+	+	·	+	+	+	+	−	+	·	+	+	+	·	+	−	·	−	−	·	−	−	+	·	−	+	15
·	+	+	·	·	·	−	·	·	·	·	+	·	·	·	·	+	·	+	·	+	·	+	·	·	·	−	·	·	+	+	·	−	·	16
−	−	·	·	·	·	+	·	·	+	·	+	·	−	·	·	·	−	·	−	·	·	−	·	·	·	·	·	−	−	·	−	·	·	17
−	·	·	·	+	−	+	−	·	+	·	·	·	−	−	·	+	+	·	−	·	+	−	·	·	·	·	·	·	·	−	+	·	·	18
·	−	+	−	+	−	·	·	·	−	+	−	+	·	+	·	·	·	+	·	+	+	·	+	·	+	·	−	−	·	−	·	+	−	19
−	−	·	−	−	−	·	+	·	+	−	·	+	−	·	−	−	−	·	−	·	·	·	−	−	−	−	−	−	−	−	·	·	−	20
·	+	·	+	·	·	·	+	−	·	−	·	·	+	·	·	·	+	−	+	−	·	+	+	+	−	−	−	·	−	−	+	−	−	21
·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	·	·	·	·	·	·	·	·	·	−	·	·	·	·	−	22
+	+	−	·	+	·	·	+	+	+	+	−	+	+	+	+	+	·	−	+	·	·	·	+	+	+	·	+	+	+	−	·	+	+	23
+	·	·	·	·	·	·	−	·	+	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	−	·	·	·	·	·	·	24
−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	25
·	·	·	−	·	·	·	−	−	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	26
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	·	27
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	·	28
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	29
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	30
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	31
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	32
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	33
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	34
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	35
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	36
−	−	·	·	·	−	−	−	·	−	−	·	−	+	·	+	+	−	+	−	·	−	+	−	·	·	·	·	·	·	·	·	·	−	37
27	19	30	25	20	16	20	31	22	31	17	23	19	20	23	15	28	26	23	22	21	23	25	18	21	20	36	29	32	41	28	87	40	40	*E*

I have avoided the use of spot area as an estimate of compound amount as used by e.g. Jaworska and Nybom (1967), Olsson (1967), Dass and Nybom (1967), Oldén and Nybom (1968), etc. The relationship between area and amount cannot be implied to be even approximately linear, depending on

Table 9. Regional study. *Hierochloë odorata* 2n=42. — Regional subdivision cf. p. 233.

E	41	40	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	
0	·	·	·	·	|	·	·	·	·	·	·	·	·	+	+	·	·	·	·	|	|	|	·	·	|	+	|	+	·	+	+	|	·	|	+	+	+	+	|	+	+	ATF 3
3	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	+	·	+	·	·	+	+	+	+	|	+	+	+	+	+	+	+	+	AMF 5
7	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	+	·	·	|	·	·	|	+	+	+	|	|	+	+	+	+	+	+	+	AMC 3
5	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	+	·	·	·	·	|	+	+	+	|	+	+	+	+	+	+	+	+	AMD 4
2	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	|	+	·	·	·	|	+	+	+	+	|	+	+	+	+	+	+	+	+	ANU 3
5	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	|	·	+	|	·	+	,	·	+	+	+	+	|	+	+	+	+	+	+	+	+	ALB 3
0	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	+	+	·	|	·	|	+	+	|	·	+	+	+	+	+	|	+	+	+	+	+	+	+	+	AGL 2
4	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	|	·	+	·	·	+	·	·	·	+	|	+	+	+	|	+	+	+	+	+	+	+	+	AGD 6
5	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	+	·	+	+	|	+	·	·	·	+	+	+	+	+	|	+	+	+	+	+	+	+	+	AGH 3
4	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	+	+	·	+	·	+	|	·	·	·	+	+	+	+	+	|	+	+	+	+	+	+	+	+	AGK 2
9	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	+	·	·	|	|	+	·	·	·	+	+	+	+	+	|	+	+	+	+	+	+	+	+	AGI 2
9	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	+	·	·	+	·	·	|	+	+	+	|	+	+	+	+	+	+	+	+	AFO 5
8	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	+	|	·	+	|	+	·	+	+	+	|	+	+	+	+	+	+	+	+	ADH 1
7	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	|	·	+	·	·	·	+	+	+	|	+	|	+	+	+	+	+	+	AFR 4
9	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	+	·	+	·	+	|	+	+	+	|	+	|	+	+	+	+	+	+	AFS 6
0	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	·	+	·	+	·	+	+	+	+	+	|	+	+	+	+	+	+	+	+	AFT 3
8	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	·	·	|	·	·	+	·	+	·	+	+	+	+	+	|	+	|	+	+	+	+	+	+	AFU 4
9	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	|	|	·	+	·	|	·	|	|	+	+	+	|	+	|	+	+	+	+	+	|	AGC 6
7	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	|	|	·	|	·	+	|	+	+	+	|	+	+	+	+	+	+	+	+	BAX 2
9	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	+	·	+	·	|	+	+	+	+	|	+	|	+	+	+	+	+	+	AFX 1
2	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	|	|	·	·	|	|	·	+	·	+	·	|	+	+	+	+	|	+	+	+	+	+	+	+	+	AFH 5
5	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	+	·	·	+	·	·	|	·	+	·	+	+	+	+	+	·	+	|	+	+	+	+	+	+	AFM 5
1	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	+	+	·	+	·	|	|	+	+	+	|	+	+	+	+	+	+	+	+	AFN 2
7	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	·	·	|	·	·	|	|	+	·	|	+	+	+	+	|	+	+	+	+	+	+	+	+	AFK 4
7	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	+	·	·	+	|	|	+	|	+	·	+	|	+	+	+	|	|	|	+	+	+	+	+	+	AFL 2
1	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	·	·	|	|	+	|	·	+	·	|	+	+	+	+	|	+	+	+	+	+	+	+	+	AHN 6
9	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	|	·	|	·	+	·	+	|	+	+	+	|	+	+	+	+	+	+	+	+	AHO 5
31	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	+	·	·	·	·	|	·	·	+	+	·	|	+	+	+	|	+	+	+	+	+	+	+	+	AHF 5
5	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	+	·	·	|	·	·	|	+	+	·	+	+	+	+	+	|	+	+	+	+	+	+	+	+	AFC 4
13	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	·	·	·	·	·	+	|	+	·	+	|	+	+	+	·	+	|	+	+	+	+	+	+	AFB 6
25	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	|	·	·	|	|	·	·	|	+	+	|	|	+	+	+	|	+	+	+	+	+	+	+	+	AEX 2
14	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	·	·	|	·	·	|	+	+	|	|	+	+	+	+	|	|	+	+	+	+	+	+	+	AEU 3
30	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	|	·	·	|	|	·	·	|	+	+	+	+	+	+	+	·	+	|	+	+	+	+	+	+	AFA 3
22	·	·	·	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	·	·	+	·	|	·	+	+	+	|	+	+	+	+	+	+	+	+	APP 1
20	·	·	·	·	|	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	·	+	·	·	|	+	·	+	+	+	|	+	+	+	+	+	+	+	+	BAF 1
12	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	|	·	·	·	·	+	·	·	·	+	|	+	+	+	|	+	+	+	+	+	+	+	+	AHS 1
20	·	·	·	·	|	·	·	·	·	·	·	·	·	+	+	·	·	·	+	·	·	·	|	·	·	·	·	|	|	+	+	+	|	+	+	+	+	+	+	+	+	BAA 2
14	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	·	·	·	+	·	·	·	|	|	+	+	+	·	+	+	+	+	+	+	+	+	AXR 6
16	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	|	+	·	·	·	·	+	·	·	·	+	|	+	+	+	|	+	+	+	+	+	+	+	+	AXP 1
20	·	·	·	·	+	·	·	·	·	·	·	·	·	+	+	·	·	·	+	·	·	·	·	·	·	·	·	|	+	+	+	+	|	+	+	+	+	+	+	+	+	AXU 3
54	|	|	|	|	·	·	·	·	·	·	·	·	·	+	+	·	·	+	·	|	|	|	·	|	+	+	|	+	|	+	+	·	|	|	+	+	+	+	|	+	+	AOD 1
E	41	40	39	38	37	36	35	34	33	32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1	

starting-spot area, different diffusion in layer, difficulties in consistent definition of spot outline, etc. The calculations recommended by NYBOM (1966, 1967) are hardly applicable to non-identified compounds.

The rough estimation of intensity used in the present work may be less misleading and is far simpler to perform (cf. BREHM & OWNBEY 1965).

The scale 0, 2, 3 used can be subjected to discussion but has the desirable effect that the numerical values reflect firstly the presence or absence of a spot but also to some extent its intensity. The distance (squared as it will be in the analysis of variance) between 0 and 2 is 4 units, between 0 and 3 9 units but between 2 and 3 only 1 unit. Variation in intensity of a spot (and in all likelihood in amount of the compound responsible) is registered but not very heavily weighted. Variation between absent and weak spot, being somewhat uncertain in the vicinity of the perception threshold, is given an intermediate weight, and variation between absent and strong spot is given a considerable weight. This quantitative estimate is of course limited to comparisons comprising one spot at a time, the same intensity of two different spots not necessarily indicating the same amounts of substances.

One objection to the use of statistics at all is the risk of a non-random choice of collections to be included in the Tables 7—14. The importance of using material collected at random for statistical treatment has been pointed out by several authors. In the present material the intensity of sampling has of course been much greater within the mainly studied region in North-west Europe than in other parts of the distribution areas of the taxa concerned. However, within Fennoscandia and Denmark the density of collections is probably roughly proportional to the abundance of the taxa. From other parts of the areas the material is so scanty that it will not have any great influence on the values as a whole.

The use of non-identified spots in statistics can be dangerous. One and the same glycoside can give rise to a group of spots due to unintentional hydrolysis or other decomposition (cf. ALSTON 1965 p. 273). Also in cases when the occurrence of more than one glycoside with the same aglycone is no artifact, it contributes excessively to the biochemical distance or any other index and should not in this respect be given equal weight as more fundamental characters.

FAHSELT and OWNBEY (1968) found by means of gradual hydrolysis and rechromatography that different glycosides in *Dicentra* can be included in a decomposition chain ending with the same aglycone.

GRANT and ZANDSTRA (1968) obtained matching coefficients, based upon non-identified and non-hydrolyzed compounds from some *Lotus* species run on silica gel, conflicting with the results of HARNEY and GRANT (1964) using identified hydrolyzed compounds of the same species run on paper. Both results conflict also with the coefficients of similarity or paired affinity indices calculated from both hydrolyzed and non-hydrolyzed compounds from the species concerned run on paper (HARNEY & GRANT 1965). Whether the inconsistency is due to choice of specimens, layer, type of compounds, numerical treatment or some other factors is difficult to elucidate.

A study of the variation in each glycoside is, however, defensible in the estimate of deviations as used in the present work. The co-occurrence of

Table 10. Regional study. *Hierochloë odorata* 2n=56. *incl.

	Trs		STrd		Hdm	Opl	TL						LL	Nb	Jmt	Mpd		Hrj	Dlr											
	AUA 5	ATU 2	ARI 4	ARH 1	ARB 3	ARF 3	ACO 2	AAR 1	BBF 5	ABF 2	ATP 2	ABC 4	ANC 5	ATR 1	AMB 4	ANN 1	ANM 6	ACX 3	ALM 4	ALL 1	ALK 1	ALI 6	ALH 4	ALG 3	ALF 5	ALE 3	AGO 1	AGN 2	AGM 2	ALD 2
1	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+
3	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	−	−	+	+	+	+	+	+	+	+	+	+
4	+	−	+	−	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+
5	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+
6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
7	+	+	+	−	−	·	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	·
8	−	+	+	+	·	+	+	−	−	+	−	+	+	+	−	+	+	−	−	+	+	+	+	−	+	+	+	−	−	−
9	+	−	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+
10	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−
11	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+
12	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
13	+	−	−	−	+	+	−	+	+	−	·	+	+	−	−	−	+	+	+	−	+	+	+	+	+	−	−	+	−	−
14	+	·	−	+	·	−	−	+	·	+	−	+	+	+	·	−	·	·	−	+	+	+	·	+	·	−	−	·	·	−
15	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+
16	−	+	+	−	+	+	+	+	+	+	·	+	+	+	+	+	+	+	+	−	+	·	+	+	+	+	·	+	+	+
17	+	+	+	−	+	−	·	+	+	−	+	+	+	−	+	+	+	+	+	+	−	−	+	+	+	+	−	+	−	+
18	−	·	·	·	·	·	−	−	·	−	+	·	−	+	·	·	·	·	+	−	+	+	·	·	·	+	+	·	·	·
19	·	+	+	+	+	+	+	·	+	+	·	·	·	·	·	·	·	−	+	+	·	·	·	·	+	·	·	+	·	·
20	−	−	·	·	·	−	·	·	−	+	·	+	−	·	·	−	−	−	·	−	·	·	·	−	·	·	·	−	·	·
21	·	·	−	·	+	·	+	·	·	·	·	·	·	+	·	+	·	·	−	·	·	·	+	·	−	−	−	−	+	+
22	·	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
23	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
24	·	·	·	·	·	·	·	−	·	·	·	+	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	·	·	·
25	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
26	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·
27	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−
28	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	−	+	+	+	+	+	+
29	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	−	+	·	·	·	·	·	+	·	+	+	+	+	+	+
30	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	+	+	+	+	+	·
31	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	+	+	+	+	+	+
32	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	+	+	+	+	+	+
33	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	+	+	+	+	+	+
34	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	+	·	+	+	+	+	+	+
35	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
36	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
37	·	·	−	−	−	−	−	−	·	−	−	−	·	·	·	·	·	·	·	−	·	−	−	·	·	·	+	·	·	−
38	+	+	+	+	+	+	·	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
39	+	+	+	+	+	+	·	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
40	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
41	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
*E***	19	13	8	12	23	17	30	13	15	14	24	20	10	15	13	10	12	11	20	11	14	20	13	10	13	11	24	13	14	19
*E**	23	17	12	16	52	21	34	17	19	17	28	24	14	18	17	39	11	15	24	14	17	23	42	14	42	40	53	42	43	43

29—34; **excl. 29—34. — Regional subdivision cf. p. 233.

		Vrm	Upl		Nrk	Vg	Li		Le	Lk	Ob	Ok	Ta			Sa				Nyl		Canada	USA	
AGR 4	AGP 3	AGS 2	ALA 2	AKU 1	AHM 2	AHI 2	AUK 1	AUL 1	ATN 3	AUM 1	AUS 2	AUT 3	BAC 1	BAE 2	ADK 4	AHR 1	AXG 2	AXH 4	AXK 6	AXN 2	AXO 1	ADF 1	AKE 3	
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	1
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	2
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	3
+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	4
+	+	+	+	+	−	+	+	+	+	+	+	−	+	+	+	+	+	+	+	−	+	+	+	5
+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	6
+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	·	+	+	+	+	−	+	−	7
−	+	·	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	8
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	−	9
+	+	+	·	·	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	10
+	+	+	+	−	+	−	+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	11
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	12
+	+	−	−	−	+	−	+	+	−	+	−	+	−	−	+	−	+	+	+	+	+	−	·	13
·	−	·	·	·	·	−	+	+	+	+	+	+	·	+	+	+	·	−	+	+	·	−	+	14
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	15
+	+	+	+	−	+	+	−	+	+	+	+	+	·	+	+	+	+	+	+	+	+	−	−	16
+	+	−	−	−	+	−	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	·	·	17
·	·	−	·	+	·	·	−	·	+	·	·	·	·	+	−	−	·	·	−	−	·	·	+	18
+	+	·	·	·	·	·	+	−	·	−	+	·	·	−	+	·	+	+	·	·	·	·	−	19
−	−	·	·	·	·	·	·	−	−	−	+	·	−	·	·	−	−	−	+	−	+	−	−	20
·	−	+	−	+	+	−	−	−	·	−	−	·	·	+	+	·	·	−	−	+	+	·	−	21
+	+	+	+	+	−	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	22
·	·	+	−	·	+	+	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	23
·	−	·	·	·	·	·	·	·	·	·	·	·	·	·	−	·	·	·	·	·	·	·	·	24
·	·	·	·	−	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	−	25
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	−	26
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	27
+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	28
·	·	+	+	+	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	29
·	·	+	+	−	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	30
·	·	+	·	+	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	31
·	·	+	·	+	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	32
·	·	+	·	+	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	+	33
·	·	+	·	+	+	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	+	34
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	35
·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	36
·	−	−	−	+	−	−	·	−	+	+	−	−	−	−	−	·	·	−	−	−	+	·	·	37
+	+	+	·	+	+	+	+	+	+	+	+	+	+	·	·	+	·	·	·	·	·	·	+	38
+	+	+	+	+	+	+	+	+	+	+	+	+	+	·	·	+	·	·	·	·	·	·	+	39
+	+	+	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	·	+	·	·	+	40
+	+	+	+	+	−	+	+	+	+	+	+	+	+	−	·	+	·	+	·	+	+	·	+	41
14	11	27	27	31	21	15	11	7	14	9	12	10	18	26	35	18	41	21	38	22	37	64	60	*E***
18	15	56	40	56	50	18	15	11	18	13	16	14	47	29	38	22	45	24	42	26	41	68	72	*E**

Table 11.

	A	B	
1	−	+	1
2	+	+	2
3	+	+	3
4	·	·	4
5	+	+	5
6	·	·	6
7	−	−	7
8	−	·	8
9	+	+	9
10	+	+	10
11	+	+	11
12	−	−	12
13	−	−	13
14	+	−	14
15	·	+	15
16	·	·	16
17	·	·	17
18	+	−	18
19	·	·	19
20	·	·	20
21	·	−	21
22	·	·	22
23	−	+	23
24	·	·	24
25	·	·	25
26	·	·	26
27	−	−	27
28	·	·	28
29	·	·	29
30	·	·	30
31	·	·	31
32	·	·	32
33	·	·	33
34	−	−	34
35	·	·	35
36	·	·	36
37	·	·	37
38	·	·	38
39	·	·	39
40	·	·	40
41	·	·	41
42	+	+	42
43	+	+	43
44	+	−	44
45	+	+	45
46	−	+	46
47	+	+	47
48	+	−	48
49	+	−	49

Table 12.

	C	D	E	
1	+	+	+	1
2	+	−	·	2
3	+	+	+	3
4	+	·	+	4
5	·	+	+	5
6	+	·	·	6
7	−	·	−	7
8	+	+	+	8
9	+	+	+	9
10	+	+	−	10
11	·	·	·	11
12	·	·	+	12
13	−	+	+	13
14	+	+	+	14
15	·	·	·	15
16	·	·	·	16
17	·	·	·	17
18	·	·	·	18
19	·	·	·	19
20	−	−	−	20
21	·	·	·	21
22	+	−	+	22
23	·	·	·	23
24	·	·	·	24
25	·	·	·	25
26	·	·	·	26
27	·	·	·	27
28	·	·	·	28
29	·	·	·	29
30	·	·	·	30
31	·	·	·	31
32	·	·	·	32
33	·	·	·	33
34	·	·	·	34
35	·	·	·	35
36	·	·	·	36
37	·	·	·	37
38	·	·	·	38
39	·	·	·	39
40	·	·	·	40
41	·	·	·	41
42	·	·	·	42
43	·	·	·	43
44	·	·	·	44
45	+	·	−	45
46	−	−	+	46
47	+	+	+	47
48	+	+	+	48
49	+	+	+	49
50	−	·	·	50
51	−	·	−	51
52	·	·	·	52

Table 13.

	B D R 3 Le	B D R 11	B G D Green-	B G K land	
1	+	−	−	−	1
2	·	−	+	+	2
3	+	·	+	+	3
4	−	+	−	−	4
5	+	+	+	+	5
6	·	·	·	·	6
7	−	+	·	·	7
8	+	−	+	+	8
9	+	+	−	−	9
10	+	−	+	+	10
11	·	−	+	+	11
12	+	+	+	+	12
13	·	−	+	−	13
14	−	−	−	·	14
15	·	+	·	−	15
16	·	−	−	·	16
17	·	+	−	·	17
18	·	·	·	·	18
19	·	·	·	·	19
20	−	+	−	−	20
21	·	·	·	·	21
22	·	·	−	−	22
23	·	·	·	−	23
24	·	·	·	·	24
25	·	·	·	·	25
26	·	·	·	·	26
27	·	·	·	·	27
28	·	·	·	·	28
29	·	·	·	·	29
30	·	·	·	·	30
31	·	·	·	·	31
32	·	·	·	·	32
33	·	·	·	·	33
34	·	·	·	·	34
35	·	·	·	·	35
36	·	·	·	·	36
37	·	·	·	·	37
38	·	·	·	·	38
39	·	·	·	·	39
40	·	·	·	·	40
41	·	·	·	·	41
42	·	·	·	·	42
43	·	·	·	·	43
44	·	·	·	·	44
45	·	·	·	·	45
46	·	·	·	·	46
47	+	−	+	+	47
48	+	−	−	−	48
49	+	−	+	+	49
50	−	−	+	+	50
51	+	·	−	−	51
52	·	−	−	·	52
53	·	−	+	−	53

Table 14.

	B F P Green-	B F B land	A K F	A K H USA	A K O	
1	+	+	+	+	−	1
2	+	+	+	+	+	2
3	+	+	+	+	+	3
4	+	+	+	−	+	4
5	+	+	+	+	+	5
6	−	+	+	+	+	6
7	+	+	+	+	+	7
8	+	+	−	−	−	8
9	−	+	−	−	−	9
10	+	+	−	−	−	10
11	+	+	+	+	+	11
12	+	+	+	+	+	12
13	−	+	·	−	·	13
14	−	+	−	−	−	14
15	+	+	+	+	+	15
16	·	·	·	·	·	16
17	·	·	−	−	−	17
18	·	·	−	+	−	18
19	·	−	·	·	·	19
20	−	−	−	−	−	20
21	·	+	·	·	−	21
22	−	+	−	·	−	22
23	·	−	+	·	·	23
24	·	·	·	·	·	24
25	·	·	·	·	·	25
26	·	·	·	·	·	26
27	·	·	·	·	·	27
28	·	·	·	·	·	28
29	·	·	·	·	·	29
30	·	·	·	·	·	30
31	·	·	·	·	·	31
32	·	·	·	·	·	32
33	·	·	·	·	·	33
34	·	·	·	·	·	34
35	·	·	·	·	·	35
36	·	·	·	·	·	36
37	·	·	·	·	·	37
38	·	·	·	·	·	38
39	·	·	·	·	·	39
40	·	·	·	·	·	40
41	·	·	·	·	·	41
42	·	·	·	·	·	42
43	·	·	·	·	·	43
44	·	·	·	·	·	44
45	·	·	·	·	·	45
46	·	·	·	·	·	46
47	+	+	+	+	+	47
48	+	+	+	+	+	48
49	+	+	+	−	+	49
50	−	+	−	−	−	50
51	·	·	−	·	−	51
52	·	·	−	−	−	52

spots mostly affects the calculations within one taxon at a time only to a minor extent. The reverse is true in *H. odorata* 2n=56, where the group 29—34 considerably raises the deviation.

The correlation coefficients calculated between spots (Figs. 3—4) can give some indications as to whether the groupings observed are likely to be due to a mere chemical dependency upon each other. The association between spots occurring in all plants of a given taxon (not necessarily the same spots in different taxa) are difficult to elucidate since no variation occurs. For the same reason they do not, however, add to the *E* values. The groups of spots with highly significant positive correlation to each other can be explained in two ways. Firstly, such spots may be suspected to have a common biogenetical background or even to be at least partly artifacts. Secondly, compounds thus correlated may be in themselves independent of each other but reveal different gene combinations prevailing in different taxa and in different parts of the distribution areas.

Where strong correlations occur in one taxon but not in others, a common chemical background is not likely. The spots 27—28 and 38—41 (and possibly some of the spots 29—34) may then be the only correlated groups to be suspected of having a common chemical background, the other positive correlations as well as the negative ones being most likely to have other causes. These coefficients thus may demonstrate certain relative differences in gene content and have some value in this respect.

Due to the great number of possible comparisons, however, some correlations can be expected to be due to chance, $p < 0.001$ and $0.001 < p < 0.01$ for the two levels of significance illustrated in Figs. 3—4, respectively.

Because of the fact that deviations in all spots are added together the *E* value obtained must be influenced by the number of spots present in the different taxa. I do not find this effect solely undesirable. However, for the sake of comparison I have given *E* values in Table 10 (*H. odorata* 2n=56) also with the spots 29—34 disregarded because of the great effect of the group.

3. The degree of repeatability and consistency of results has been estimated.

Thin-layer chromatography, being a fairly rough method as applied here, has of course inherent sources of error. Extraction cannot be presumed to

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Table 11. Regional study. *Hierochloë occidentalis.* — A: Calif., Samuel Taylor State Park 8.4. 1954 L. S. ROSE (LD). — B: Calif., Lagunitas Creek 11.1. 1949 C. SKOTTSBERG (S).

Table 12. Regional study. *Hierochloë pauciflora.* — C: Canada, Franklin Distr., Spence Bay 8.7. 1951 J. G. CHILLCOTT No. 31 (S). — D: Novaja Semlja, Matotschin Schar 25.7. 1911 T. HWASS (S). — E: Kamchatka austr., Bolshaja Reka, 7. 1921 E. HULTÉN No. 1951 (S).

Table 13. Regional study. *Hierochloë alpina.* — Regional subdivision cf. p. 233.

Table 14. Regional study. *Hierochloë monticola.*

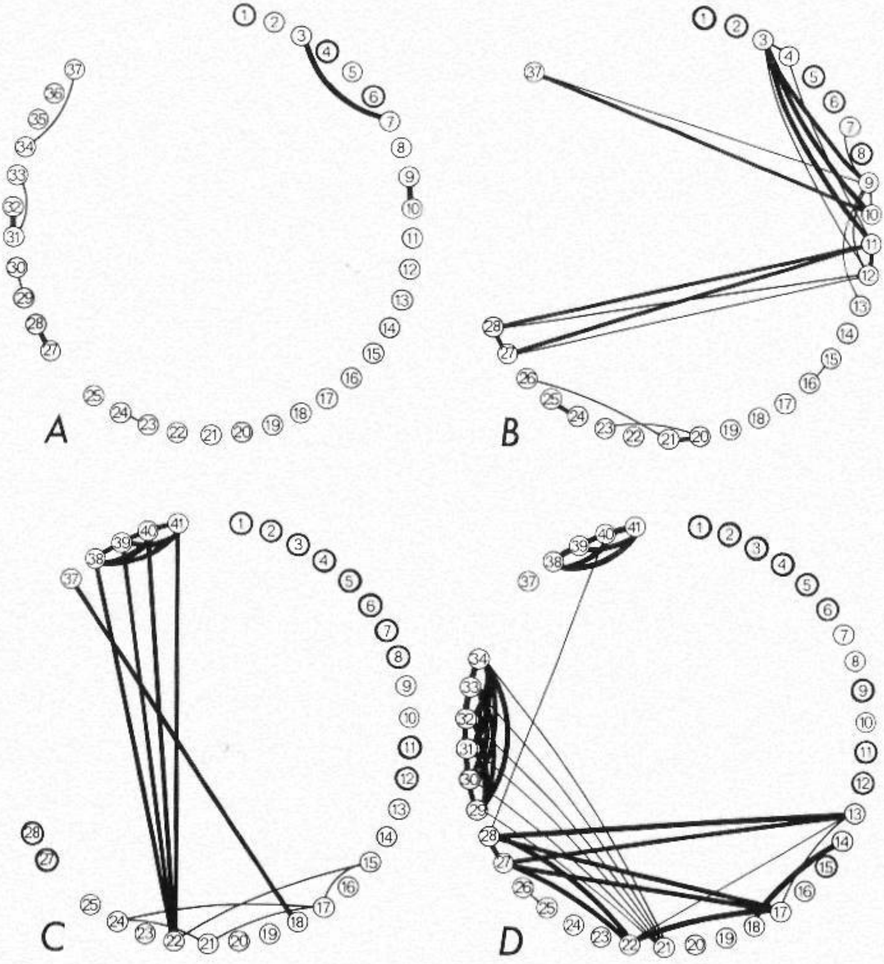

Fig. 3. Significant positive correlations between spots. Broad lines: $p < 0.001$; narrow lines: $0.001 < p < 0.01$. Spots occurring at 100 % are marked with heavy circles. — *A: Hierochloë australis.* — *B: H. odorata* 2n=28. — *C: H. odorata* 2n=42. — *D: H. odorata* 2n=56.

be absolutely uniform. The total weight of a sample is to a varying extent dependent on the content of mechanical tissue, in its turn rather inversely proportionate to the content of the studied compounds. The same extract run on two different plates can under certain conditions give a different number of spots due to varying layer, separating media, temperature, spraying with reagents etc. Such errors could sometimes be observed during the work with plates in duplicate from the same extract. Since the tables were made up from more than one plate, the occasional dropping out of a spot on a single plate has no deteriorating effect. The effect of other errors cannot be separately

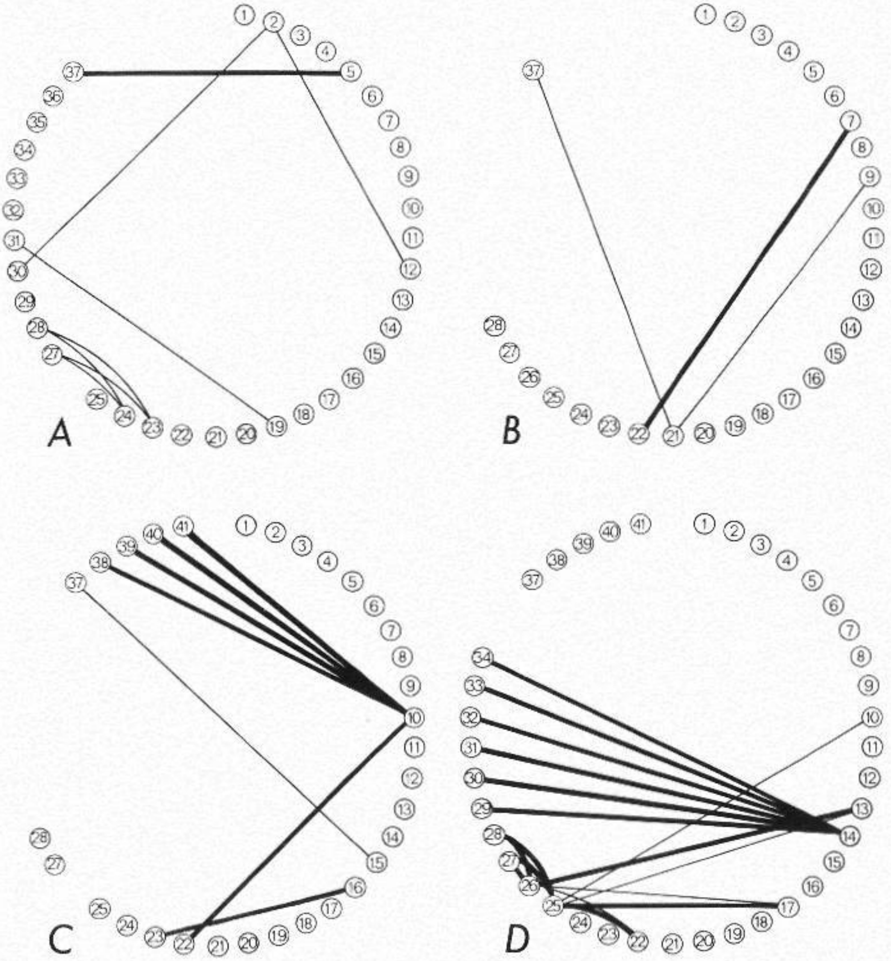

Fig. 4. Significant negative correlations between spots. Broad lines: $p < 0.001$; narrow lines: $0.001 < p < 0.01$. — *A—D* as in Fig. 3.

calculated from the present material but forms part of $E_{\text{other sources}}$. Thus their magnitude together with chance is estimated (in this material usually not amounting to 15 units), and conclusions should not be drawn from results below or too close to it.

It is perhaps somewhat risky to infer the estimate of chance and other sources of deviation from *H. odorata*, where it was possible to calculate (Tables 3 B—F, 5 B—C), to biologically different materials, i.e. the other taxa treated. Although we do not know about possible differences between taxa in reaction on habitat, I find the estimate valuable if used with caution as an approximate rating of experimental errors etc.

4. The modifying effect upon patterns is great as to season and treatment during cultivation. However, the spot combinations considered as diagnostic in most cases still permit determination of the material, experience of the modifications taken into consideration. Differences between the sampling and storing techniques are usually not very great but should be taken into account.

I have in this matter only intended a purely practical investigation in direct connexion with cultivation conditions of interest in taxonomic work. As to physiological aspects on phenolic biosynthesis see e.g. SIEGELMAN (1964) for survey and references.

Thorough experiments are described for *Spirodela* by MCCLURE and ALSTON (1964), who found fairly small modifications in an exhaustive test series under artificial conditions. BALL, BEAL and FLECKER (1967), however, found the obtained variation in a similar test with *Spirodela* to be more considerable. Most other authors touching the problems have found differences due to sampling season, plant age, growth condition, etc. (e.g., SCHWARZE 1959, YAP & REICHARDT 1964, BRAGG & MCMILLAN 1966, FREDRIKSSON 1967, POLLOCK et al. 1967, and LAROI & DUGLE 1968). No or very small differences have been reported by e.g. BÖRTITZ (1962, 1963), GRANT and WHETTER (1966), and THIELGES (1969). See also TÉTÉNYI (1970 pp. 26—34) for references concerning variation in various compounds found in medicinal plants.

If in Tables 3 B—H and 5 B—C an F-test of the different sources is performed with the degrees of freedom given in the tables, the only E values significantly larger than $E_{\text{other sources}}$ at the 5 % level are time in Table 3 B and time and treatment in Table 5 B—C. However, in these calculations no regard has been taken of the fact that the values for a large number of spots, which are to a large extent independent of each other, have been summed. Thus the number of degrees of freedom and the level of significance in the test are far too low. On the contrary, the individual intensity values do not follow the normal distribution required in an F-test, but normality is approached through the summing of independent spots.

Fairly little seems to be known about the importance of sampling and storing technique when studying non-hydrolyzed leaf phenolics. Some authors report no or negligible differences between heat dried, conventionally newly dried and old herbarium material, e.g. BÖRTITZ (1963), SMITH and LEVIN (1963), HORNE (1964), TORRES and LEVIN (1964), GRANT and WHETTER (1966), FREDRIKSSON (1967), HARBORNE (1967), LAROI and DUGLE (1968), and ARDITTI (1969).

Of course it is of interest to choose the sampling method giving the least difference compared to herbarium material, thus widening the applicability and versatility of the method. Since the present material concerning sampling and storing techniques is fairly small and the values are inconsistent, nothing in this way can be judged from it with certainty. The results indicate, however, that a possible influence of different methods should always be taken into account.

5. An obvious heterogeneity within collections has been found in *H. australis* and *H. alpina*. Sample tests have not indicated such a heterogeneity within collections in any of the *H. odorata* cytotypes.

H. australis and *H. alpina* grow in tufts. Although material studied by me has shown an apomictic tendency (WEIMARCK 1967 a and unpubl.), the tufts growing on the same locality obviously can be genotypically different, thus not being members of a clone. Since the external conditions in this experiment were the same for all plants, the differences surely have a genetical basis.

In spite of the fact that I found sexual seed-setting in *H. odorata* 2n=28, I regarded the samples studied as facultative apomicts because of the bad seed germination ability and the long creeping rhizomes forming clones (WEIMARCK 1967 a p. 230). The assumption is corroborated by the present facts giving no evidence of the genotypical variation to be expected in a cross-breeding population but indicating clonal propagation within a locality. Since the flowers are protogynous and chasmogamous, autogamy is no plausible explanation of the homogeneity in the characters studied.

The obligate or almost obligate apomixis in *H. odorata* 2n=42 and 2n=56 (WEIMARCK 1967 a) is also confirmed by the chromatographic results.

Cases of intrapopulational variation have been reported by e.g. ELLISON, ALSTON and TURNER (1962), BRUNSBERG (1965), FRÖST (1966), and FREDRIKSSON (1967).

6. The *E* value between collections of *H. australis* enters the one within collections discussed above. *H. odorata* 2n=28 and to a still greater extent *H. odorata* 2n=42 are more uniform, only some collections deviating considerably from the main part. Most of the *H. odorata* 2n=56 material also contains rather moderate differences if spots 29—34 are disregarded, but this spot group causes a considerable rise in variance.

Variation in diagnostic spots is separately discussed under 7.

Variation within taxa in chromatographically obtained characters are reported by e.g. LORENZ and SCHULTZ-SCHAEFFER (1964), TORRES and LEVIN (1964), BREHM and OWNBEY (1965), BRUNSBERG (1965), BRAGG and MCMILLAN (1966), MCCLURE and ALSTON (1966), BJÖRKQVIST (1968), ISING and FRÖST (1969), and THIELGES (1969). HARNEY and GRANT (1963, 1964) and YAP and REICHARDT (1964) did, however, not find such a variation.

References concerning infraspecific variation in flavonoid contents of medicinal plants are listed by TÉTÉNYI (1970 pp. 159—164).

I do not find it justifiable at the present time to give the two *H. odorata* 2n=56 spot pattern types the name of "chemical races" or any taxonomic rank (cf., e.g., BREHM & ALSTON 1964). In the present study concerning non-identified substances I find the information too imperfect in this respect. The same is valid for *H. odorata* 2n=28, respectively having and lacking the spot group 27—28. Since, however, some correlation seems to exist between certain morphological features and spot patterns in *H. odorata* 2n=56, the problem will be dealt with also in a later paper.

7. Most of the taxa can be distinguished with good certainty on key spot combinations. Exceptions are *H. odorata* 2n=28 versus 2n=42 and *H. alpina* versus *H. monticola*. The specificity of patterns in the rest of the material is however — at least seemingly so — not absolute.

Probably the spots have very different interest from a taxonomic point of view due to their chemical nature and the chains of synthesis responsible for their occurrence. Before the nature of the compounds are known, the taxonomic bearing of spots must be judged more or less subjectively. The grouping of spots in the tables represents an attempt to demonstrate their diagnostic value. This can easily be estimated by comparing the freq. percentages found in different taxa for a key spot. Hereby the different number of collections of taxa compared must be taken into account. One also has to be aware of the possibility that a whole group of spots may be the result of a difference in only one gene, e.g. responsible for a certain aglycone or a certain type of glycosylation.

H. odorata 2n=28 and 2n=42 are morphologically similar, whilst the 2n=56 cytotype is well distinguishable at least in Northern Europe (WEIMARCK unpubl.). The great pattern affinities between the 2n=28 and 2n=42 cytotypes suggest together with other yet unpublished facts that the latter may be an autopolyploid derivative of the former. Also BRUNSBERG (1965) found no consistent chromatographic differences between *Lathyrus pratensis* 2n=14, 21, 28 or 42.

The only absolute difference found between *H. alpina* and *H. monticola* is in spot 6, which in respect to the small material is of restricted significance. The taxa are evidently also very closely related according to other criteria (cf. SØRENSEN 1954 and WEIMARCK unpubl.).

Taxon-specific chromatographic patterns can of course be of great value when scrutinizing critical taxa, because they afford additive characters to morphological and others. The possibility of using herbarium material is especially of interest in this respect. In *Hierochloë* flowering is sometimes poor, and chromatography could perhaps be tempting as a way to determine nonreproductive material. More direct practical use of chromatographic patterns is made by FREDRIKSSON (1967), analyzing the composition of *Festuca* seed parcels. In the last-mentioned case chromatography seems to be the only method possible in practice.

Single plants have, however, turned out to lack diagnostic spots or have spots diagnostic to another taxon than that they are referred to. Octoploid *H. odorata* plants lacking the groups 29—34 and 38—41 (A X K 6, A D F 1) can with certainty be distinguished neither from tetraploid or hexaploid *H. odorata* nor from *H. australis* lacking both of the spots 35 and 36 (B A D 2, A P R 4). The hexaploid *H. odorata* plant A O D 1 would be believed to be octoploid because of the spot group 38—41.

It is by no means self-evident that, within a taxon traditionally treated as a species, plants with the same chromosome number form a phyletic unit. The unbalanced apomictic mechanism found in *Hierochloë* gives good possibilities for higher polyploids to arise from lower ones more than once. The hexaploids and octoploids within *H. odorata* may very well each consist of different evolutionary lines, some of them with affinities rather to other levels of polyploidy than to other lines on the same level.

The Swiss hexaploid *H. odorata* collection, the only strongly aberrant one in Table 9, and the two North American octoploid collections, also very deviating, may thus turn out to be wrongly placed together with other *H. odorata* material with the same chromosome numbers, respectively. Taxonomy and nomenclature of the whole complex are, however, to be treated in a later paper on the basis of these and other data.

In the present connexion the inherent danger in wide generalizations from a restricted material should be pointed out. Especially as to the widely spread *H. pauciflora* and *H. alpina* the studied material is disproportionately small.

In the present investigation I judge the information given on modification, variation within taxa, and method as at least equally interesting as that on differences between taxa. The method used also provides a means of explaining breeding systems and population structures in plants offering few other suitable characters.

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Studies on Mire Vegetation in the Archaean Area of South-Western Götaland (South Sweden)

IV. Benthic Algae and Their Distribution on the Åkhult Mire

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ABSTRACT

FLENSBURG, T. and MALMER, N.: Studies on Mire Vegetation in the Archaean Area of South-Western Götaland (South Sweden). IV. Benthic Algae and Their Distribution on the Åkhult Mire. — Bot. Notiser 123: 269—299, Lund.

This study complements two earlier mire investigations in central South Sweden, one on the macrophytic vegetation and its habitat conditions on the Åkhult mire (MALMER 1962 a) and one on the micro algae of the mire Store Mosse (FLENSBURG 1967). A list of the 225 taxa of micro algae (some of them new to South Sweden) recorded in 170 samples from the Åkhult mire is given together with short notes about their distribution on the mire.

There are only small differences in the flora of micro algae between the Åkhult mire and the Store Mosse. It is shown that the micro algae have the same general distribution pattern on the Åkhult mire as the macrophytes. No taxa confined only to bog areas have been found.

INTRODUCTION

In an earlier paper (MALMER 1962 a) one of the present authors has given a thorough description of the macrophytic vegetation (vascular plants, bryophytes and lichens) on the Åkhult mire (Central Småland, Fig. 1) together with a description of the habitat conditions, especially with reference to the water level conditions and the chemistry of peat and water. The present study on the benthic algae with special reference to the desmids and diatoms is intended to complete the picture of the vegetation given in the previous paper.

The other one of the present authors has performed a special study (FLENSBURG 1965, 1967) on desmids and other benthic algae including notes on the macrophytic vegetation in the extensive mire area Store

Mosse (Western Småland, Fig. 1). The localities investigated there covered a wide range of habitats. The present study completes this broad survey with more detailed investigations on the micro algae within a narrower range of habitats less well represented in the Store Mosse area. Especially the distribution of the species in relation to the hydrologic mineral soil water limit will be discussed here. — Further information about the benthic algae of the mires in the South Swedish upland have been given by e.g., THUNMARK (1942), DU RIETZ (1950 a, b) and FETZMANN (1961).

In this paper a list of the benthic algae recorded from the mire will be presented together with a survey of their distribution with reference to the vegetational gradients (cf. the chapter about the directions of variation in the vegetation in MALMER 1962 a pp. 44—47). The sociology and ecology will be more thoroughly discussed in a following paper.

The laboratory work as well as the nomenclature of the algae follows FLENSBURG 1967. Concerning macrophytic vegetation nomenclature references are given in MALMER 1962 a p. 20. Also in the terminology of the mires and the mire vegetation that paper is followed (MALMER 1962 a pp. 42—47, 86—139, MALMER 1965).

This investigation has been carried out at the Department of Plant Ecology, University of Lund. It has been made possible through grants from Statens Naturvetenskapliga Forskningsråd. The field work and the investigations on the habitat conditions have been done by MALMER. FLENSBURG is responsible for all the determinations of the algae and has written the section with the list of species. The general discussions have been written in cooperation. Technical assistance has been given by Mrs. INGRID ENGBERG, Miss HANNA LUNDBERG and Mrs. MIMMI VARGA.

INVESTIGATION AREA

The Åkhult mire is situated in Kronobergs county, about 40 km NNW the city of Växjö (cf. map Fig. 1). It represents a bog mire (DU RIETZ 1959, MALMER 1965), i.e., a mire complex mainly with bog areas. There are two main bog areas (cf. Fig. 2), viz., one large, eccentrically sloping (the Great Bog) and one smaller, rather concentrically sloping (the Small Bog). Along the northeastern margin there are fen areas both of the narrow lagg fen type and of a broader, much more extensive type. A further description is given in MALMER 1962 a pp. 52—60.

The investigations have been performed only within three special parts of the mire, all of them along the northeastern margin. In the

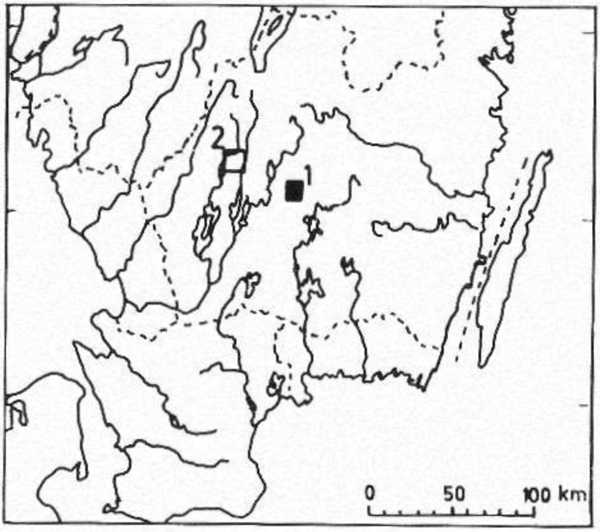

Fig. 1. Map of southern Sweden with the situation of the Åkhult mire (1) and the mire Store Mosse (2) indicated.

Lönnstorpet area in the northwestern part of the mire there is one narrow lagg fen area and one broad fen area. The Stattute area representing the central part of mire comprises a broad and extensive fen area together with adjacent parts of the Great Bog. The surface is rather even. There is no distinct difference in level between the fen and the bog. A number of small and shallow pools (the row of brook pools) divide the fen into two parts, viz., the Inner Fen adjacent to the mineral soil and the Outer Fen adjacent to the Great Bog. The row of brook pools represents a distinct water course which receives most of its water from the Lönnstorpet area. The Bygget area comprises the eastern part of the mire with a lagg fen and a fen soak together with the adjacent parts of the Small Bog. There is a considerable difference in level between the fen and bog areas.

The vegetation represents bog and poor fen vegetation in the sense of Du Rietz (1949, 1954; cf. Malmer 1965). With reference to the distribution of the macrophytic species, six groups of species may be distinguished and arranged along the poor — rich vegetation gradient (Malmer 1962 a pp. 76—79). One of these groups (the *Sphagnum plumulosum* group) regarded as the richest one comprises species as *Carex dioeca, C. tumidicarpa, Trichophorum alpinum, Campylium stellatum,* and *Sphagnum plumulosum.* These species occur only in the fens of the Lönnstorpet area and only in few individuals. The *Menyan-*

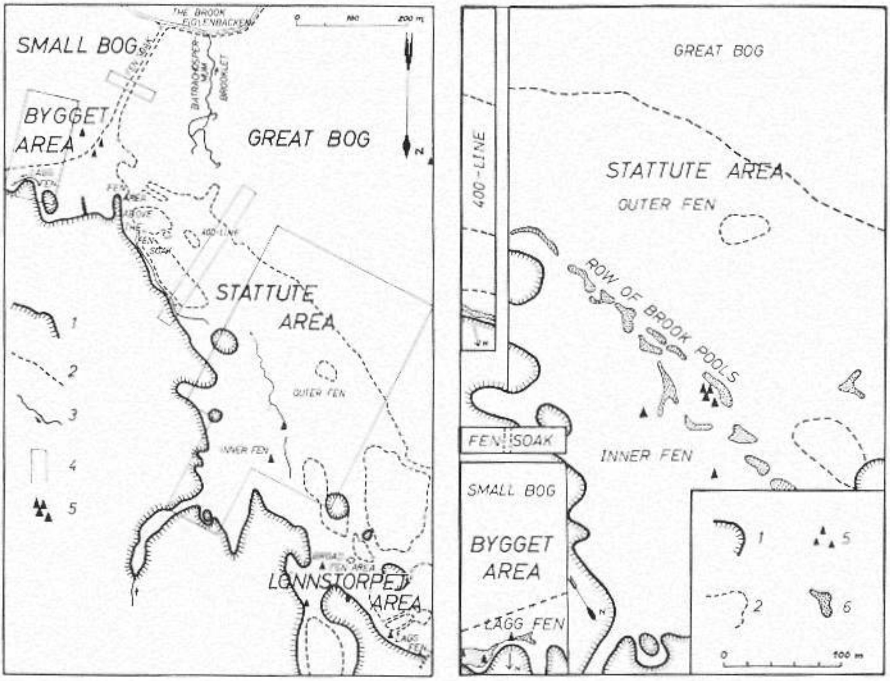

Fig. 2. Maps of the investigated area on the Åkhult mire. — 1. Border of the mineral soil. 2. The hydrologic border between fen and bog. 3. Brooklet. 4. Border of the special areas. 5. Great boulder stone. 6. Area with rather deep water (> 0.5 m). Further explanations in text. The right figure is used as a basic map for the Figs. 3, 5—14, and 16—23.

thes trifoliata group has a wider distribution and is much more common. They are encountered all over the fens of the Lönnstorpet and Bygget areas. In the Stattute area they occur in the Inner Fen and along the row of brook pools. To this group belong, e.g., *Menyanthes trifoliata, Utricularia intermedia, Carex lasiocarpa,* and *Sphagnum inundatum.* The *Eriophorum angustifolium* group comprises the species *Carex limosa, Eriophorum angustifolium, Scheuchzeria palustris, Sphagnum apiculatum,* and *S. pulchrum* among others. They are all common together with the species of the *Menyanthes trifoliata* group. In addition they occur in a broad area of the Outer Fen adjacent to the row of brook pools (the *Eriophorum angustifolium* zone in Fig. 3). Among the fen plants, the *Narthecium ossifragum* group (e.g., *Erica tetralix, Narthecium ossifragum, Carex pauciflora, Rhynchospora fusca,* and *Sphagnum auriculatum*) represents the most widespread ones. They

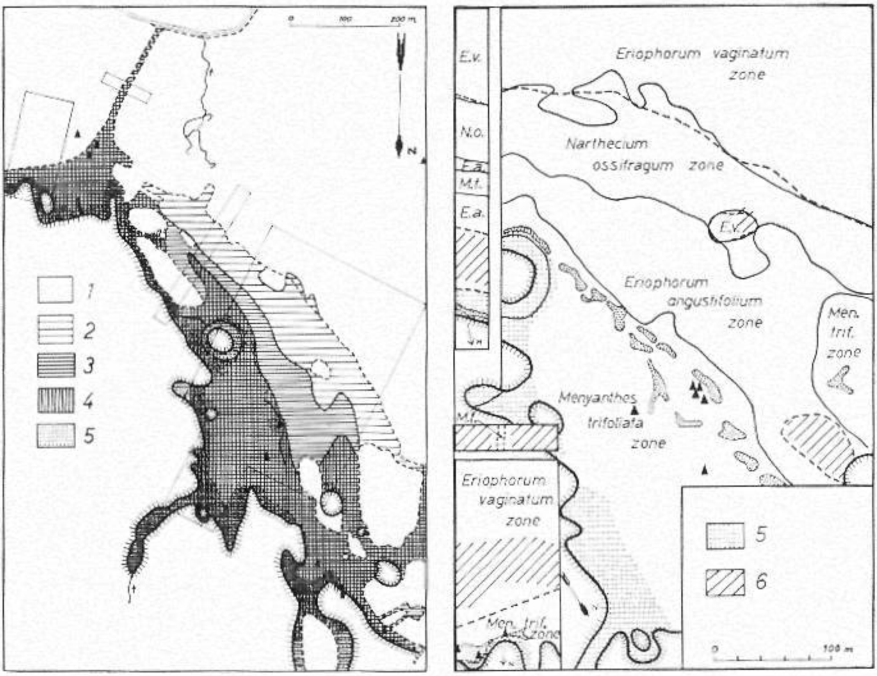

Fig. 3. To the left the distribution of the species groups among the macrophytes (except the *Sphagnum plumulosum* group) in the investigation area on the Åkhult mire. To the right the vegetation zones within the special areas. — 1. Only species of the *Eriophorum vaginatum* group. 2. This group together with the *Narthecium ossifragum* group. 3. These two groups together with the *Eriophorum angustifolium* group. 4. The distribution of the *Menyanthes trifoliata* group. 5. Mire margin vegetation. 6. Wooded bog area.

are found all over the fen areas with mire expanse vegetation. In the Outer Fen of the Stattute area they occur in the *Narthecium ossifragum* zone (Fig. 3) up to the hydrologic mineral soil water limit.

In the open bog plain areas of the Great Bog and the Small Bog (the main part of the *Eriophorum vaginatum* zone) two groups of macrophytic plant species occur. One comprises species as *Andromeda polifolia, Calluna vulgaris, Vaccinium oxycoccus, Drosera rotundifolia, Eriophorum vaginatum, Trichophorum caespitosum, Sphagnum magellanicum, S. rubellum, Cladopodiella fluitans,* and *Gymnocolea inflata,* which are rather evenly distributed all over the mire or at least over the mire expanse areas. *Drosera anglica, D. intermedia, Rhynchospora alba,* and *Sphagnum papillosum* may be referred to this group too, in spite of the fact that in this zone they occur only on the Great Bog and not on the Small Bog. The second group comprises only a few species. esp. *Sphagnum balticum*, *S. cuspidatum*, and *S. tenellum*, which occur only on the woodless bog plain areas and in the Outer Fen but not in the *Menyanthes trifoliata* zone.

This description demonstrates the gradual transition found in the macrophytic vegetation of the mire expanse type. The *Eriophorum vaginatum* zone of the bog areas represents one extreme, viz., the poorest one. The *Menyanthes trifoliata* zone and especially the Lönnstorpet area represents the other extreme, here designated the richest one. In the Outer Fen of the Stattute area there is a gradual transition over more than 100 m between these extremes, but in the lagg fens they are bordering along a sharp and distinct limit between bog and fen.

In this paper the distribution of the benthic micro algae will be studied with special reference to this poor—rich gradient. It is of great interest in this case that the hydrologic conditions are well known. The limit between bog and fen has been determined through hydrologic measurements and it has been shown that only precipitation water reaches the *Eriophorum vaginatum* zone of the bogs. In the *Narthecium ossifragum* and *Eriophorum angustifolium* zones there is only a restricted supply of mineral soil water. The *Menyanthes trifoliata* zone as well as most of the mire margin areas are supplied with much water from the surroundings while the precipitation water forms only a small part (cf. MALMER 1962 a pp. 160—166, 181—183).

THE BENTHIC MICRO ALGAE

The Samples

The samples were fixed in formalin shortly after the sampling and preserved until it was possible to work on them in 1968. Due to this treatment the investigation is restricted mainly to desmids, diatoms, and a few other groups. It has been necessary to leave the flagellates and similar groups for future investigations (cf. FETZMANN 1961).

All samples are from small and shallow pools in areas with a macrophytic vegetation of mire expanse type, i.e., from mud-bottoms with a vegetation of the *Sphagnum cuspidatum - inundatum* series (MALMER 1962 a pp. 86 ff.). Most of them treated in this investigation were taken in May and September 1954 at points where the water level was measured that year and where samples for chemical analyses of water and peat also were taken (cf. map Fig. 4). In addition there are supplementary samples from August 1949 and July 1952. From 1954 there are three samples from the Lönnstorpet area (two from the narrow lagg fen area and one from the broad fen area), 119 from the Stattute

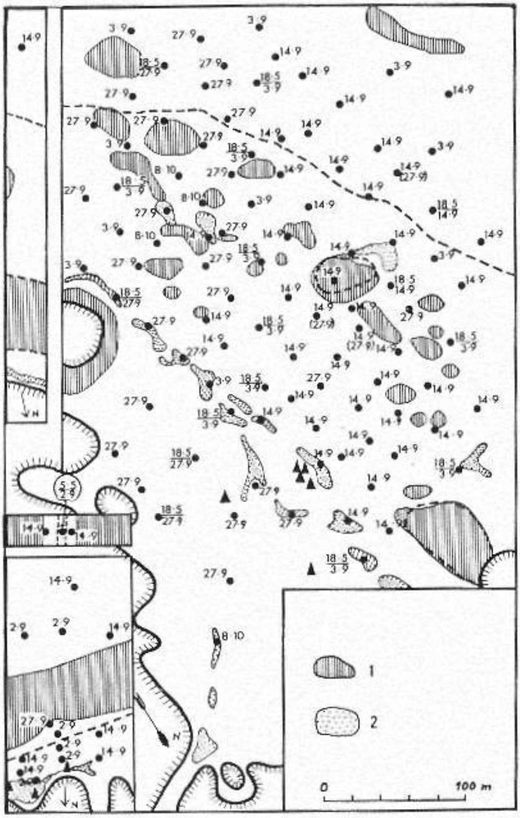

Fig. 4. The sampling points and date of sampling for benthic micro algae in 1954 within the special areas (cf. Appendix I, Map 1 and Appendix IV, Maps 3—6 in MALMER 1962 a.) — 1. Large area with hummocks. 2. Large area with mudbottom.

area and six from the Bygget area. In the samples from 1949 and 1952 there are two from the broad fen of the Lönnstorpet area, 26 from the Stattute area and four from the fen soak of the Bygget area.

In all 225 taxa (here as in the subsequent discussions including both species and varieties) have been recorded. Among them 157 are desmids and 39 diatoms. In the Lönnstorpet area 135 taxa have been noted, in the Stattute area 155 and in the Bygget area 55. All taxa are listed in the following section together with generalized notes about there distribution.

What is indicated on the maps or said about distribution, number of species, etc., refer to the sampling in 1954 when not especially stated.

List of Recorded Species

CYANOPHYTA

CHROOCOCCALES

Aphanocapsa sp. found in one sample from 1952 in the Stattute area (Outer Fen).

Chroococcus minutus (KÜTZ.) NÄG. in some sample from the Stattute area, viz., in the Outer Fen and on the bog. Sometimes very frequent in the samples.

Chroococcus turgidus (KÜTZ.) NÄG. In the Lönnstorpet and Stattute areas in nearly all samples and in all parts of the areas but in the Bygget area only in one bog sample. Often a great number of colonies in the samples. Wide distribution in the Store Mosse area, too.

Gloeocapsa sp. This species has been noted in the Lönnstorpet area and in a few bog samples from the Stattute and Bygget areas. In Store Mosse found in Lake Kävsjön only.

Merismopedia glauca (EHRBG.) NÄG. Found in some samples from the Stattute area, both in the Inner Fen and the Outer Fen. In Store Mosse most common in the rich fen areas.

Synechococcus aeruginosus NÄG. Found in a few samples from the Outer Fen of the Stattute area. On Store Mosse mainly in rich fen areas.

HORMOGONALES

Anabaena sp. Breadth about 5μ. This undeterminable species has been found in all parts of the Lönnstorpet and the Stattute areas. It is questionable whether this common species is taxonomically uniform.

Hapalosiphon sp. Breadth 5μ. Noted twice near the hydrologic mineral soil water limit in the Stattute area, viz., on the bog 1954 and in Outer Fen 1949.

Lyngbya sp. Noted in one brook pool sample from the Stattute area 1949.

Oscillatoria sp. Breadth about 5μ. An undeterminable but very common species. Found in all parts of the Lönnstorpet, Stattute and Bygget areas except in bog areas.

Nostoc paludosum KÜTZ. Breadth about 3μ. Noted in some samples from the Stattute area (the row of brook pools, Outer Fen and the bog).

Nostoc sp. (globular colonies). Undetermined species noted in one sample in the Outer Fen of the Stattute area.

Schizothrix sp. Found in the Stattute area (one sample, Outer Fen 1949) and in the Bygget area (1952).

Scytonema sp. Breadth 5—10μ. In some samples from the Stattute area, along the row of brook pools as well as in the Inner and Outer Fen.

Stigonema sp. Breadth about 20μ. Noted in two samples from the Stattute area, one from the row of brook pools and one from the Outer Fen.

OEDOGONIALES

Bulbochaete sp. In the Lönnstorpet area and all parts of the fen in the Stattute area. It seems to be the same species as in Store Mosse.

Oedogonium sp. Breadth 5—10μ. Common in all parts of the Lönnstorpet, Stattute and Bygget areas. Probably a taxonomically uniform species.

CHAETOPHORALES

Draparnaldia sp. Breadth 40μ. Only in the Lönnstorpet area.

CHLOROPHYTA

PROTOCOCCALES

Crucigenia rectangularis (BR.) GAY. Found in one sample from the row of brook pools in the Stattute area. Not reported by THUNMARK 1942 or found on Store Mosse.

Oocystis solitaria WITTROCK. Very common in all parts of the Stattute area. Not found on Store Mosse.

Scenedesmus alternans REINSCH. Only found in the Lönnstorpet area. Not observed on Store Mosse.

Scenedesmus arcuatus LEMM. As *S. alternans.*

Scenedesmus bijugatus (TURP.) KÜTZ. As *S. alternans.* On Store Mosse found in Lake Kävsjön.

Tetraëdron sp. Noted in one sample (Outer Fen) of the Stattute area.

CONJUGATAE

ZYGNEMALES

Mougeotia spp. Two species, just as on Store Mosse. One narrow one (breadth 5—10μ), one broad one (breadth 15—23μ). Both species common in all parts of the Stattute area. The narrow one also in the Bygget area (both bog and fen) and in the Lönnstorpet area. Generally both seems to be rather eurytopic.

Spirogyra sp. Breadth 6—15μ; single chromatophore. Found only in the Lönnstorpet area and in the Bygget area (the Small Bog). Probably the same species.

Zygnema sp. Breadth 25μ. Found only in the Lönnstorpet area.

Zygogonium ericetorum KÜTZ. One of the most common species on this mire. Found in nearly all samples from all parts of the mire. Often very luxuriant, but always sterile. Similar appearance and distribution as on Store Mosse.

DESMIDIALES

Actinotaenium adelochondrum (ELFVING) TEILING. Only in the Stattute area where it is common in the Outer Fen and along the row of brook pools. Found scattered on the bog, too. Not found on Store Mosse or reported in THUNMARK 1942.

Actinotaenium cucurbita (BRÉB.) TEILING. One of the most common desmids of the mire. Found in nearly all samples in the Stattute area. Also common in all parts of the Bygget and the Lönnstorpet areas. On Store Mosse mainly distributed in areas with moderately rich fen, poor fen and bog vegetation.

Actinotaenium cucurbitinum (BISSET) TEILING. Only found in the Lönnstorpet area. A rich fen species on Store Mosse.

Arthrodesmus octocornis EHRBG. Only found in the Lönnstorpet area.

Bambusina Borreri (RALFS) CLEVE. Common in all parts of the Stattute area except on the bog, where it has been found only in five samples most of them near the mineral soil water limit. Noted also in all fen sites of the Lönnstorpet and Bygget areas. Widespread on Store Mosse, but rare on the bog.

Closterium abruptum W. WEST. In the Lönnstorpet area, along the row of brook pools in the Stattute area and in the fen of the Bygget area.

Closterium acutum BRÉB. var. *variabile* (LEMMERM.) KRIEGER. Noted only in one brook pool sample and one bog sample from the Stattute area.

Closterium angustatum KÜTZ. Found only in the Lönnstorpet area.

Closterium archerianum CLEVE. As *C. angustatum*.

Closterium baillyanum BRÉB. (sensu GRÖNBLAD 1919). Found in the Lönnstorpet area and in the Stattute area (Fig. 5). Common on Store Mosse, esp. in the rich fen areas there.

Closterium calosporum WITTROCK. Found only in the Lönnstorpet area. Mainly a rich fen species on Store Mosse and very common in Lake Kävsjön.

Closterium costatum CORDA. As *C. calosporum*.

Closterium cynthia DE NOT. s. str. As *C. calosporum*.

Closterium cynthia DE NOT. var. *Jenneri* (RALFS) KRIEGER. As *C. cynthia* s.str.

Closterium dianae EHRBG. In the Lönnstorpet area and in a few samples from the row of brook pools in the Stattute area. On Store Mosse as *C. calosporum*.

Closterium dianae EHRBG. var. *pseudodianae* (ROY) KRIEGER. Only in some samples from the row of brook pools in the Stattute area. On Store Mosse most frequent in Blådöpet. — No transitional forms to the main species either on the Åkhult mire or on the Store Mosse. Therefore it seems probable that it may be given the rank of separate species as proposed by other authors (*C. pseudodianae* ROY).

Closterium didymotocum RALFS. Noted from the Lönnstorpet area and in some brook pool samples from the Stattute area.

Closterium gracile BRÉB. Noted in the Lönnstorpet area and along the row of brook pools and in the Inner Fen in the Stattute area.

Closterium gracile BRÉB. var. *elongatum* WEST & WEST. Found 1952 in one sample from the row of brook pools in the Stattute area.

Closterium intermedium RALFS. Found in the Lönnstorpet area, along the row of brook pools and in the Inner Fen of the Stattute area and in the fen of the Bygget area.

Closterium juncidum RALFS. Only in the Lönnstorpet and Bygget areas (fen sites).

Closterium Kützingii BRÉB. Found only in the lagg fen of the Bygget area. Mainly a rich fen species in the Store Mosse area.

Closterium libellula FOCKE. Found in the Lönnstorpet area and in one brook pool sample from the Stattute area.

Closterium lunula (MÜLL.) NITZSCH. Found only in the Lönnstorpet area.

Closterium macilentum BRÉB. Found in two samples from the row of brook pools in the Stattute area in 1952 in the Lönnstorpet area, too.

Closterium navicula (BRÉB.) LÜTKEM. Found in the Lönnstorpet and Bygget areas.

Closterium pronum BRÉB. This species has a wider ecological amplitude than most of the other *Closterium* spp. with scattered occurrences in the Stattute area and the Bygget area (Fig. 5). In Store Mosse a similar distribution.

Closterium Ralfsii BRÉB. and its var. *hybridum* RABENH. (no clear differences between them seem to exist, see FLENSBURG 1967 p. 58). Both found only in the Lönnstorpet area.

Closterium rostratum EHRBG. A few occurrences in the Lönnstorpet area, in the Stattute area (near the brook pools) and in the Bygget area (the lagg fen).

Closterium setaceum EHRBG. Found in the Lönnstorpet area and in one brook pool sample from the Stattute area. Very common in Lake Kävsjön.

Closterium striolatum EHRBG. Found in the fen of the Lönnstorpet area as well as in the Stattute and Bygget areas (Fig. 5). Wide ecologic amplitude in Store Mosse.

Closterium tumidulum GAY. Noted only in one sample from the fen soak in the Bygget area. Not found on Store Mosse or reported in THUNMARK 1942.

Closterium turgidum EHRBG. Found only in the Lönnstorpet area.

Closterium ulna FOCKE. Noted in fen sites of the Lönnstorpet area, in the Stattute area (along the row of brook pools) and in the Bygget area. Similar distribution on Store Mosse.

Closterium venus KÜTZ. Found only in the Lönnstorpet area.

Cosmarium amoenum BRÉB. Only in the Stattute area along the row of brook pools and some fen sites close to them.

Cosmarium angulosum BRÉB. Found in one sample from the Outer Fen and one from the row of brook pools in the Stattute area. Not found on Store Mosse or reported in THUNMARK 1942.

Cosmarium Blyttii WILLE. Found in the Lönnstorpet area and the Stattute area (along the row of brook pools).

Cosmarium Boeckii WILLE. Found only in the Lönnstorpet area.

Cosmarium contractum KIRCHN. Only in the Stattute area along the row brook pools and some fen sites close to them as well as in the fen of the Bygget area.

Cosmarium contractum KIRCHN. var. *ellipsoideum* (ELFVING) WEST & WEST. Found in the Lönnstorpet area and in the Stattute area (a few samples from the Outer Fen).

Cosmarium cymatonotophorum WEST. Found in one sample from the Outer Fen near the row of brook pools in the Stattute area. Not found in Store Mosse or reported in THUNMARK 1942.

Cosmarium depressum (NÄG.) LUNDELL. Found only in one sample from the Stattute area (the Outer Fen) and in two samples from the Small Bog in the Bygget area. On the last mentioned site it corresponds to var. *reniforme* WEST & WEST but is here regarded as an ecologic modification. On the Store Mosse common in Lake Kävsjön.

Cosmarium difficile LÜTKEM. Found only in the Lönnstorpet area. Common in Lake Kävsjön.

Cosmarium globosum BULNH. Found only in the Lönnstorpet area.

Cosmarium Hammeri REINSCH. Found in the Stattute area, especially in the Outer Fen, but also along the row of brook pools and in the Inner Fen.

Cosmarium impressulum ELFVING. Found only in the Lönnstorpet area. Fairly common in Lake Kävsjön.

Cosmarium margaritiferum MENEGH. As *C. impressulum*.

Cosmarium moniliforme (TURP.) RALFS. Found only in the Lönnstorpet area.

Cosmarium norimbergense REINSCH. Noted in two brook pool samples in the Stattute area. Not observed on Store Mosse and not reported in THUNMARK 1942.

Cosmarium pachydermum LUNDELL. Found only in the Lönnstorpet area. Fairly common around Lake Kävsjön.

Cosmarium pseudoexiguum RACIB. (Fig. 15). Only in the Stattute area where it is a common and characteristic species (Fig. 6) in the samples from 1954. In 1949 and 1952 recorded only in one sample each year. Not observed on Store Mosse and not reported in THUNMARK 1942.

Cosmarium pseudopyramidatum LUNDELL. In the Lönnstorpet area and in the Stattute area (Fig. 16). Its distribution is contrary to that of *C. pseudoexiguum*. Only in one sample were both species found together. Common in Lake Kävsjön.

Cosmarium punctulatum BRÉB. var. *subpunctulatum* (NORDSTEDT) BØRGESEN. Found only in the Lönnstorpet area. Scattered in Lake Kävsjön.

Cosmarium pygmaeum ARCHER. Found in the fen sites of the Lönnstorpet area, in the Stattute and the Bygget area even in bog sites (Fig. 7). In the Store Mosse found only scattered around Lake Kävsjön. May be a heterogeneous taxon.

Cosmarium pyramidatum BRÉB. Found in the Lönnstorpet area and in the Stattute area along the row of brook pools and in one sample from the Outer Fen. Not as common as *C. pseudopyramidatum*. In Store Mosse there is the reverse situation.

Cosmarium quadratulum (GAY) DE TONI. Found in one sample in the Outer Fen of the Stattute area near the row of brook pools. Not found in the Store Mosse area and not reported in TUHNMARK 1942.

Cosmarium Ralfsii BRÉB. Noted only in the Stattute area, most of the finds from the Outer Fen and the brook pools. Rare on Store Mosse, too.

Cosmarium rectangulare GRUNOW. Found in the Stattute area along the row of brook pools and in a few samples from the Outer Fen. In Store Mosse most common in Lake Kävsjön.

Cosmarium Regnesii REINSCH. Only in the Lönnstorpet area. On Store Mosse found only in Lake Kävsjön.

Cosmarium sphagnicolum WEST & WEST. Found in the Lönnstorpet area and in the Stattute area where it has been found in all parts even on the bog. On Store Mosse only in Lake Kävsjön.

Cosmarium subarctoum (LAGERH.) RACIB. Found in the Lönnstorpet area and along the row of brook pools in the Stattute area. Not found in Store Mosse and not reported in THUNMARK 1942.

Cosmarium subcrenatum HANTZSCH. Only in the Lönnstorpet area. Rare in Lake Kävsjön.

Cosmarium subquadrans WEST & WEST. Noted only in the Stattute area, mainly in the Outer Fen but also in two samples from the bog. On Store Mosse rare and found only in Lake Kävsjön.

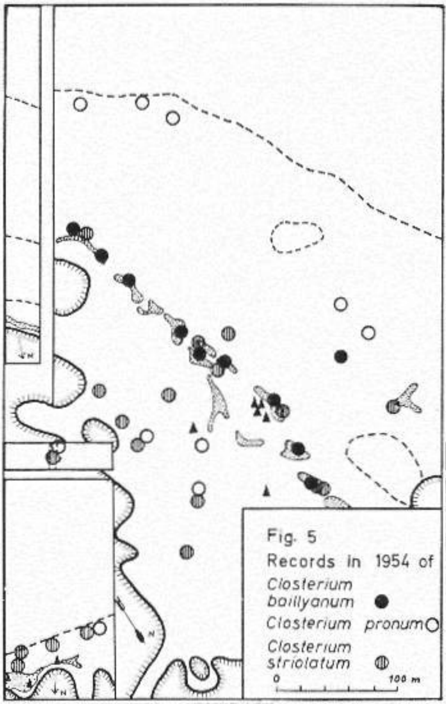

Fig. 5
Records in 1954 of
Closterium baillyanum ●
Closterium pronum ○
Closterium striolatum ◍

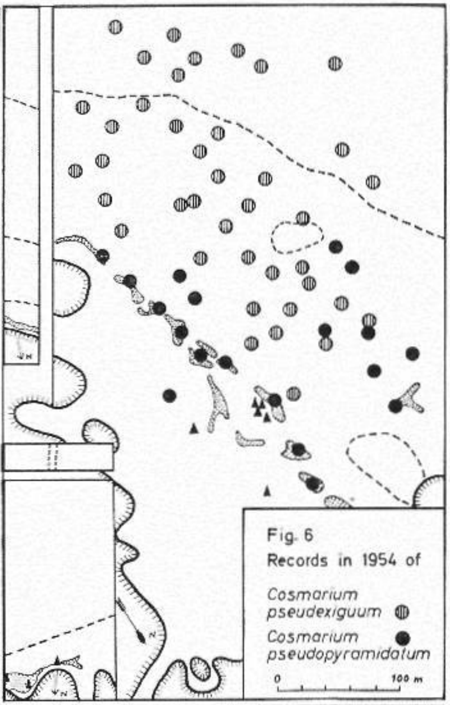

Fig. 6
Records in 1954 of
Cosmarium pseudexiguum ◍
Cosmarium pseudopyramidatum ●

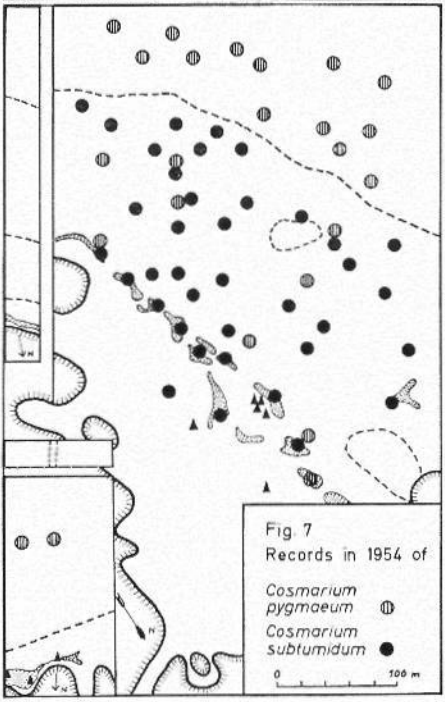

Fig. 7
Records in 1954 of
Cosmarium pygmaeum ◍
Cosmarium subtumidum ●

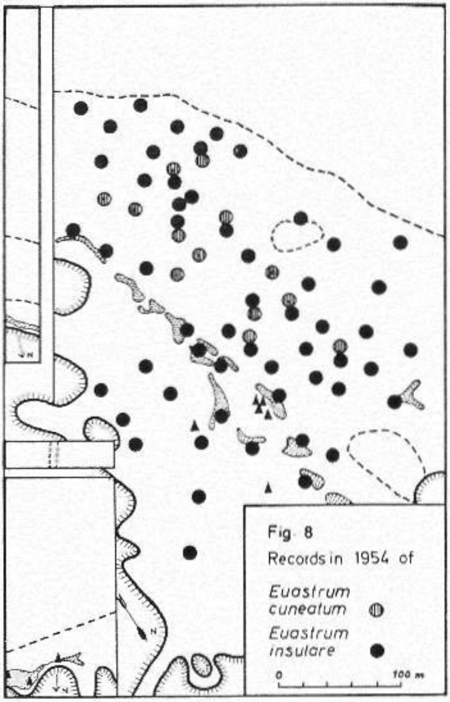

Fig. 8
Records in 1954 of
Euastrum cuneatum ◍
Euastrum insulare ●

Cosmarium subtumidum NORDSTEDT. Common in the Stattute area (Fig. 7). In Store Mosse common in Lake Kävsjön and some other areas.

Cosmarium subundulatum WILLE. Noted in one sample from the Outer Fen of the Stattute area. Not found in Store Mosse but reported in THUNMARK 1942.

Cosmarium tinctum RALFS. Noted in two samples, one from the Lönnstorpet area and one from the Stattute area (a brook pool).

Cosmarium venustum BRÉB. Found in the Lönnstorpet area and all over the fen areas of the Stattute area. More common on the Åkhult mire than on Store Mosse.

Cylindrocystis Brebissonii MENEGH. One of the most common benthic micro algae on the Åkhult mire. Found in samples from all parts of the Lönnstorpet, the Stattute and the Bygget areas. Does not seem to show preference for any part. In the Store Mosse area it is most common on bog sites.

Cylindrocystis Brebissonii MENEGH. var. *minor* WEST & WEST. Observed in one sample from the Outer Fen in the Stattute area. Not found on Store Mosse or reported in THUNMARK 1942.

Cylindrocystis crassa DE BARY. Found in two samples from the Stattute area, one from the bog and one from the Inner Fen. Not found on Store Mosse or reported by THUNMARK 1942.

Desmidium cylindricum BRÉB. Found only in the Lönnstorpet area. In Store Mosse most common in Blådöpet.

Docidium baculum BRÉB. Found in one sample from a brook pool in the Stattute area. Not found in Store Mosse, but reported in THUNMARK 1942.

Docidium undulatum BAIL. As *D. baculum*, but not in the same sample. Not found on Store Mosse or reported in THUNMARK 1942.

Euastrum ampullaceum RALFS. Found in the Lönnstorpet area. Common in the Stattute area along the row of brook pools and in the Outer Fen, as well as in the fen of the Bygget area. Similar distribution type on Store Mosse.

Euastrum ansatum EHRBG. Noted in the Lönnstorpet area and in two fen samples from the Stattute area. The most common *Euastrum* sp. in Lake Kävsjön and the rich fen areas of Store Mosse.

Euastrum bidentatum NÄG. In the Lönnstorpet area and in the Stattute area (a few samples along the row of brook pools). In Store Mosse most common in Blådöpet.

Euastrum binale (TURB.) EHRBG. Found in the Lönnstorpet area, in the Stattute area (along the row of brook pools and in the Outer Fen) and in fen sites of the Bygget area. Here an exclusive fen species, not found in bog areas as on Store Mosse.

Euastrum crassicolle LUNDELL. Found in fen samples from the Stattute area, one taken in 1954 and six in 1949 and 1952, both the Inner och Outer Fen. Not observed in Store Mosse or reported in THUNMARK 1942.

Euastrum crassum (BRÉB.) KÜTZ. Found in the fen sites of the Lönnstorpet area. In the Stattute area common along the row of brook pools and in the Outer Fen but only in two samples from the Inner Fen. On Store Mosse not found in the rich fen areas.

Euastrum cuneatum JENNER. Found in the Stattute area (Fig. 8). Not observed on Store Mosse but found in bog areas of the mire Komosse (FLENSBURG unpublished) and reported in THUNMARK 1942.

Euastrum denticulatum (KIRCHN.) GAY. Found in the Lönnstorpet area and in two samples from the Stattute area near the row of brook pools. Common in Lake Kävsjön.

Euastrum didelta RALFS. Found in the Lönnstorpet area and in the Stattute area (along the row of brook pools, in the Inner and Outer Fen).

Euastrum dubium NÄG. Found scattered in the Stattute area (along the row of brook pools, in the Inner and Outer Fen).

Euastrum elegans (BRÉB.) KÜTZ. s. str. Found in the Lönnstorpet area and a few samples along the row of brook pools in the Stattute area.

Euastrum elegans (BRÉB.) KÜTZ. var. *novae-semliae* WILLE. Greater than *E. elegans* s.str. Found in the Stattute area along the row of brook pools and in the Outer Fen. Not found in Store Mosse or reported in THUNMARK 1942.

Euastrum evolutum (NORDSTEDT) WEST & WEST var. *Glaziowii* (BØRGESEN) WEST & WEST. Found in one sample from the Stattute area 1952 (the row of brook pools). Not found on Store Mosse or reported in THUNMARK 1942.

Euastrum gemmatum BRÉB. Found in one sample from the Lönnstorpet area 1952. Found only twice in Lake Kävsjön.

Euastrum humerosum RALFS. In 1954 found only in the Lönnstorpet area but in 1952 also in the Stattute area. Not found in Store Mosse but reported in THUNMARK 1942.

Euastrum insigne HASS. Found in the Stattute area, along the row of brook pools as well as in the Inner and Outer Fen. Only on one locality in the Store Mosse area.

Euastrum insulare (WITTROCK) ROY. In the Lönnstorpet area and the Stattute area (Fig. 8). In Store Mosse most common in Lake Kävsjön.

Euastrum montanum WEST & WEST. Found in the Stattute area along the row of brook pools and in the Inner Fen. Not found in Store Mosse or reported in THUNMARK 1942.

Euastrum oblongum (GREV.) RALFS. Found only in the Lönnstorpet area. On Store Mosse one of the most common *Euastrum* species.

Euastrum pectinatum BRÉB. Found in both the Lönnstorpet area and in the Stattute area along the row of brook pools and in the Inner Fen. On Store Mosse common in Lake Kävsjön.

Euastrum pingue ELFVING. Found in one sample from the Inner Fen of the Stattute area from 1952. Not found on Store Mosse or reported in THUNMARK 1942.

Euastrum pinnatum RALFS. Found in one sample from a brook pool in the Stattute area. Only occasional on Store Mosse.

Euastrum sinuosum LENORM. var. *aboënse* (ELFVING) CEDERGREN. Found in one sample from the Outer Fen in the Stattute area 1949. The main species, but not this variety, found in Lake Kävsjön.

Euastrum ventricosum LUNDELL. Found in a few samples from the Stattute area (all parts of the fen) and in the lagg fen of the Bygget area. Not found in Store Mosse.

Euastrum verrucosum EHRBG. Found in two samples from the Stattute area (a brook pool and in the Outer Fen). Common in Lake Kävsjön.

Hyalotheca dissiliens (SMITH) BRÉB. Found scattered in fen areas in the Lönnstorpet, Stattute and Bygget areas. Fairly common in Lake Kävsjön.

Hyalotheca mucosa (MERT.) EHRBG. Found only in the Lönnstorpet area. Scattered on Store Mosse.

Micrasterias angulosa HANTZSCH. Found only in the Lönnstorpet area. Fairly common in Lake Kävsjön.

Micrasterias Jenneri RALFS. Found only in the Stattute area (Fig. 9). Mainly a poor fen species on Store Mosse.

Micrasterias oscitans RALFS. As *M. Jenneri* (Fig. 9). Not found on Store Mosse, but reported by THUNMARK 1942.

Micrasterias papillifera BRÉB. Found only in the Lönnstorpet area. Fairly common in Lake Kävsjön.

Micrasterias rotata (GREV.) RALFS. Found in the Lönnstorpet area. Common in Lake Kävsjön and the rich fen areas on Store Mosse.

Micrasterias truncata (CORDA) BRÉB. Found in the Lönnstorpet area and in two samples from the row of brook pools in the Stattute area. Common in Lake Kävsjön.

Netrium digitus ITZIGSH. & ROTHE. One of the most common desmids of the mire and noted in all the three areas (cf. Fig. 10). Very common both in the poor and rich fen areas of Store Mosse.

Netrium digitus ITZIGSH. & ROTHE var. *lamellosum* (BRÉB.) GRÖNBLAD. Replaces *N. digitus* s. str. in the lagg fen site of the Lönnstorpet area.

Netrium interruptum (BRÉB.) LÜTKEM. Found 1952 in one sample from the Lönnstorpet area and one from the row of brook pools in the Stattute area. Scattered on Store Mosse.

Netrium oblongum (DE BARY) LÜTKEM. Found in the Stattute and Bygget areas (Fig. 10). In many samples *N. digitus* and *N. oblongum* occur together. On Store Mosse this species is confined mainly to bog areas and rarely found together with *N. digitus*.

Netrium oblongum (DE BARY) LÜTKEM. var. *cylindricum* WEST & WEST. Found in 1949 and 1952 in the Lönnstorpet area and in some samples from the Stattute area along the row of brook pools. Not observed in Store Mosse or reported in THUNMARK 1942.

Penium borgeanum SKUJA. Found only in the Stattute area (Fig. 11). Not observed in Store Mosse or reported in THUNMARK 1942.

Penium cylindrus (EHRBG.) BRÉB. Found in the fen sites of the Lönnstorpet and Bygget areas. Rare on Store Mosse.

Penium polymorphum PERTY. Found only in the lagg fen of the Bygget area. Not observed in bog areas where this species is fairly common in Store Mosse.

Penium silvae-nigrae RABANUS s. str. Found in the Stattute and Bygget areas (Fig. 12). On Store Mosse very rare out of the bog areas.

Penium silvae-nigrae RABANUS var. *parallelum* KRIEGER. As *P. silvae-nigrae* s. str. (Fig. 12). In Store Mosse found only on bog areas.

Pleurotaenium minutum (RALFS) DELP. Common in the Outer Fen in the

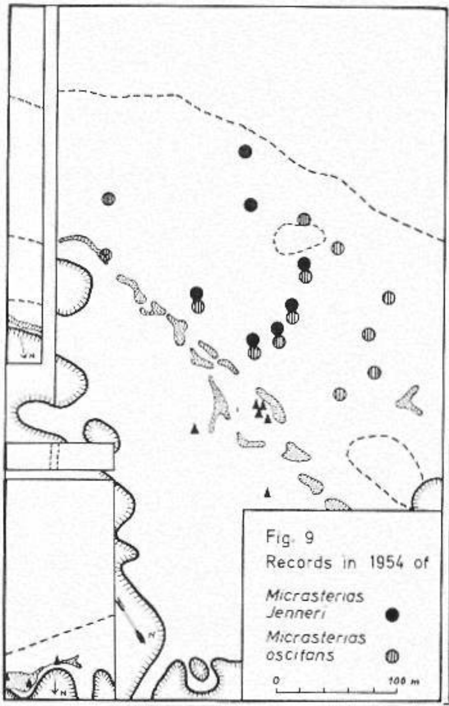
Fig. 9
Records in 1954 of
Micrasterias Jenneri ●
Micrasterias oscitans ◍

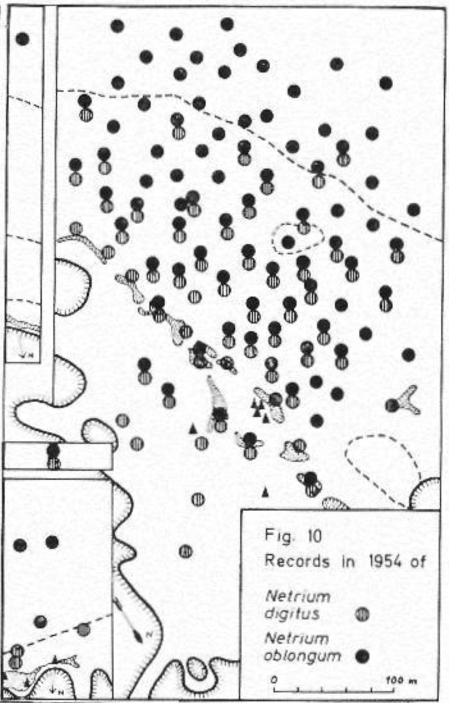
Fig. 10
Records in 1954 of
Netrium digitus ◍
Netrium oblongum ●

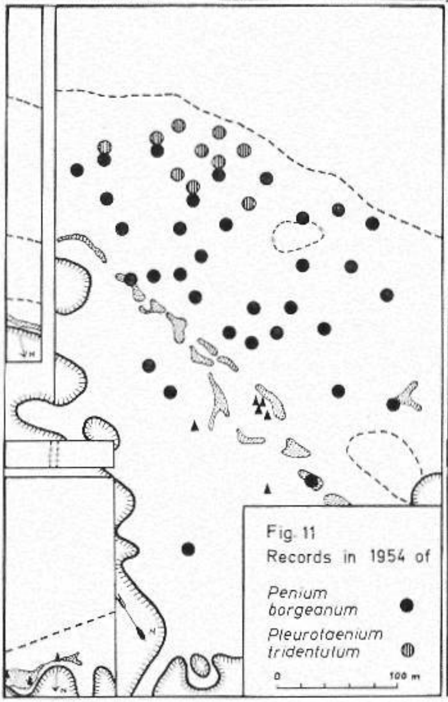
Fig. 11
Records in 1954 of
Penium borgeanum ●
Pleurotaenium tridentulum ◍

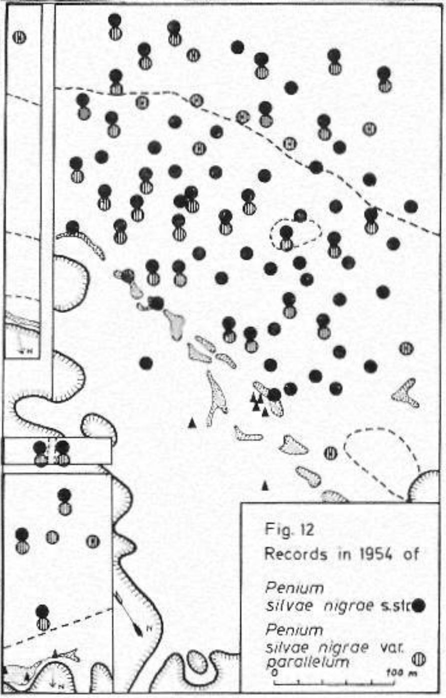
Fig. 12
Records in 1954 of
Penium silvae nigrae s.str. ●
Penium silvae nigrae var. *parallelum* ◍

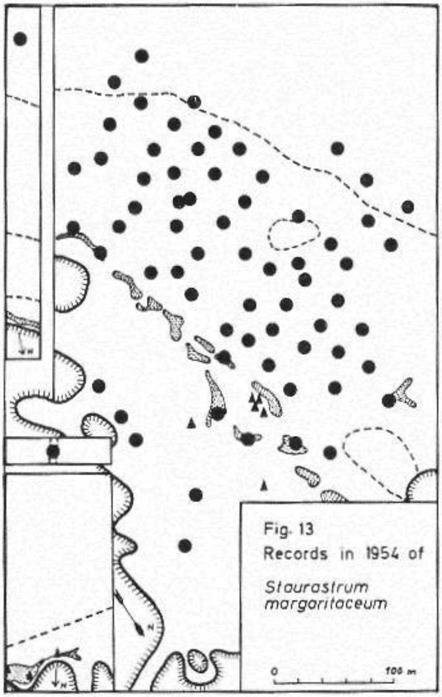

Fig. 13
Records in 1954 of
Staurastrum margaritaceum

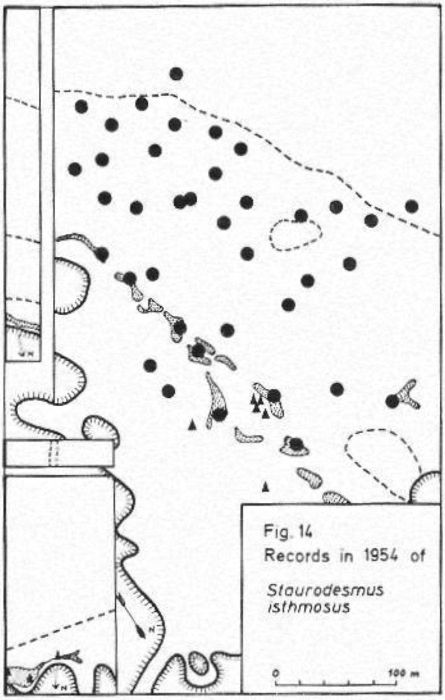

Fig. 14
Records in 1954 of
Staurodesmus isthmosus

Stattute area. Noted also in three samples from the Great Bog. Found in the Bygget area in the lagg fen. On Stone Mosse in bog and poor fen areas.

Pleurotaenium trabecula (EHRBG.) NÄG. Found in the Lönnstorpet area and along the row of brook pools in the Stattute area. Common in Lake Kävsjön.

Pleurotaenium tridentulum (WOLLE) W. WEST. (Fig. 15). Found in samples from a small part of the Stattute area (Fig. 11). Such a limited distribution may be characteristic as similar distribution types have been observed on Store Mosse.

Spirotaenia condensata BRÉB. Found in one sample from the Lönnstorpet area from 1952.

Spondylosium secedens (DE BARY) ARCHER. Found only in one sample from a brook pool in the Stattute area.

Staurastrum alternans BRÉB. Found in the Lönnstorpet area and in the Bygget area, in both areas in the lagg fen. In Store Mosse common in Lake Kävsjön.

Staurastrum controversum BRÉB. Found only in the Lönnstorpet area.

Staurastrum cyrtocerum BRÉB. Found only in one sample from the Inner Fen in the Stattute area. Not found in Store Mosse or reported in THUNMARK 1942.

Staurastrum dilatatum EHRBG. Noted only in the Lönnstorpet area. Scattered on Store Mosse.

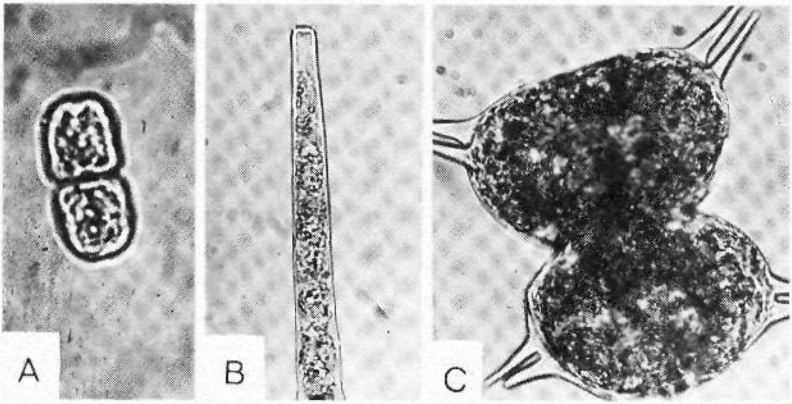

Fig. 15. — A: *Cosmarium pseudoexiguum* (25×12 μ). — B: *Pleurotaenium tridentulum* (one semicell, total size 260×17 μ). — C: *Staurastrum longispinum* (130× 125 μ with spines).

Staurastrum hexacerum (Ehrbg.) Wittrock. Found only in the Lönnstorpet area.

Staurastrum longispinum (Bail.) Archer. (Fig. 15.) This very large and characteristic species is found in one brook pool sample from the Stattute area. Not found in Store Mosse or reported in Thunmark 1942.

Staurastrum margaritaceum (Ehrbg.) Menegh. Found in the Stattute and Bygget areas (Fig. 13). On Store Mosse eurytopic but less common.

Staurastrum monticulosum Bréb. Found in the Lönnstorpet area and in the Stattute area (in the Outer Fen and in two bog samples). Not found on Store Mosse or reported in Thunmark 1942.

Staurastrum muricatum Bréb. Found in the Outer Fen of the Stattute area. Not found in Store Mosse, but reported in Thunmark 1942.

Staurastrum orbiculare Ralfs s. str. Found in the Outer Fen in the Stattute area and in the fen soak of the Bygget area.

Staurastrum orbiculare Ralfs var. *depressum* Roy & Bissett. As *S. orbiculare* s.str. In Lake Kävsjön the most common one among the varieties of this species.

Staurastrum orbiculare Ralfs var. *Ralfsii* West & West. Found in the fen soak of the Bygget area.

Staurastrum Simonyi Heimerl. In the Stattute area common in the Outer Fen and on the bog, more scattered in the Inner Fen and along the brook pools. Also in the fen sites of the Bygget area. Rare on Store Mosse.

Staurastrum teliferum Ralfs. Noted in the Lönnstorpet area and in the Stattute area (one sample from the Outer Fen). In Store Mosse common in Lake Kävsjön.

Staurastrum vestitum Ralfs. Found in the Lönnstorpet area and in the Stattute area in a few samples from the row of brook pools. In Store Mosse most common in Lake Kävsjön.

Staurodesmus brevispina (BRÉB.) CROASDALE. Found in one sample from 1949 in the Lönnstorpet area.

Staurodesmus controversus (WEST) TEILING. Found in one sample from a brook pool in the Stattute area 1954 and one from the fen soak in the Bygget area 1949. Not observed on Store Mosse or reported in THUNMARK 1942.

Staurodesmus dejectus (BRÉB.) TEILING. Found in the Lönnstorpet area. In Store Mosse noted in Lake Kävsjön.

Staurodesmus extensus (BORGE) TEILING. Found in a few samples from the row of brook pools and in one sample from the Outer Fen in the Stattute area. Not observed on Store Mosse or reported in THUNMARK 1942.

Staurodesmus incus (BRÉB.) TEILING. Found in one sample from the row of brook pools in the Stattute area.

Staurodesmus isthmosus (HEIMERL.) CROASDALE. The most common *Staurodesmus* species on the mire. Found in the Lönnstorpet area and in the Stattute area (Fig. 14). Not found in Store Mosse or reported in THUNMARK 1942.

Staurodesmus Joshuae (GUTW.) TEILING. Found in the Lönnstorpet area. In Store Mosse common in Lake Kävsjön.

Staurodesmus megacanthus (LUNDELL) THUNMARK. Found in one sample from a brook pool in the Stattute area.

Staurodesmus spencerianus (MASKELL) TEILING. Found in a few samples from the Outer Fen of the Stattute area. In Store Mosse sporadic in Lake Kävsjön.

Staurodesmus triangularis (LAGERHEIM) TEILING. Only found in the Lönnstorpet area. Not observed on the Store Mosse or reported by THUNMARK 1942.

Tetmemorus Brebissonii (MENEGH.) RALFS s. str. Found in the Lönnstorpet area and in three samples from the Stattute area (Fig. 16). In Store Mosse common in Blådöpet.

Tetmemorus Brebissonii (MENEGH.) RALFS var. *intermedius* FLENSBURG. Common in the Stattute area (Fig. 16). This variety is the only one in the bog areas. Here — but not on Store Mosse — it has been found in the same samples as *T. Brebissonii* var. *minor*. In one Outer Fen sample *T. Brebissonii* s. str. also has been found together with both these varieties.

Tetmemorus Brebissonii (MENEGH.) RALFS var. *minor* DE BARY. Found in the Lönnstorpet area. Common in the Stattute area (Fig. 16). In Store Mosse only in Blådöpet.

Tetmemorus granulatus (BRÉB.) RALFS. Found in the Lönnstorpet, Stattute and Bygget areas (Fig. 17). Common on Store Mosse in fen areas.

Tetmemorus laevis (KÜTZ.) RALFS. Found in the Lönnstorpet area and along the row of brook pools in the Stattute area. Quite rare on Store Mosse.

Tetmemorus laevis (KÜTZ.) RALFS var. *minutus* (DE BARY) KRIEGER. More common than *T. laevis* s. str. Found in the Stattute and Bygget areas (Fig. 18). Similar distribution as on Store Mosse.

Xanthidium antilopaeum (BRÉB.) KÜTZ. Found in the Lönnstorpet area and in one sample in the Stattute area (Fig. 19). Scattered on Store Mosse. *X. antilopaeum* var. *laeve* SCHMIDLE, which in Store Mosse also occurs in the bog, has not been noted in the Åkhult mire.

Xanthidium armatum (BRÉB.) RABENH. Found in the Lönnstorpet and Stattute areas (Fig. 19). Scattered on Store Mosse.

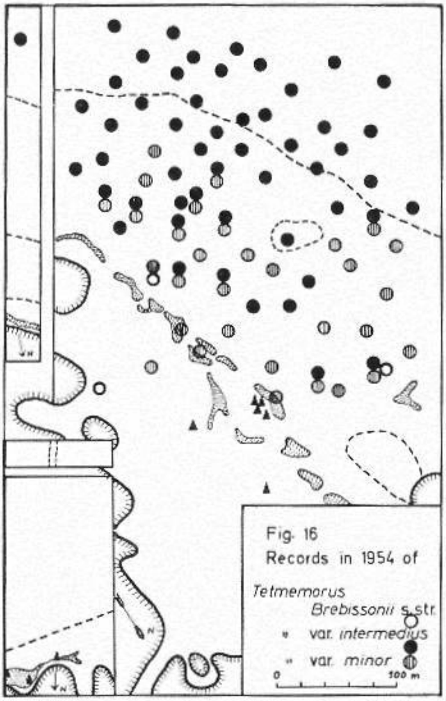

Fig. 16
Records in 1954 of

Tetmemorus
Brebissonii s. str. ○
" var. *intermedius* ●
" var. *minor* ◍

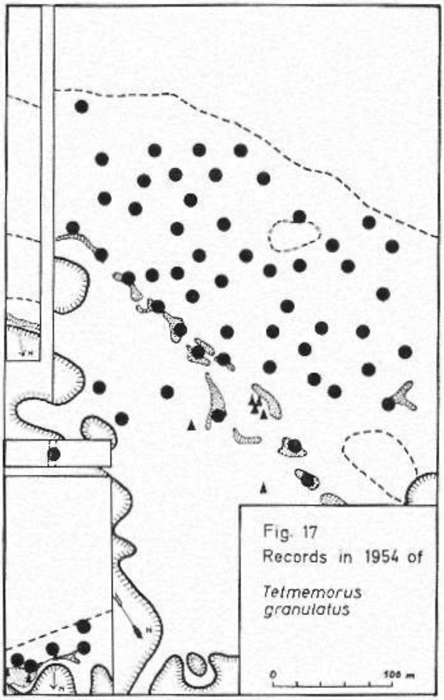

Fig. 17
Records in 1954 of

Tetmemorus granulatus

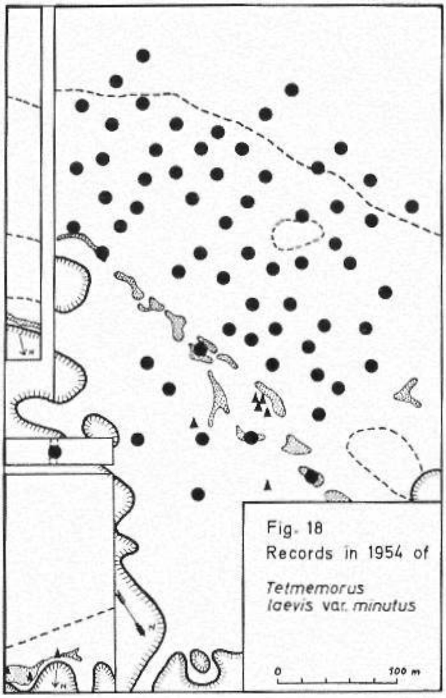

Fig. 18
Records in 1954 of

Tetmemorus laevis var. *minutus*

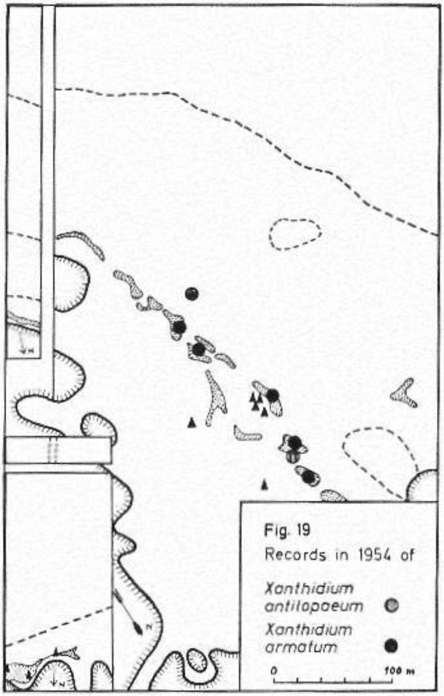

Fig. 19
Records in 1954 of

Xanthidium antilopaeum ◍
Xanthidium armatum ●

CHRYSOPHYTA

PANTOSTOMATINEAE

Dinobryon divergens IMHOF. Very common in all parts of the Stattute area, where it occurs in most of the samples. A *Dinobryon* species, probably this one, has also been found in the lagg fen of the Bygget area. *D. divergens* is much more common on the Åkhult mire than on Store Mosse, where it is as rare as the other *Dinobryon* species.

PROTOMASTIGINEAE

Rhipidodendron Huxleyi KENT. Noted in one sample from the row of brook pools in the Stattute area 1952. In Store Mosse common around Lake Kävsjön. and in Blådöpet.

DIATOMEAE

Achnanthes flexella (KÜTZ.) BRUN. Noted in one brook pool sample in the Stattute area.

Cymbella gracilis (RABENH.) CLEVE. Found in the Lönnstorpet area and in two brook pool samples in the Stattute area. In Store Mosse in Lake Kävsjön.

Cymbella hebridica (GREGORY) GRUNOW. Noted from the lagg fen of the Lönnstorpet area. Common in Lake Kävsjön.

Eunotia alpina (NÄG.) HUSTEDT. Found in one brook pool sample from the Stattute area.

Eunotia arcus EHRBG. Found in the Lönnstorpet area. Rare in Store Mosse.

Eunotia exigua (BRÉB.) GRUNOW. Found in the Lönnstorpet, Stattute, and Bygget areas (Fig. 20). On bog areas not as common as on Store Mosse.

Eunotia gracilis (EHRBG.) RABENH. Found in the Lönnstorpet area. In the Stattute area scattered along the row of brook pools and in the Outer Fen as well as in one sample from the bog near the mineral soil water limit. In the Bygget area in the lagg fen. In Store Mosse common in Lake Kävsjön, scattered in other fen areas.

Eunotia lunaris (EHRBG.) GRUNOW. Rather common in the Lönnstorpet, Stattute, and Bygget areas (Fig. 20). One of the most common algae on Store Mosse.

Eunotia lunaris (EHRBG.) GRUNOW var. *subarcuata* (NÄG.) GRUNOW. Found in the Lönnstorpet area and in some brook samples in the Stattute area.

Eunotia paludosa GRUNOW. Found only in the Lönnstorpet area. Not found in Store Mosse

Eunotia parallela EHRBG. Found in the Lönnstorpet area, in the Stattute area (common along the row of brook pools, in the Inner Fen and the western part of the Outer Fen) and in the lagg fen of the Bygget area. Rare in Store Mosse.

Eunotia pectinalis (KÜTZ.) RABENH. Found only in the Stattute area in some samples along the row of brook pools in the Inner and Outer Fen and in three bog samples. In Store Mosse most common in Lake Kävsjön.

Eunotia robusta RALFS. Found only in the Lönnstorpet area. In Store Mosse quite common in Lake Kävsjön.

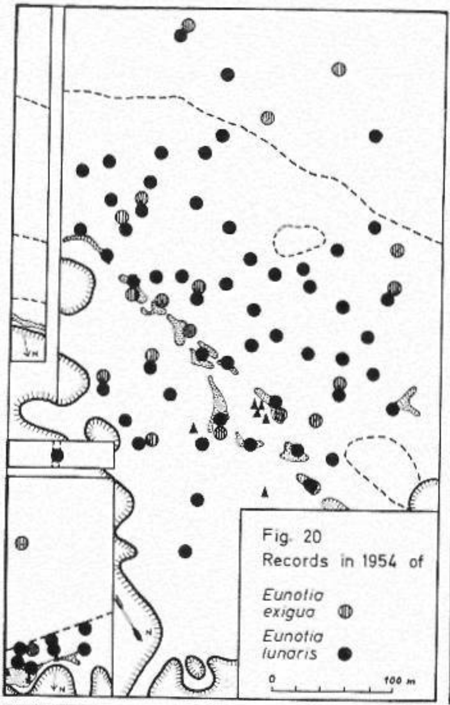

Fig. 20
Records in 1954 of
Eunotia exigua ◍
Eunotia lunaris ●

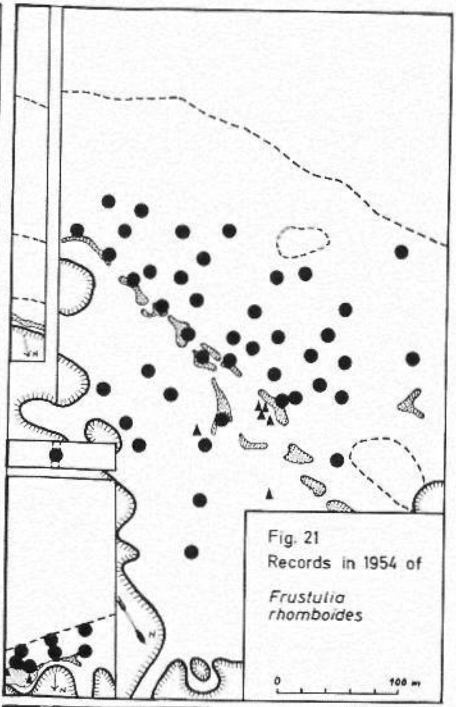

Fig. 21
Records in 1954 of
Frustulia rhomboides

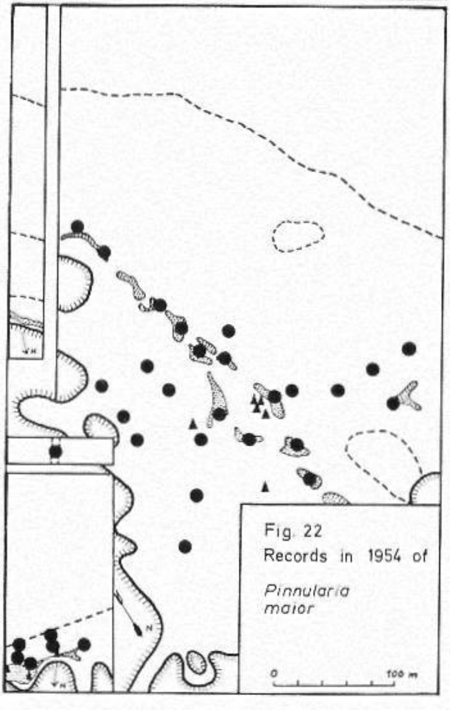

Fig. 22
Records in 1954 of
Pinnularia maior

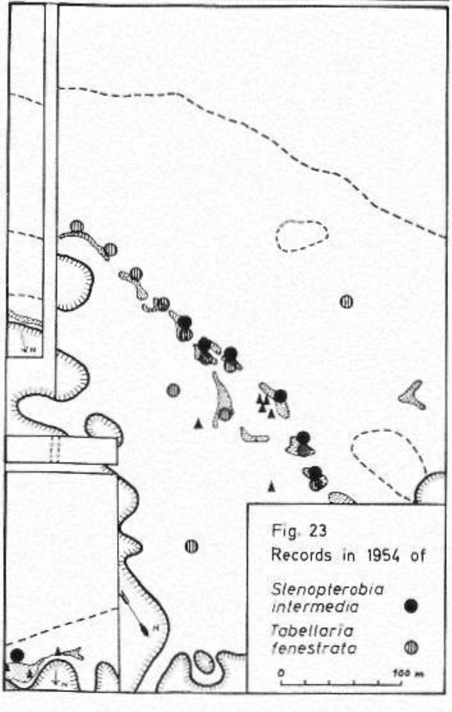

Fig. 23
Records in 1954 of
Stenopterobia intermedia ●
Tabellaria fenestrata ◍

Frustulia rhomboides EHRBG. Found in the Lönnstorpet, Stattute, and Bygget areas (Fig. 21). As on Store Mosse it does not occur on the bog.

Frustulia saxonica (RABENH.) DE TONI. One of the most common algae of the mire, found in all parts and in nearly all samples. In some samples it has a frequency of 75 %. Eurytopic on Store Mosse, too.

Gomphonema acuminatum EHRBG. var. *Brebissonii* (KÜTZ.) CLEVE. Found only in the Lönnstorpet area. Scattered in the rich fen areas of Store Mosse.

Navicula subtilissima CLEVE. Found in samples from all investigated parts of the mire. Usually very common, contrary to the conditions in Store Mosse where it is very rare.

Navicula sp. Undeterminable species found in the lagg of the Lönnstorpet area.

Nitzschia gracilis HANTZSCH. Found in two samples from 1949 in the Stattute area from 1952 in the fen soak of the Bygget area. Not found on Store Mosse or reported in THUNMARK 1942.

Nitzschia hantzschiana RABENH. Found only in the Lönnstorpet area.

Nitzschia sublinearis HUSTEDT. Found only in one brook pool sample in the Stattute area. Not found in Store Mosse or reported in THUNMARK 1942.

Pinnularia dactylus EHRBG. Found only in the Lönnstorpet area. Rare on Store Mosse.

Pinnularia gibba EHRBG. Found in the Lönnstorpet area, in the Stattute area (common along the row of brook pools as well as in the Inner and the Outer Fen) and in the fen sites of the Bygget area. Never found on the bog sites. Common in Store Mosse.

Pinnularia interrupta W. SMITH. Found only in the Lönnstorpet area. In Store Mosse most common in rich fen sites.

Pinnularia maior KÜTZ. Found in the Lönnstorpet, Stattute and Bygget areas (Fig. 22). Common on Store Mosse, especially in Lake Kävsjön and rich fen areas.

Pinnularia mesolepta (EHRBG.) W. SMITH. Found in one sample from the lagg fen of the Bygget area and 1952 in one sample from the Lönnstorpet area. On Store Mosse as *P. maior*.

Pinnularia microstauron (EHRBG.) CLEVE. Found in the Lönnstorpet area. Common along the row of brook pools and in the Outer Fen of the Stattute area as well as in the fen sites of the Bygget area. Scattered in most parts on Store Mosse except the bog areas.

Pinnularia nobilis EHRBG. Found in samples from 1949 and 1952 in the Lönnstorpet area as well as in three fen samples from different parts of the Stattute area. In Store Mosse in Lake Kävsjön and the rich fen sites.

Pinnularia stauroptera (GRUNOW) CLEVE. Here treated separated from *P. gibba* contrary to FLENSBURG 1967. Found in the Lönnstorpet area. Common along the row of brook pools as well as in the Inner and the Outer Fen of the Stattute area. In the Bygget area found in the lagg fen. This species has been noted also on Store Mosse.

Pinnularia viridis (NITZSCH) EHRBG. incl. var. *sudetica* (HILSE) HUSTEDT. Very common in all parts of the mire, both in fen and bog areas. Often in great quantities. Very widespread also on Store Mosse.

Stauroneis phoenicenteron EHRBG. Found in the Lönnstorpet area and in one brook pool sample from the Stattute area. In Store Mosse most common in rich fen sites.

Stenopterobia intermedia (LEWIS) FRICKE. Found in the Lönnstorpet and Stattute areas (Fig. 23). In Store Mosse most common in rich fen sites.

Synedra acus KÜTZ. Found only in the Lönnstorpet area. Not found on Store Mosse or reported in THUNMARK 1942.

Synedra ulna (NITZSCH) EHRBG. Noted in the Lönnstorpet area, in the Stattute area in a few fen samples and in fen sites of the Bygget area. In Store Mosse common in Lake Kävsjön.

Tabellaria fenestrata (LYNGB.) HUSTEDT. Found in the Lönnstorpet, Stattute and Bygget areas (Fig. 23, the dot in the Bygget area refer to this species). In Store Mosse around Lake Kävsjön and in the rich fen sites.

Tabellaria flocculosa (ROTH) KÜTZ. Found in the Lönnstorpet area, in the Stattute area in a few brook pool samples and in the Bygget area in the lagg fen. On Store Mosse as *T. fenestrata*.

PYRRHOPHYTA

PERIDINEAE (DINOMONADINEAE)

Glenodinium neglectum SCHILL. Found in the Lönnstorpet area. In Store Mosse mainly in Blådöpet.

Glenodinium uliginosum SCHILL. Found in the Lönnstorpet area and in the Stattute area where it is common along the row of brook pools and scattered in the rest of the area, even on the bog. In Store Mosse common in Lake Kävsjön but not found on the bog.

Peridinium cinctum (MÜLLER) EHRBG. Found in two brook pool samples from the Stattute area, in a sample from 1949 also in the Lönnstorpet area.

Peridinium quadridens STEIN. Found in one brook pool sample from the Stattute area. Not found in Store Mosse or reported in THUNMARK 1942.

DISTRIBUTION TYPES AMONG THE BENTHIC ALGAE

Even if many samples of benthic micro algae are studied these samples form only an extremely small part of the total area covered by such algae communities. Further only parts of the samples are studied microscopically. This means that there is a great chance to overlook occurrences of individual taxa. The seasonal and yearly variation in the occurrence of the algae influence the results of the studies, too. When comparing with the distribution of macrophytes one must always keep in mind that such plants are easily observed all over the mire during most of the vegetation period when walking round.

These problems may be illustrated with a comparison between the samples of algae from those points in the Stattute and Bygget areas which were sampled both in May and September 1954 (Table 1). The

Table 1. Number of species noted at the points sampled both in May and September 1954. Number of localities 17. Median value and range given.

	Number of species	Species noted only in one sample	
		Number	Percentage
May	27	7	25 %
	13—44	3—14	10 %—48 %
September	30	12	36 %
	12—54	1—24	6 %—50 %
Both occasions	39	18	51 %
	15—68	4—38	20 %—62 %

number of species noted in the samples on the two sampling occasions does not differ very much. On an average about half the number of taxa recorded from each point was noted only once. However, nearly all these taxa occur with a frequency less than 0.5 %. In the samples with a low number of taxa (samples from bog areas and most of the Outer Fen) the differences are much less, even measured as percentage, than in the samples with a great number of taxa, e.g., from the points 210 and 311 (total number 42 and 68, noted only once 27 and 38). Further it may be mentioned that the investigation of the samples from 1949 and 1952 has added only 14 new taxa or 7 % of the number recorded in 1954 while 75 taxa were not found.

This indicates that well-founded conclusions concerning the distribution of the micro algae mainly can be given only for such taxa which seem to occur with a rather high frequency and when a sufficient number of samples have been investigated. Therefore, any general grouping like that for the macrophytes of all the micro algae recorded on the mire is impossible. However, in spite of these facts it is possible to demonstrate distinct distribution types among the algae.

A great number of the benthic micro algae have only been noted in the fen sites of the Lönnstorpet area, e.g., several *Closterium* species, (*calosporum, costatum, lunula, Ralfsii,* etc.), *Cosmarium impressulum, C. moniliforme, Desmidium cylindricum, Euastrum oblongum, Micrasterias angulosa, M. rotata, Staurastrum controversum, S. dilatatum, Staurodesmus Joshuae,* and *Eunotia arcus.* These algae have a distribution corresponding to that of the *Sphagnum plumulosum* group among the macrophytes. These macrophytes are, however, few and of little importance in the vegetation.

Another group of species among the micro algae is found in the fen sites of the Lönnstorpet area and/or along the row of brook pools in the Stattute area, but not elsewhere in the mire. Some of them, e.g., *Closterium dianae, C. libellula, C. setaceum, Euastrum elegans, Micrasterias truncata,* and *Xanthidium antilopaeum* (Fig. 19) have in the Stattute area been found only in the upper (northwestern) part of the row of brook pools. In this area a few macrophytes referred to the *Sphagnum plumulosum* group have been found (e.g., *Hammarbya paludosa, Riccardia pinguis*). Some other algae in this group, however, have a wider distribution and have been found all along the row of brook pools, e.g., *Closterium baillyanum* (Fig. 5), *C. didymotocum, Cosmarium Blyttii, Euastrum bidentatum, Tetmemorus laevis* s.str. (Fig. 18), *Xanthidium armatum* (Fig. 19), and *Stenopterobia intermedia* (Fig. 23). Among the macrophytes such a distribution has been demonstrated for, e.g., *Utricularia minor,* referred to the *Menyanthes trifoliata* group.

A number of algae have a distribution resembling that of the most widespread species (e.g., *Menyanthes trifoliata*) in the *Menyanthes trifoliata* group, e.g., *Closterium abruptum, C. gracile, C. striolatum* (Fig. 5), *Euastrum pectinatum, Pinnularia maior* (Fig. 22), and *Tabellaria fenestrata* (Fig. 23). These algae occur all over the *Menyanthes trifoliata* zone, i.e., in the fen sites of the Lönnstorpet and Bygget areas as well as in the Inner Fen and along the row of brook pools in the Stattute area.

With reference to the macrophytic vegetation there is obviously a differentiation in the *Menyanthes trifoliata* zone between the Lönnstorpet, Stattute and Bygget areas along the poor—rich gradient in the vegetation (cf. MALMER 1962 a p. 128). Concerning the benthic micro algae 135 taxa have been noted in the two investigated sites in the Lönnstorpet area, among them 51 taxa (23 % of the total number on the mire), which only have been found there. As many as 132 algal taxa have been recorded in this zone in the Stattute area but the number of samples (28) is much greater than in the Lönnstorpet area. Many species have only been noted in one or two samples, especially in the sites along the row of brook pools. In the eight fen sites of the Bygget area only 53 taxa have been observed. The mean number of species noted in the samples is 85 in the Lönnstorpet area, 42 along the row of brook pools, 26 in the other parts of the *Menyanthes trifoliata* zone in the Stattute area and only 19 in the Bygget area. Comparisons with other investigations (THUNMARK 1942, DU RIETZ 1950 a—c, FLENSBURG 1967) show that with regard to the taxa of micro algae recorded, the Lönnstorpet area ought to be regarded as richer than the other areas and that there is a distinct gradient from this area to the others as well as within them. As far as distributions of taxa are concerned the differentiation of the *Menyanthes trifoliata* zone along this rich—poor gradient seems to be more conspicuous in the algal than in the macrophytic vegetation.

In the Outer Fen of the Stattute area 107 taxa of micro algae have been noted. Among them there are several occurring in the *Menyanthes trifoliata* zone and in the adjacent parts of the Outer Fen but lacking further bogwards, e.g. *Cosmarium Hammeri, C. pseudopyramidatum* (Fig. 6), *C. Ralfsii, C. venustum, Eunotia parallela, Frustulia rhomboides* (Fig. 21), *Pinnularia gibba, P. microstauron*, and *P. stauroptera*. Sharp distribution limits are difficult to distinguish but in most cases they seem to correspond rather well with the limits for the species of the *Eriophorum angustifolium* group among the macrophytes.

Many taxa in the Outer Fen have a distinct distribution limit coinciding rather well with the hydrologic mineral soil water limit, e.g., *Cosmarium subtumidum* (Fig. 7), *Euastrum ampullaceum, E. crassum, E. insulare* (Fig. 8), *Netrium digitus* (Fig. 10), *Penium borgeanum* (Fig. 11), *Tetmemorus Brebissonii* var. *minor* (Fig. 16), *T. granulatus* (Fig. 17). These species have a distribution resembling that of the *Narthecium ossifragum* group among the macrophytes. On the Åkhult mire they ought to be regarded as exclusive fen plants as all the other taxa treated above. A few species (e.g., *Pleurotaenium minutum* and *Staurodesmus isthmosus* (Fig. 14) which have been noted more or less occasionally in bog samples close to the mineral soil water limit but not elsewhere on the bog may be included in this group, too.

Some species in the Outer Fen have not been noted in more than a few samples outside this area, in spite of the fact that they are rather common there, e.g., *Cosmarium Ralfsii, Euastrum cuneatum* (Fig. 8), *Micrasterias Jenneri* (Fig. 10), *M. oscitans* (Fig. 10), *Penium borgeanum* (Fig. 11), *Pleurotaenium minutum* and *P. tridentulum* (Fig. 11). Among the macrophytes, e.g., *Lycopodium inundatum, Sphagnum compactum*, and *S. molle* have a distribution corresponding to that of these micro algae.

The number of species in the bog areas is lower than in the other parts. Excluding four taxa noted only in one or two samples near the mineral soil water limit in the Stattute area, 42 taxa have been found in the bog areas (41 on the Great Bog and 16 on the Small Bog). Most of them are rather evenly distributed over most of the investigated parts of the mire. Among them, e.g., *Chroococcus turgidus, Mougeotia* sp. (5—10 μ), *Zygogonium ericetorum, Actinotaenium cucurbita, Cosmarium pygmaeum* (Fig. 7), *Cylindrocystis Brebissonii, Frustulia saxo-*

nica, Navicula subtilissima, and *Pinnularia viridis* occur on both the Small Bog and the Great Bog. Rather evenly distributed but lacking on the Small Bog are, e.g., *Anabaena* sp., *Oocystis solitaria, Bambusina Borreri, Staurastrum margaritaceum* (Fig. 13), *Tetmemorus laevis* var. *minutus* (Fig. 18), *Eunotia lunaris* (Fig. 20), and *Dinobryon divergens.* Six taxa, viz., *Cosmarium depressum* (lacking on the Great Bog), *C. pseudoexiguum* (Fig. 6), *Netrium oblongum* s.str. (Fig. 10), *Penium silvae-nigrae* (Fig. 12), *P. silvae-nigrae* var. *parallelum* (Fig. 12), *Staurastrum Simonyi* (lacking on the Small Bog), and *Tetmemorus Brebissonii* var. *intermedius* (Fig. 16) have their main distribution in bog areas. Outside these areas they occur mainly in the Outer Fen. Only occasionally they have been noted in the *Menyanthes trifoliata* zone. No taxa have been found only in bog areas.

The distribution types of these facultative bog taxa among the micro algae correspond well with those among the macrophytes of the bog areas as described above (pp. 273—274). Even such a peculiar one as that of *Sphagnum imbricatum,* which occurs mainly in the bogs and in the *Menyanthes trifoliata* zone (cf. MALMER 1962 a p. 65) can be demonstrated among the micro algae, e.g., by *Eunotia exigua* (Fig. 20) and *Glenodinium uliginosum.*

DISCUSSION

As for the macrophytes the distribution pattern on the Åkhult mire for the micro algae treated here shows a rather gradual transition from the Lönnstorpet area (regarded as the richest part) to the bog areas, especially the Small Bog (designated as the poorest part along this gradient). However, when regarding just the floristic distribution limits among the micro algae the border line just outside the row of brook pools between the *Menyanthes trifoliata* zone and the Outer Fen seems to be especially important in the investigated parts of the Stattute area. The same limit, but still more distinct, is found between fen and bog in the Bygget area. It is indicated with two main groups of algae, viz., the more than 100 taxa which occur only in the *Menyanthes trifoliata* zone and the less numerous which are more or less confined to the Outer Fen and the bog areas. Neither in the Outer Fen nor along the hydrologic mineral soil water limit does it seem possible to distinguish any limit equally well indicated.

In the Outer Fen there is a transition from the *Menyanthes trifoliata* zone with its great number of taxa to the *Eriophorum vaginatum* zone of the Great Bog with its low number. Especially interesting in this case is the occurrence of transitional border zones between taxonomically related species as *Netrium digitus* and *Netrium oblongum* s.str. (Fig. 10), *Tetmemorus Brebissonii* var. *minor* and *Tetmemorus Brebissonii* var. *intermedius* (Fig. 16) or the not as especially related considered *Cosmarium pseudopyramidatum* and *C. pseudoexiguum* (Fig. 6).

The general pattern for the distribution of the micro algae on the Åkhult mire demonstrated above is in accordance with that found on the Store Mosse. The greater number of taxa noted there (about 400) depends on the greater variation of investigated sites as even lake shores and different types of rich fen areas have been included.

Many taxa, which on the Åkhult mire occur only in the *Menyanthes trifoliata* zone, are much more widespread on Store Mosse (FLENSBURG 1967). This is especially obvious for the taxa more or less confined to the fen sites in the Lönnstorpet area and the row of brook pools, most of which seem to have their main distribution in mire areas with rich fen vegetation, e.g. *Euastrum oblongum*. However, there are also taxa as, e.g., *Penium polymorphum* and *Pinnularia subcapitata* which are very rare or lacking on the Åkhult mire in spite of the fact that they are common even in the bog areas of Store Mosse.

Some widespread taxa on the Åkhult mire are for some reason very rare or lacking on the Store Mosse. Among them *Oocystis solitaria, Cosmarium pygmaeum, Euastrum cuneatum, Penium borgeanum, Dinobryon divergens*, and *Navicula subtilissima* were equally common 1949 and 1952 as 1954 while *Cosmarium pseudoexiguum* and *Staurodesmus isthmosus* seem to have been much less common and *Euastrum crassicolle* much more common in 1952 than in 1954. These three species have not been reported from central South Sweden before.

This survey of the benthic micro algae on the Åkhult mire and their distribution has demonstrated a great resemblance in the general distribution pattern between the macrophytes and the algae as far as the poor—rich gradient of variation in the vegetation is concerned. The available samples have not made it possible to study the other gradients. A general discussion about the habitat conditions on the Åkhult mire in relation to the poor—rich gradient in the vegetation is found in MALMER 1962 a pp. 181—183, 213—216, 218 and 1962 b pp. 10—11.

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New and Noteworthy Species of Primulaceae from the 'Flora Iranica'-Area

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ABSTRACT

WENDELBO, P.: New and Noteworthy Species of Primulaceae from the 'Flora Iranica'-Area. — Bot. Notiser 123: 300—309, Lund.

The following new taxa are described: *Androsace podlechii* of sect. *Chamaejasme* (NE. Afghanistan); *Dionysia esfandiarii* of sect. *Anacamptophyllum* (S. Iran); *D. freitagii* of sect. *Dionysiastrum* (N. Afghanistan); and *D. termeana* of sect. *Dionysia* (S. Iran). *Primula algida* ADAM, *P. gaubaeana* BORNM. and *P. kaufmanniana* REGEL are recorded as new to the flora of Afghanistan. *Primula dueckelmannii* GILLI previously known only from the type collection, has been recollected. It is endemic to NE. Afghanistan. The find of *P. gaubaeana* in SW. Afghanistan is of considerable phytogeographical interest as the species was previously known from SW. Iran only.

INTRODUCTION

Large areas of Afghanistan and Iran, the main countries covered by K. H. RECHINGER's 'Flora iranica', are still unexplored or inadequately known from a botanical point of view. Every collection from the more remote parts of these countries reveals interesting and often surprising finds. The family *Primulaceae* was treated for this flora by WENDELBO (1965). In addition to a previously described species of *Dionysia* (WENDELBO 1967), recent collections contain no less than 4 new species of this family and several other finds of considerable interest. Three of the new species described below belong to the genus *Dionysia* comprising obligate chasmophytes many of which are narrow endemics. 28 species were treated in the last monograph (WENDELBO 1961 a), since then 10 species have been added including the ones described in this paper (WENDELBO 1964, 1967). There is every reason to expect further new species of *Dionysia* to be discovered in the future.

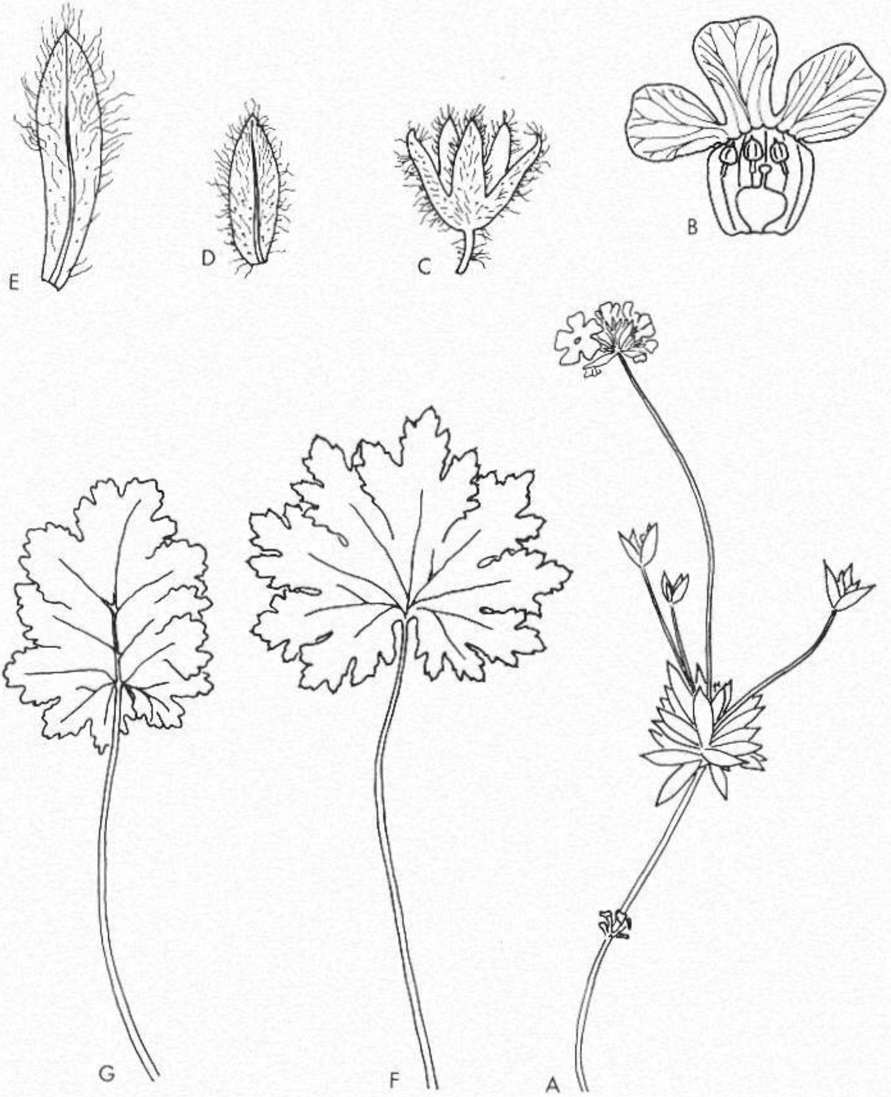

Fig. 1. — A—E: *Androsace podlechii* WENDELBO; PODLECH 11741 (M). — A: Habit, hairs not drawn. — B: Part of corolla with ovary. — C: Calyx with pedicel. — D: Bract. — E: Leaf. — F: *Primula dueckelmannii* GILLI; PODLECH 10624 (M). Leaf, hairs not drawn. — G: *P. kaufmanniana* REGEL; PODLECH 11093 (M). Leaf, hairs not drawn. — A ×1; B—E ×4; F—G ×0.5. — ELLEN SCHJÖLBERG del.

Androsace podlechii WENDELBO, sp. nov. — Fig. 1 A—E

Sect. *Chamaejasme* C. KOCH

Herba perennis stolonifera, pilis usque ad 1.2 mm longis articulatis et glandulis brevibus capitatis obsita. *Stolones* 1—3, e rosulis foliorum orientes usque ad 3 cm longi, interdum foliis dissitis obsiti, demum brunnescentes, glabri. *Folia* rosulata, 6—13 mm longa, 1.6—3.3 mm lata, anguste elliptico-obovata, acuta. Scapi e centro rosulae foliorum orientes, 4—8 cm longi. *Umbella* 5—8-flora, densa. *Bracteae* c. 5 mm longae, elliptico-ovatae. *Pedicelli* 1.5—2 mm longi. *Calyx* vix 4 mm longus, campanulatus, per 2/3 longitudinis in lobos ovato-oblongos obtusos divisus. *Corolla* rotata, verosimiliter alba purpurascenti-suffusa, annulus flavus; tubus c. 3.5 mm longus, doliiformis; lobi c. 3.5 mm longi, vix 3 mm lati, subobovati, apice retusi. *Filamenta* 0.5 mm longa, supra medium tubum inserta; antherae 0.6 mm longae, mucronulatae. *Ovarium* depresso-globosum. Stylus 1 mm longus; stigma capitatum.

Afghanistan. Takhar: Khost-o-Fereng, slopes northeast of the Yawnu-pass towards the upper Kala-valley, 3100 m, granite, 10.VII.1965, D. PODLECH 11741 (holotypus M).

The new species is rather similar to *A. akbaitalensis* DERG. and *A. olgae* OVCZ. It differs from the former in the narrowly elliptic-obovate leaves with a different pubescence, the much larger calyx with comparatively much longer, ovate-oblong — not broadly triangular-ovate — teeth, as well as in the much larger corolla. It differs from *A. olgae* first of all in the larger calyx with comparatively much longer and narrower lobes. The calyx of *A. podlechii* looks green because of the more open and spreading pubescence. It also has a corolla which is larger in all parts.

The new species is named in honour of its discoverer Dr. D. PODLECH of Munich who collected extensively in NE. Afghanistan in 1965.

Dionysia esfandiarii WENDELBO, sp. nov. — Fig. 2 M—N

Sect. *Anacamptophyllum* MELCHIOR

Caespites parvos densissimos griseo-pilosos, efarinosos, c. 7 cm diametro formans. *Rami* foliis pallide cinerascenti-brunneis obsiti. *Folia* petiolo incluso c. 4 mm longa, lineari-oblonga, apice rotundata; lamina 1—1.5 mm longa, 0.6—0.8 mm lata, margine integra revoluta, supra pilis patentibus usque antrorsis apice et margine revoluto pilis retrorsopatentibus usque retrorsis obsitae; petiolus latus, indistinctus, margine pilis dispersis, faciebus pilis brevioribus obsitus; pili usque ad 0.5 mm longi, articulati. *Bracteae* 2, lineares, acuminatae, brevissimae 2.5×0.2 mm, longissimae 4×0.4 mm, subtus pilis patentibus retrorsis, margine pilis patentibus, supra pilis ± antrorsis obsitae; pili c. 0.3 mm longi. *Flores* solitarii, sessiles. *Calyx* probabiliter non complete evolutus vix 4 mm longus, usque ad dimidum circiter in lobos lineari-triangulatos acuminatos fissus, extus pilis retrorsis, in margine loborum pilis patentibus, intus pilis antrorsis obsitus; pili usque ad 0.4 mm longi. *Corolla* inevoluta tantum nota, violacea, extus pubescens, pilis c. 0.1 mm longis; lobi obcordati. *Ovarium* quinque-ovulatum.

Iran. Fars: Abadeh, Bavanat, Kuh Khataban, 3100 m, 23.VI.1969, TERMÉ 8128 E (holotypus GB, isotypus IRAN.)

D. esfandiarii is a very distinct new species of the sect. *Anacamptophyllum* MELCHIOR subsect. *Revolutae* WENDELBO. It differs from all the other species of its subsection in the combination of being densely tufted, having an entire leaf margin and a violet flower as well as in its peculiar pubescence consisting of retrorse and antrorse long hairs. Unfortunately the plant is in a young state and it has been impossible to study fully developed flowers.

D. esfandiarii is named in honour of Dr. E. ESFANDIARI, the head of the "Herbarium Ministerii Iranici Agriculturae", Teheran.

Dionysia freitagii WENDELBO, sp. nov. — Fig. 2 A—F

Sect. *Dionysiastrum* SMOLJAN.

Caespites densos cinerascenti-virides, glanduloso-puberulos, efarinosos, usque ad 30 cm diametro formans. *Rami* lignosi, usque ad 4 mm diametro, rosula foliorum cinerascenti-viridi terminati, foliis emarcidis violaceo-brunneis partim rosulatis, rosulis 5—15 mm inter se remotis, partim inter rosulas dispersis obsiti. *Folia* usque ad 5 mm longa et 3 mm lata, ea surculorum juvenilium et basalia rosularum elliptica, basi in petiolum inferne dilatatum attenuata, apice rotundata usque ad acuta; folia cetera rosularum subrhombica usque aliquantum angulato-elliptica, basi lata, apice acuta usque ad subacuta, nervatura supra prominente. *Bracteae* 2, c. 1.5 mm longae, una elliptica, breviter late petiolata, altera anguste elliptico-oblonga. *Flores* solitarii, subsessiles, heterostyli. *Calyx* 4.5—5 mm longus, anguste campanulatus, usque paulo infra medium in lobos anguste elliptico-oblongos subacutos divisus, extus et intus glanduloso-puberulus. *Corolla* hypocrateroides, violacea vel purpureo-violacea?, extus glanduloso-puberula; tubus 15—16 mm longus; lobi c. 5 mm longi, late obovati, apice emarginati. *Antherae* vix 2 mm longae, in floribus brevistylis paulo exsertae, in floribus longistylis manifeste ultra medium tubi insertis. *Ovarium* 3—5-ovulatum. *Stylus* longus faucem corollae tubi vix attingens; stylus brevis c. 2/3 corollae tubi attingens; stigma capitatum. *Capsula* c. 3 mm longa, ovoidea, valvis 8—9 dehiscens. *Semina* 3—5, submatura, c. 2 mm longa, elliptica, plana.

Afghanistan. Balkh: Ali Kuh, mountain 18 km S of Mazar-i Sharif, 1300—1700 m, 29.V.1969, HEDGE, WENDELBO & EKBERG W. 8497 (holotypus GB, isotypus E); 18 km S of Mazar, Sultan Baba Ali Sher, 800 m, FREITAG 185.

The new species has leaves that are more or less dimorphic, those of the shoots and of the base of the rosettes are elliptic with a rounded to acute apex and have a short broad petiole which is again widened at the base. The leaves of the middle part of the rosette are subrhombic with a more or less acute apex, and are narrowed from above the middle into a rather broad base.

Dionysia freitagii must be referred to the section *Dionysiastrum* SMOLJAN. and is most closely related to *D. viscidula* WENDELBO. It differs from that species in the larger corolla and calyx, the smaller indistinct bracts, in the comparatively broader and more acute rosette leaves, and in the distinctly shorter glands. *D. viscidula* is so far only known from the valley Darrah Zang near Maimana about 200 kilometers to the south-west from the locality of *D. freitagii*.

The species is named in honour of its discoverer Dr. H. FREITAG working at the Department of Botany, University of Kabul as member of the "Partnerschafts-Team der Mathematisch-Naturwissenschaftlichen Fakultät Bonn a.d. Universität Kabul".

Fig. 2. — A—F: *Dionysia freitagii* WENDELBO; HEDGE, WENDELBO & EKBERG W 8497 (GB). Glands not drawn. — A: Corolla of longstyled flower. — B: Corolla of shortstyled flower. — C: Calyx split open. — D: Bracts. — E—F: Leaves. — G—L: *D. termeana* WENDELBO; TERMÉ 8131 (GB). — G: Corolla of longstyled flower, glands not drawn. — H: Calyx split open. — I: Bracts. — J—L: Leaves. — M—N: *D. esfandiarii* WENDELBO; TERMÉ 8128 (GB). — M: Leaf from above. — N: Leaf from below. — A—N ×4. — ELLEN SCHJÖLBERG del.

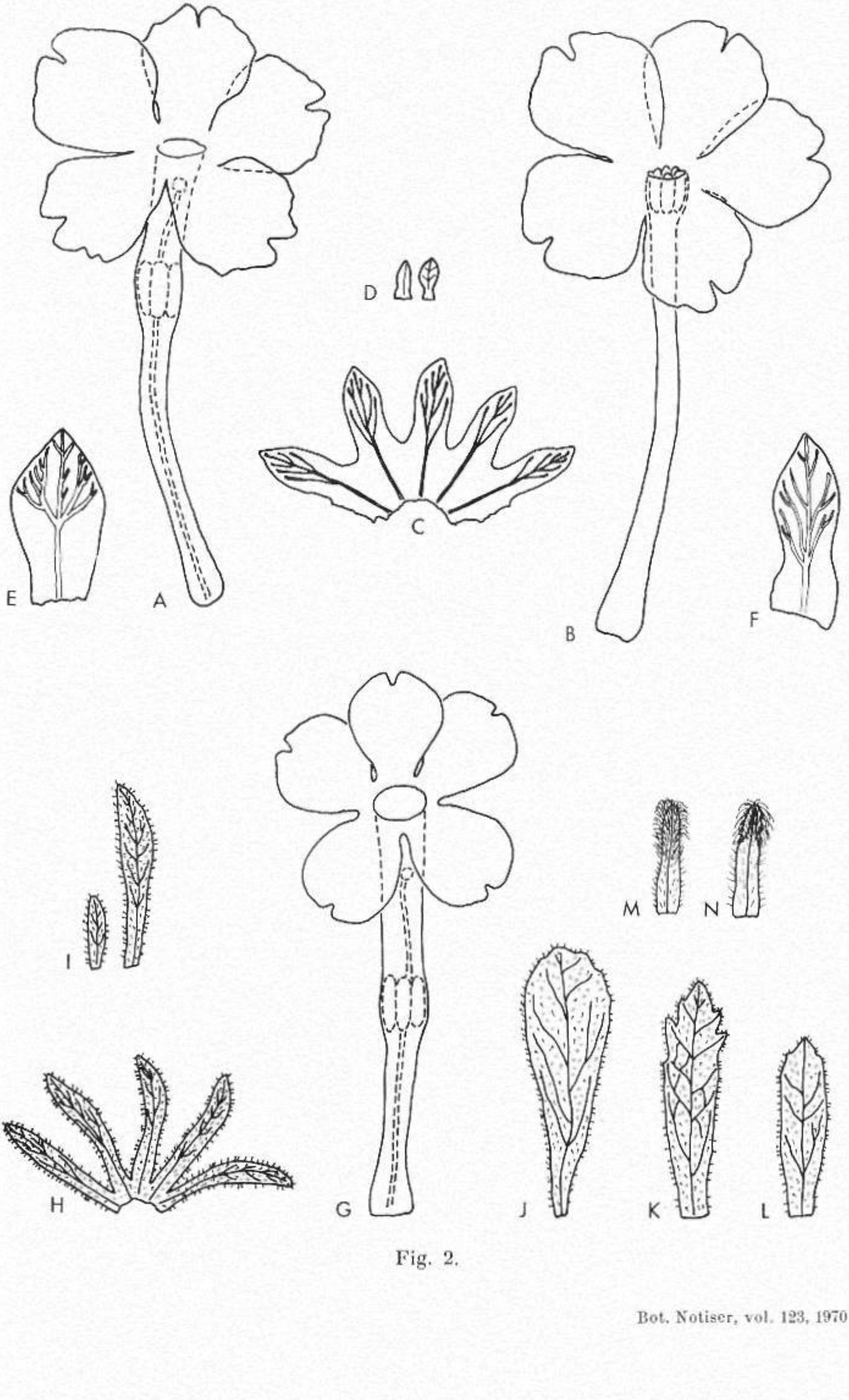

Fig. 2.

Dionysia termeana WENDELBO, sp. nov. — Fig. 2 G—L

Sect. *Dionysia*

Laxe caespitosa, glanduloso-pubescens, efarinosa, foliis emarcidis rosulatis, rosulis foliorum in ramis inter se 1—1.5 cm remotis. *Folia* reticulato-nervosa, glandulosa; glandulae vix 0.2 mm longae; folia exteriora rosularum et folia surculorum juvenilium usque ad 11 mm longa, 4—5 mm lata, ± obovato-spathulata, subintegra vel ± distincte 1—6-crenata, obtusa usque subacuta; folia interiora 6—9(—11) mm longa, 2—2.5 mm lata, lineari-oblonga, subintegra vel usque ad 5—6-crenata, obtusa usque subacuta. *Bracteae* 2, 2.5 et 7 mm longae, anguste ellipticae, usque oblanceolatae, obtusae. *Flores* solitarii, sessiles, heterostyli. *Calyx* 5—6 mm longus, usque ad basin fere in lobos ± lineares, obtusos, c. 0.7 mm latos fissus. *Corolla* hypocrateroides, flava; tubus floris longistyli 15—17 mm longus; lobi 4—5 mm longi, 3.5—4 mm lati, emarginati. *Antherae* 1.5—2 mm longae. *Capsula* quinque valvis. *Semina* c. 8.

Iran. Fars: Sissakht, Kuh Daena to Gadaneh-Bidjan, 20.VI.1969, TERMÉ 8131 E (holotypus GB, isotypus IRAN).

Undoubtedly this new species belongs to sect. *Dionysia* subsect. *Caespitosae* WENDELBO. It differs, however, from all other species of its subsection in having emarginate corolla-lobes, and also in the calyx which is split to the very base. *D. termeana* comes closest to *D. diapensiifolia* BOISS. and *D. gaubae* BORNM., but differs in addition to the characters mentioned above, also from the former in the much looser tufts with separated rosules of old leaves, from the latter in the apparently much larger tufts and in the longer and narrower inner leaves of the rosette.

D. termeana is named in honour of its discoverer Ing. FEREYDOUN TERMÉ of the Department of Botany, Plant Pest and Diseases Research Institute, Teheran.

Primula algida ADAM in WEBER & MOHR, Beiträge Naturk. 1:46 (1805)

WENDELBO in Flora iranica 9:11 (1965).

Afghanistan. Wakhan: Dario Wazit, N of Wazit gorge, 4600 m, BRECKLE A 1247.

Previously this species has not been found in Afghanistan, but it is recorded from the Pamir-Alai area in the USSR somewhat to the north.

There is a considerable gap in the distribution of *P. algida* as it is known from C. Asia and then from Caucasus and the Kurdish mountains. It is much the same area as that of the likewise alpine *Allium oreophilum* C. A. MEY. Very few species seem to have a similar disjunct area.

Primula dueckelmannii GILLI, Feddes Repert. 62: 22 (1959). — Fig. 1 F

WENDELBO in Flora iranica 9: 5 (1965).

Afghanistan. Takhar: Koh-i-Ishkamish, ca. 7 km south-east of Ishkamish, shady slopes, 1500 m, PODLECH 10624. — Badakhshan, above Jawarsan, c. 30 km S of Keshm, 1600 m, HEDGE & WENDELBO W. 9320.

This species was previously known from the type collection which consisted of flowering plants only. It flowers in the beginning of April (GILLI 1959 p. 22). The material of PODLECH collected 14 May 1965 is in fruit. The capsules are ellipsoid, 7—8 mm long, 45 mm broad and somewhat protruding from the calyx.

P. dueckelmannii (W. 9320) was found as willed fragments under stones at c. 1600 m altitude in *Pistacia vera* — *Amygdalus bucharica* — *Acer pentapomicum* woodland with scattered *Juniperus* cfr. *semiglobosa*. This is probably a typical locality and there is reason to think that the rarity of this species is due the fact that this type of forest has been destroyed over extensive areas. The likewise rare endemic *Salvia pterocalyx* HEDGE was found in the same place and very probably these two species have more or less the same distributional area which they share with a whole group of other endemic species (Fig. 3).

Primula gaubaeana BORNM. Mitt. Thür. Bot. Ver. N.F. 47: 132—137 (1941)

WENDELBO in Flora iranica 9: 4, Tab. 1, Fig. 1 (1965).

Afghanistan. Farah: 15 km N of Golestan, stream-side with *Carex* sp. and *Epipactis* sp., 2100—2200 m, 23.IV.1969, flowers yellow, HEDGE & EKBERG W. 7282.

The Afghan plants do not differ significantly from available Iranian material. The calyx may be somewhat larger and the bracts may have a somewhat different shape. Even if these differences should be constant the Afghan population should probably not be treated as more than a geographical race of the rank of subspecies.

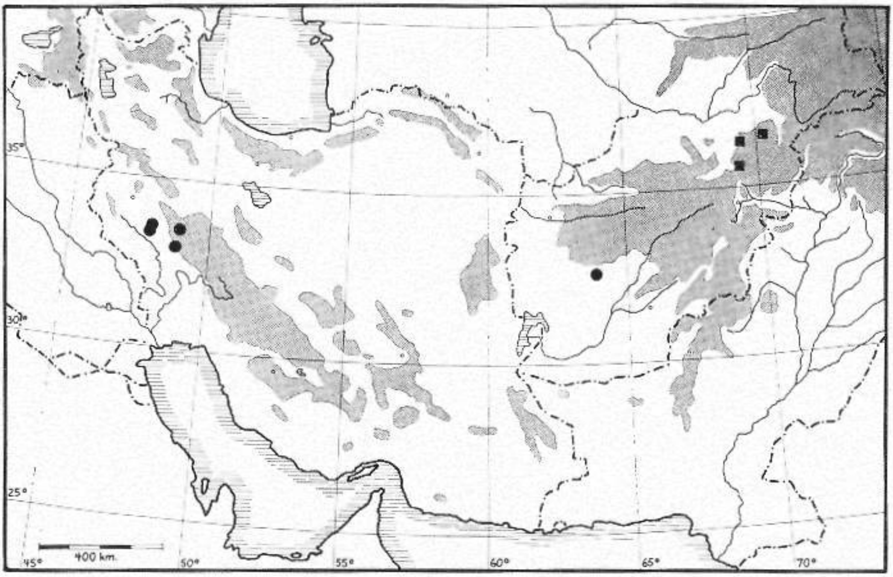

Fig. 3. Total distribution of *Primula dueckelmannii* GILLI (■) and *P. gaubaeana* BORNM. (●). Half-tone indicates areas with mountains above 2400 m.

The find of *P. gaubaeana* in Afghanistan is of considerable phytogeographical interest. The locality 15 km north of Golestan in the province of Farah (32°45′N, 63°45′E) is situated about 1400 km east of the previously known localities in Iran (Fig. 3). The 6 known species of *Primula* subgenus *Sphondylia* are scattered over a large area: NW. Himalayas, Afghanistan, Ethiopian mountains, Yemen, Sinai, W. Iran and SE. Turkey (WENDELBO 1961 b). They are undoubtedly relics from a period with a moister climate when ancestral forms of this group were scattered over this area. The geographical area of *P. gaubaeana* must earlier have covered South Iran and parts of Afghanistan. Even if the western and eastern populations have been separated for a long span of time no marked differentiation has taken place in this case. The disjunct area of *P. gaubaeana* is remarkable, but a good parallel is found in the distribution of certain large-leaved *Dionysiae*. Thus *D. bornmuelleri* (PAX) CLAY in West Iran has its closest relatives in two Afghan species, *D. paradoxa* WENDELBO and *D. balsamea* WENDELBO & RECH. f. (WENDELBO 1964).

Primula kaufmanniana REGEL, Acta Horti Petrop. 3:131 (1874). — Fig. 1 G

FEDOROV in Fl. USSR 18:126, Tab. IV, Fig. 1 (1952).

Afghanistan. Baghlan: Andarab-valley, southern side-valley of the Taganak valley at Darrah-i-Shu, 3000 m, PODLECH 11093. — Badakhshan, Khumbuk area, S. of Keshm, side valley to the SW of Robat, 3000 m, HEDGE & WENDELBO W. 9403.

These are the first records of this species from Afghanistan and from outside the USSR. It is an extension of the area by about 250 km to the SW.

The Afghan specimens match the description and figure of FEDOROV (l.c.). I have also seen several sheets of *P. kaufmanniana* kindly sent on loan by Dr. I. T. VASSILCZENKO from the Leningrad herbarium. The only other species of sect. *Cortusoides* in Afghanistan is the rare endemic *P. dueckelmannii* GILLI (see above) which differs markedly in the much more deeply cut leaves (Fig. 1 F—G).

P. kaufmanniana (W. 9403) was found at c. 3000 m altitude near the upper limit of the *Juniperus* cfr. *semiglobosa* belt were it grew in rich subalpine vegetation.

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Vegetation Types of Planted Spruce Forests in Scania, Southern Sweden

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ABSTRACT

NIHLGÅRD, B.: Vegetation Types of Planted Spruce Forests in Scania, Southern Sweden. — Bot. Notiser 123: 310—337, Lund.

Vegetation analyses and soil investigations from 87 localities with planted spruce forest, situated south of the natural border area for *Picea abies* in Scania, have been performed. Most of the stands are old with a well developed ground vegetation, some are young, and some are situated side by side with beech forests. In this way a picture of the different vegetation types, of the development of the vegetation in young and dense spruce plantations and of the floristic changes when beech forests are replaced by spruce is obtained.

Five different vegetation types, separated by different dominating species, are discussed from an ecological point of view, considering in particular, the soil and light conditions. Rough estimations of the productivity of the tree layer are also discussed.

The main species dominating in the vegetation types are: *Dicranum majus, D. scoparium, D. undulatum, Hypnum cupressiforme, Plagiothecium* spp., *Pleurozium schreberi, Deschampsia flexuosa, Oxalis acetosella, Dryopteris austriaca, Rubus idaeus, Sorbus aucuparia, Sambucus nigra* and *S. racemosa*.

INTRODUCTION

The southern boundary of the natural distribution of spruce (*Picea abies*) in Sweden, passes through the north part of Scania (Fig. 1). According to pollen analytic investigations (FRIES 1965) this border area has existed for about 1500 years. However, during the last 100 years spruce has also been planted outside its natural borders in the southern deciduous forest region, which belongs to the Nemoral zone (SJÖRS 1965). The plantations have been performed either on formerly grazed heathlands and arable land or replacing beech forests. Owing to the relatively low financial potential of beech forests and grazing pastures, the spruce plantations have increased during recent decades and it seems probable that in the near future spruce forests will prevail in the deciduous region also.

Having in view a clarification of the vegetation types and the floristic changes which we can expect to find to an ever increasing extent in step with the increasing area of planted spruce forests, the present studies have been made in the southern deciduous forest region of Scania during the years 1966—1969.

INVESTIGATION METHODS

A great number of planted spruce forests south of the natural border of *Picea abies* in Scania have been investigated. The sites chosen for analysis were situated over the whole area (Fig. 1), representing all the different vegetation types obtainable. The stands were 20—85 years old and thus information on the succession of vegetation with age and thinnings was also obtained. The vegetation of the stands was delimited by analysing one large square only, about 2000 m^2, at each locality. Only homogeneous areas representative of the forests were chosen and investgated, thereby avoiding boundary vegetation.

In order to demonstrate the floristic differences that develop when spruce is planted on former beech forest areas, some localities with both beech and adjacent old spruce forests were analysed. The selection of these double localities was governed by two criteria:

1. The two stands should lie side by side on as flat ground as possible: if situated on a slope the inclination should be uniform.

2. It should be proved, by speaking to the landowner or by studying old land-surveying maps, that beech forest once preceded the planted spruce forest.

On the double localities the stands have been delimited by the choice of two large squares, each 1000—2500 m^2, which have been placed as near each other as possible, in practice at a distance of 30—50 m. In this way the primary differences of the mineral soil composition between the stands ought to be small. Areas with boundary vegetation, and in the spruce forest areas with beech litter were avoided as far as possible.

The vegetation analysis comprised investigations of the tree, shrub, field, and bottom layers inside the large square.

The tree layer was investigated on the following data:

1. Stand density was determined in the spruce forests by counting numbers of trees inside five squares of 100 m^2. In the beech forests all trees inside the large square were counted.

2. Cover of the tree crowns was estimated as a percentage of the area of the large square.

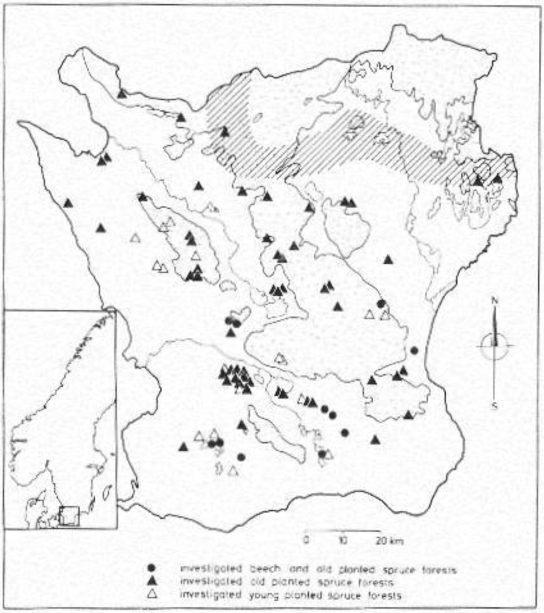


Fig. 1. Map of Scania in Southern Sweden, showing the situation of the investigated localities. The southern border area of the natural distribution of spruce is marked with hatched lines (after HESSELMANN & SCHOTTE 1906). Areas situated more than 100 metres above sea level are dotted. Map of Scandinavia inserted.

3. Age of the trees was determined by boring at breast height in a typical tree with an increment borer. This was possible in the spruce forests where the trees were of the same age. In the beech forest the trees were unevenaged and then the average age was estimated from random borings, and using information obtained from other localities.

4. Measurements of height of the trees and tree crowns were performed using a Blume-Leiss instrument. To obtain average values some typical, subjectively chosen trees were measured from each stand.

5. Average values of diameter of the trees were obtained after measuring ten trees from each stand.

The shrub layer. The cover of the shrub layer was estimated as a percentage of the large square. *Rubus idaeus* was not included.

The field and bottom layers (=the groundlayer) were analysed by placing ten small squares each of 16 m^2, in a fixed pattern, in order to get a uniform distribution inside the large square. The species inside the small squares were noted and their cover, according to the five-degree scale of HULT—SERNANDER—DU RIETZ, was estimated. Species in the large square, which were not represented in the small squares, were afterwards added to the list and are marked with + in the tables. Bryophytes and lichens on stones or stumps were not included in the analysis.

In the vegetation survey tables the small square frequency (F) and the characteristic degree of cover (C) are given as F^C. F denotes the number of small squares in which the species occur calculated as a percentage of the total number of small squares. C is an average value of the degree of cover. At its calculation the degrees of cover for each small square are first transformed to mean absolute values of the area covered and then the average of these is retransformed to degree of cover (cf. PERSSON 1961). In Table 1 and Fig. 2 the cover of the vegetation in m^2/m^2 is given. This has been calculated from the units in the HULT—SERNANDER—DU RIETZ scale. Using a small square of 16 m^2 the following means are valid:

$$1 = 0.5\ m^2,\ 2 = 1.5\ m^2,\ 3 = 3.0\ m^2,\ 4 = 6.0\ m^2 \text{ and } 5 = 12.0\ m^2.$$

The total small square area analysed at each locality is 160 m^2. By summing the plant cover of every species in the ten small squares this value is often exceeded, which obviously is natural; firstly because both the field and bottom layers are summed, and secondly because there is a natural stratification in several layers even in the field layer. The calculation certainly gives very rough values but these are useful in comparisons and in illustrating the development of the vegetation in planted spruce forests.

The nomenclature for phanerogams and ferns follows WEIMARCK (1963), bryophytes ARNELL (1956), NYHOLM (1954—1965) and JENSEN (1939).

It has not been possible to separate *Dryopteris assimilis* (NANNFELDT 1966) from *D. austriaca*. Both species appear in the investigated forests.

Besides the vegetation analyses investigations on the soil type were performed. One profile of 50—100 cm depth was dug inside each large square. — The validity of this profile was checked with smaller pits over the whole square. — In particular the thicknesses of the different upper horizons, the soil structure and texture were noted. Soil samples for determination of pH were taken in the mor or mull horizon (F/H or A_1), in the horizon just below the mor or mull (A_2 or B_1) and in the B/C-horizon usually at a depth of about 50 cm. pH was determined on duplicated fresh soil samples both in extracts of water and of 0.2 M KCl. The volume proportion soil: solution was 1: 2 and the extraction time one hour.

THE DEVELOPMENT OF THE VEGETATION IN SPRUCE PLANTATIONS

The development of the vegetation in spruce forests is earlier treated inter alia by OTT (1966) who studied the effects of thinnings, RHEINHEIMER (1959) and SCHLÜTER (1966) who studied the light and the vegetation in glades. The above authors found that small differences in light could cause great differences in vegetation. RHEINHEIMER (1957) reports that in planted spruce forests near Hamburg, three species were commonly occurring, viz. *Plagiothecium curvifolium*, *Lophocolea heterophylla*, and *Lepidozia reptans*. BECHER (1963) has followed the disappearance of the ground vegetation in small spruce plantation squares and noticed that almost every one of the former beech forest species disappeared. THILL (in NOIRFALISE 1964) reports

Table 1. Vegetation survey table showing the immigration of species in the bottom and field layers of young planted spruce forests in Scania. The stands are arranged according to increasing cover of the vegetation. Species dominating in old spruce forests are underlined. (juv) = juvenile plants. *Plagiothecium* spp. includes *P. curvifolium*, *P. denticulatum* and *P. succulentum*. *Dryopteris* spp. (juv) includes *D. spinulosa* and *D. austriaca*. *Galeopsis* spp. includes *G. bifida* and *G. tetrahit*. *Sambucus* spp. includes *S. nigra* and *S. racemosa*. *Quercus* spp. includes *Q. petraea* and *Q. robur*.

Spruce forest stand No.	51	41	52	3	20	11	6	49	23	21	18	17	1	2	13	47	48
Cover of the vegetation, m^2/m^2	0.03	0.05	0.08	0.10	0.11	0.13	0.14	0.15	0.17	0.18	0.19	0.19	0.21	0.23	0.24	0.26	0.27
Cover of the tree crowns, %	95	100	95	90	80	80	85	90	85	80	80	85	85	90	80	80	80
Number of trees/100 m^2	18	42	24	26	11	12	8	32	9	9	12	13	12	13	15	8	12
Age at breast height, years	34	20	25	26	35	32	40	25	48	47	40	35	37	38	40	53	53
Diameter at breast height, cm	16	8	12	15	17	20	22	15	25	20	20	18	20	19	18	25	18
Height of the trees, m	18	11	13	13	21	19	19	11	25	24	20	21	21	21	18	20	18
Species \ Total number of species	2	4	8	12	11	20	15	21	15	19	18	19	16	18	24	16	22
Plagiothecium spp.	50^1	80^1	70^1	70^1	30^1	30^2	100^1	90^1	90^1	70^1	100^1	90^1	100^1	100^1	90^1	80^1	100^1
Lophocolea heterophylla	50^1	70^1	40^1	90^1	100^1	60^1	100^1	70^1	100^1	90^1	100^1	100^1	100^1	100^1	100^1	20^1	100^1
Polytrichum formosum	–	10^1	10^1	–	–	–	10^1	–	–	20^1	–	20^1	20^1	–	–	–	–
Mnium affine	–	+	–	–	–	–	–	+	–	–	–	–	–	–	–	–	20^1
Mnium hornum	–	–	20^1	20^1	–	–	10^1	–	–	20^1	10^1	30^1	60^1	30^1	+	–	–
Dicranum scoparium	–	–	30^1	10^1	–	–	–	20^1	–	10^1	20^1	–	80^1	50^1	–	–	10^1
Pohlia nutans	–	–	30^1	–	–	–	–	–	–	10^1	–	–	+	10^1	–	–	–
Vaccinium myrtillus	–	–	10^1	–	–	–	–	–	–	40^1	–	–	–	–	–	–	–
Deschampsia flexuosa	–	–	10^1	–	–	–	–	10^1	–	–	–	–	50^1	–	–	90^1	80^1
Athyrium filix-femina (juv)	–	–	–	20^1	20^1	+	+	20^1	+	–	–	20^1	–	10^1	+	–	–
Dryopteris spp. (juv)	–	–	–	20^1	50^1	20^1	40^1	20^1	40^1	40^1	40^1	50^1	40^1	50^1	40^1	–	10^1
Rubus idaeus (juv)	–	–	–	30^1	80^1	20^1	20^1	20^1	20^1	90^1	90^1	60^1	10^1	90^1	70^1	80^1	90^1
Oxalis acetosella	–	–	–	+	10^1	10^1	40^1	–	70^1	10^1	60^1	50^1	30^1	30^1	100^1	–	20^1
Moerhingia trinervia	–	–	–	10^1	–	10^1	–	+	10^1	10^1	–	–	–	30^1	–	–	10^1
Atrichum undulatum	–	–	–	10^1	–	10^1	10^1	20^1	–	–	–	40^1	–	–	20^1	–	10^1
Viola riviniana	–	–	–	10^1	–	–	–	–	–	–	+	–	–	–	40^1	+	–
Deschampsia caespitosa	–	–	–	10^1	–	–	–	–	–	–	–	–	–	–	–	–	–
Dicranella heteromalla	–	–	–	–	10^1	10^1	50^1	10^1	–	–	20^1	40^1	40^1	20^1	30^1	–	–
Galeopsis spp. (juv)	–	–	–	–	40^1	–	–	–	40^1	10^1	70^1	20^1	–	–	70^1	–	–
Senecio sylvaticus	–	–	–	–	+	–	–	–	–	10^1	–	–	–	–	–	–	–
Corylus avellana (juv)	–	–	–	–	10^1	–	–	–	–	–	–	–	–	–	–	–	–
Chamaenerion angustifolium (juv)	–	–	–	–	–	+	10^1	+	20^1	10^1	20^1	+	–	20^1	+	50^1	60^1
Urtica dioica	–	–	–	–	–	10^1	–	10^1	–	–	10^1	–	20^1	–	10^1	–	–
Sambucus spp. (juv)	–	–	–	–	–	–	10^1	–	30^1	–	–	+	–	20^1	20^1	50^1	80^1
Quercus spp. (juv)	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	20^1	20^1	20^1
Dryopteris filix-mas	–	–	–	–	–	10^1	–	–	–	–	–	10^1	–	–	+	10^1	–
Poa nemoralis	–	–	–	–	–	+	–	+	–	–	+	10^1	–	–	–	80^1	–
Mercurialis perennis	–	–	–	–	–	10^1	–	–	–	–	+	–	–	–	–	–	–
Schrophularia nodosa	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–	30^1	–	–
Impatiens noli-tangere	–	–	–	–	–	10^2	–	–	–	–	–	–	–	–	–	–	–
Hypericum sp. (juv)	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–	–	–	–
Picea abies (juv)	–	–	–	–	–	30^1	–	–	–	–	–	–	–	80^1	–	–	–
Galium saxatile	–	–	–	–	–	–	10^1	–	–	–	10^1	–	10^1	+	–	90^1	40^1
Hypnum cupressiforme	–	–	–	–	–	–	20^1	–	–	–	–	+	100^1	20^1	–	30^1	30^1
Betula verrucosa (juv)	–	–	–	–	–	–	20^1	–	–	10^1	–	–	–	–	–	–	–
Anemone nemorosa	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–	–	–
Galium odoratum	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–
Sorbus aucuparia (juv)	–	–	–	–	–	–	–	10^1	90^1	90^1	30^1	50^1	–	90^1	10^1	30^1	100^1
Carex pilulifera	–	–	–	–	–	–	–	+	10^1	10^1	–	–	+	–	–	+	–
Taraxacum vulgare	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–	10^1
Pleurozium schreberi	–	–	–	–	–	–	–	40^1	–	–	–	–	–	–	–	–	–
Veronica officinalis	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–	–
Eurynchium stokesii	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–	–
Maianthemum bifolium	–	–	–	–	–	–	–	–	40^1	+	10^1	–	+	–	–	10^1	–
Convallaria majalis	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–	10^1	–	–
Milium effusum	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–
Ribes sp. (juv)	–	–	–	–	–	–	–	–	+	–	–	–	–	–	10^1	–	20^1
Trientalis europaea	–	–	–	–	–	–	–	–	–	30^1	–	–	–	–	–	–	–
Stellaria media	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–
Ulmus glabra (juv)	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–
Plagiothecium undulatum	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–
Brachythecium reflexum	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–
Rhytidiadelphus loreus	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–
Lactuca muralis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10^1	–	20^1
Fraxinus exelsior (juv)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30^1	–	–
Circaea lutetiana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–
Geranium robertianum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10^1	–	+
Dryopteris austriaca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10^1	10^1

that in the Ardennes the planted spruce forests were almost lacking vegetation until 40—50 years of age when they were thinned out.

At the age of about ten or fifteen years the spruce plantation has grown to such an extent that insufficient light reaches the field and bottom layers, thereby causing their gradual disappearance. The ground is then covered by spruce needles. Usually there will be nothing left of the old ground vegetation, and the species that occur after the first thinnings can be regarded as newly spread plants. It is at this stage of development that this investigation starts.

Table 1 shows a number of vegetation analyses done in dense spruce plantations, where the field and bottom layers cover less than one quarter of the investigation area. Each column corresponds to one site (situation see Fig. 1).

The age at breast height varies from 20 to 50 years, the number of trees/100 m^2 is 8—42 and the cover of the tree crowns varies from 80 to 100 per cent. All the species of the ground layer are found as scattered individuals; many only as small plants showing evidence of lack of light. Even in the densest stands it is possible to find a small liverwort, *Lophocolea heterophylla*, and a *Plagiothecium* species, usually *P. curvifolium* or *P. denticulatum*. These species occur in almost every stand at all stages of maturity (cf. Table 2 A). Other species appearing at an early stage and found in almost every stand are *Dryopteris* spp. (juv), *Rubus idaeus* (juv), *Oxalis acetosella*, *Chamaenerion angustifolium* (juv) and *Sorbus aucuparia* (juv).

Polytrichum formosum, *Mnium hornum*, *Moehringia trinervia*, *Atrichum undulatum*, *Dicranella heteromalla*, and *Sambucus* can also be regarded as shade tolerant species, while e.g. *Deschampsia flexuosa*, although it can be found as small straws in glades in dense spruce forests, is most prominent in older and lighter stands.

The development of the vegetation is dependent on the cover of the tree crowns and density and these properties are usually correlated with the age of the stand. In Fig. 2 the age of the stands at breast height is correlated with the cover of the vegetation. Most of the old stands in Table 2 are also included. It is obvious that it is not until the stand is 45—50 years of age that the bottom, field, and shrub layers are of real importance and cover the whole ground area. At this age the cover of the tree crowns is usually 70—80 % and the number of trees per 100 m^2 is 5—8. In such a stand a mature vegetation type slowly appears.

It is possible to summarize the development of the ground vegetation in a planted spruce forest by dividing it into four developmental stages:

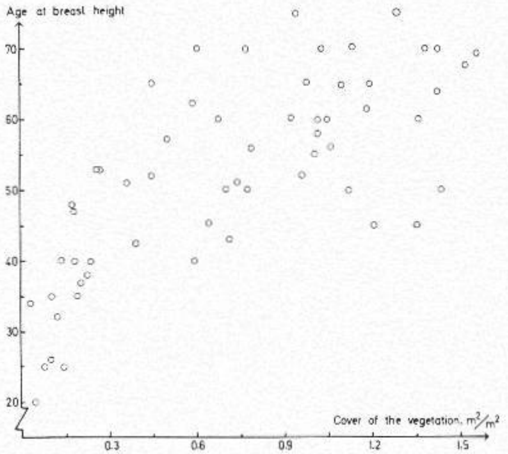


Fig. 2. Diagram showing the relation between the age of the trees at breast height and the cover of the bottom, field and shrub layers.

1. The depletion stage, lasting from the time of planting to about 15 years of age. During this stage the initial ground vegetation disappears.
2. The bare ground stage, at 15—30 years of age, is described as the time when ground vegetation is almost lacking.
3. The immigration stage, at 30—60 years of age, is the time when ordinary spruce forest species appear.
4. The mature stage appears from about 60 years of age and typical vegetation types can be distinguished.

The rotation of spruce in Southern Sweden is 60—70 years and thus the fourth stage is often short or not fully realised.

VEGETATION TYPES IN OLD PLANTED SPRUCE FORESTS

Of the 84 localities investigated 67 were used for describing the vegetation types in old planted spruce forests (situation, see Fig. 1). The condition governing the selection of these sites was that the vegetation of the bottom, field, and shrub layers together should cover at least 50 % of the area. However, a few forests, which from a forestry point of view could be regarded as mature and ready for total cutting, were also included.

a. The Vegetation

When comparing the vegetation from the 67 localities it was found that many of them were very similar, at least with regard to dominating species. On this criterion they were grouped in 27 different columns (Table 2). In this survey table the frequency values are rounded off to the nearest five.

In Table 2 A high frequency species, i.e. species with a frequency of > 50 % in at least one column, are gathered. A continuous change in the vegetation from the left to the right is seen, with very close relationships between adjacent columns. However, it is possible to differentiate into groups or types if dominating species are taken into account. Thus five main types have been established.

I. The moss dominated types are found mainly in the northern part of the investigated area or on the Scanian ridges, where stony and sandy moraines poor in nutrients, prevail (cf. WEIMARCK 1950). The main dominating species are *Dicranum majus*, *D. scoparium*, *D. undulatum*, *Hypnum cupressiforme*, *Plagiothecium curvifolium*, *P. denticulatum*, *P. undulatum*, and *Pleurozium schreberi* (Fig. 3). The vegetation dominated by *Dicranum majus* and *Plagiothecium* species is found in more shady forests and probably on more moist soils, than those dominated by *Dicranum undulatum*, *D. scoparium*, *Hypnum cupressiforme*, and *Pleurozium schreberi*. Though somewhat indifferent the latter species are found e.g. on dry sandy soils in the Vomb area in the centre of south Scania. Most of the high frequency species of the moss dominated forests also occur in other types, but *Dicranum majus*, *D. undulatum*, *Ptilium crista-castrensis*, and *Hylocomium splendens* have their main distribution in type I. *Deschampsia flexuosa* sometimes becomes a co-dominating species, particularly on dry soils and in sun-exposed stands. This vegetation is closely related to the following type.

II. In the *Deschampsia flexuosa* types *Deschampsia flexuosa* is the main species. This type is found on apparently dry localities on stony moraine with a thick mor horizon. It is a vegetation also found at the edges of young or middle-aged planted forests, where the light conditions are sufficient. In consequence it occurs only in sufficiently thinned forests where the cover of the tree crowns is as little as 50—60 %. In the most heavily thinned forests the ground vegetation has the character of edge vegetation and *Deschampsia flexuosa* can reach fertility which normally is rare in enclosed stands. Type II can be divided into two subtypes: II A, where in particular, *Dicranum scoparium* is co-dominating and II B, where *Deschampsia* is dominating alone. The *Deschampsia* — moss subtype may be regarded as a successional stage where *Deschampsia flexuosa* is increasing with increased

Number of Large squares / Small squares	1/10	2/20	1/10	4/40	2/20	1/10	2/20	2/20	5/50	1/10	3/30	1/10	2/20	2/20	1/10	2/20	3/30	3/30	2/20	7/70	5/50	5/50	1/10	2/20	2/20	3/30	2/20
Vegetation types	Moss dominated types				Deschampsia types					Deschampsia - Oxalis types										Rubus - Oxalis types				Sambucus - Oxalis types			
Species	I				II A		II B			III A			III B					III C		IV A	IV B		IV C	V A			V B
A. High frequency species Field and bottom layers (F^C)																											
Dicranum undulatum	50^1	–	100^3	100^3	10^1	–	15^1	–	–	–	–	70^1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dicranum majus	100^3	100^4	–	–	30^1	–	–	–	–	–	–	–	35^1	–	–	–	5^1	5^1	–	–	–	–	–	–	–	–	–
Ptilium crista-castrensis	30^1	–	60^1	20^1	–	–	–	–	–	–	25^1	–	–	–	–	–	5^1	5^1	–	–	–	–	–	–	–	–	–
Hylocomium splendens	–	5^1	30^1	15^1	–	50^1	–	–	–	–	10^1	–	–	–	40^1	–	–	5^1	–	–	10^1	–	–	–	–	–	–
Calluna vulgaris	10^1	–	–	20^1	50^1	–	10^3	5^1	5	–	–	–	5^1	15^1	–	–	5	–	–	5^1	5^1	–	–	–	–	–	–
Vaccinium myrtillus	20^1	60^2	–	35^1	–	60^1	20^1	45^1	35^1	10^1	25^1	10^1	15^1	80^1	60^1	75^1	65^1	10^1	–	5^1	30^1	–	–	–	–	–	–
Pleurozium schreberi	100^3	55^2	100^4	85^2	–	100^1	20^2	–	5^1	–	45^1	–	40^1	–	–	15^1	40^1	25^1	–	–	35^1	–	–	–	–	–	–
Plagiothecium undulatum	80^1	40^1	–	10^1	15^1	–	–	10^1	15^1	–	25^1	30^1	40^1	10^1	50^1	–	40^1	–	–	10^1	5^2	–	–	20^1	–	–	–
Dicranum scoparium	80^2	50^2	100^4	80^1	100^3	80^2	30^1	85^1	40^1	60^1	50^1	–	35^1	75^1	20^1	50^1	100^1	30^1	5^1	20^1	50^1	5^1	–	–	–	5^1	–
Polytrichum formosum	70^1	95^2	–	55^1	50^1	90^1	20^1	45^1	40^1	40^1	45^1	30^1	55^3	35^1	70^1	50^1	75^1	15^1	10^1	25^1	40^1	5^1	–	–	–	–	–
Trientalis europaea	+	10^1	–	10^1	15^1	–	25^1	15^1	50^2	–	+	–	10^1	5^1	–	55^2	75^1	10^1	20^1	10^1	5^1	5^1	–	–	–	–	–
Galium saxatile	+	–	+	15^1	20^1	–	60^1	10^1	40^1	–	60^1	50^1	50^1	65^1	60^1	40^1	55^1	25^1	20^1	20^1	50^1	20^1	–	–	–	–	–
Luzula pilosa	20^1	+	10^1	–	35^1	70^1	–	–	20^1	50^1	25^1	40^1	50^1	30^1	80^1	40^1	90^1	55^1	15^1	10^1	30^1	5^1	–	–	–	–	–
Carex pilulifera	10^1	15^1	–	10^1	20^1	–	25^1	15^1	25^1	30^1	20^1	20^1	65^1	35^1	–	15^1	35^1	5^1	75^1	25^1	35^1	5^1	20^1	10^1	+	–	–
Hypnum cupressiforme	100^4	35^1	100^3	85^2	40^2	100^1	45^1	75^1	45^1	–	25^1	80^1	80^1	75^1	–	+	25^1	30^1	–	40^1	5^1	5^1	–	25^1	35^1	5^1	–
Quercus spp. (juv)	10^1	–	40^1	5^1	15^1	50^1	–	10^1	10^1	+	30^1	10^1	5^1	5^1	40^1	20^1	10^1	15^1	+	10^1	5^1	5^1	–	5^1	–	10^1	–
Deschampsia flexuosa	100^1	70^3	70^1	100^4	100^3	100^5	80^2	100^3	100^4	100^5	100^4	100^3	90^3	80^2	100^2	100^5	75^3	100^4	100^4	45^1	35^1	65^1	–	20^1	–	–	–
Plagiothecium spp.	100^2	70^3	90^1	85^1	100^1	80^1	65^1	95^1	85^2	100^3	100^1	100^1	100^1	100^1	100^2	65^1	100^1	95^1	100^1	95^1	100^1	100^1	70^1	100^1	100^1	85^1	–
Lophocolea heterophylla	100^1	60^1	80^1	65^1	50^1	60^1	30^1	60^1	50^1	50^1	95^1	100^1	100^1	75^1	80^1	65^1	75^1	65^1	100^1	85^1	95^1	90^1	–	100^1	100^1	80^1	65^1
Dryopteris spinulosa	+	25^1	+	10^1	10^1	+	20^1	60^1	60^1	60^1	40^1	50^1	60^1	65^1	30^1	40^1	70^1	40^1	50^1	65^1	50^1	70^1	40^1	25^1	50^1	35^1	10^1
Picea abies (juv)	80^1	40^1	100^1	60^1	10^1	60^1	+	60^1	25^1	+	55^1	100^1	100^1	45^1	–	55^1	85^1	60^1	25^1	30^1	30^1	45^1	–	85^1	–	5^1	15^1
Betula spp. (juv)	–	5^1	–	15^1	–	–	20^1	50^1	15^1	–	–	20^1	20^1	5^1	10^1	10^1	20^1	10^1	30^1	10^1	5^1	–	–	–	–	5^1	–
Sorbus aucuparia (juv)	–	20^1	10^1	5^1	30^1	40^1	50^1	45^1	45^1	10^1	35^1	–	10^1	20^1	50^1	35^1	85^1	40^1	35^1	40^1	20^1	+	–	75^1	55^1	15^1	–
Maianthemum bifolium	–	15^1	–	10^1	–	30	+	20^1	30^1	30^2	35^3	–	+	15^1	100^3	55^1	10^1	25^2	35^2	40^1	5^1	35^1	–	–	5	5^1	–
Mnium hornum	–	45^1	10^1	10^1	25^1	–	10^1	50^1	10^1	–	20^1	40^1	65^2	20^1	100^1	50^1	75^1	10^1	30^1	30^1	40^1	15^1	–	–	15^1	15^1	–
Chamaenerion angustifolium	–	10^1	–	20^1	15^1	20^1	15^1	35^1	15^1	20^1	50^1	100^1	50^1	45^1	–	25^1	25^1	10^1	25^1	70^1	50^1	50^1	50^1	100^1	40^1	65^1	–
Oxalis acetosella	–	10^1	–	10^1	20^1	30^2	–	20^1	15^1	100^2	100^4	100^4	80^3	70^3	100^3	100^4	90^4	100^4	100^4	100^1	100^1	100^1	100^5	100^5	100^5	85^3	–
Pohlia nutans	–	–	50^1	15^1	–	–	35^1	–	10^1	10^1	5^1	10^1	5^1	5^1	–	–	10^1	5^1	5^1	10^1	5^1	5^1	–	–	–	10^1	10^1
Mnium affine	–	–	30^1	20^1	–	–	–	–	–	–	15^1	10^1	–	–	30^1	–	25^1	5^1	50^1	15^1	20^1	30^1	20^1	25^1	–	–	–
Dryopteris austriaca	–	10^1	–	–	25^1	–	5^1	30^1	20^1	–	35^1	70^1	100^3	100^3	100^4	60^2	100^3	–	–	30^1	30^1	–	–	100^2	45^1	–	–
Rubus idaeus	–	20^1	–	–	15^1	10^1	15^1	–	20^1	30^1	35^1	90^1	90^1	75^1	30^1	70^3	85^2	95^2	95^2	75^1	100^4	100^4	100^3	100^1	40^1	50^1	–
Moehringia trinervia	–	–	–	–	–	+	–	–	15^1	–	10^1	50^1	15^1	–	30^1	10^1	–	60^1	20^1	40^1	10^1	50^1	–	95^1	65^1	65^1	80^1
Sambucus spp. (juv)	–	–	–	–	–	–	+	–	5^1	+	10^1	–	–	5^1	–	–	–	–	+	15^1	+	10^1	–	90^1	75^1	75^1	80^1
Lactuca muralis	–	–	–	–	–	10^1	–	+	–	–	5^1	20^1	–	–	–	–	5^1	10^1	10^1	15^1	5^1	30^1	–	100^1	5^1	–	–
Thuidium thamariscinum	–	–	–	–	–	–	–	–	5	–	–	10^1	5^1	–	20^1	–	5^1	–	–	35^1	5^1	5^1	50^1	15^1	40^1	–	–
Atrichum undulatum	–	–	–	–	–	–	–	–	5^1	10^1	5^1	–	–	–	–	–	5^1	5^1	50^1	15^1	5^1	15^1	–	5^1	–	25^1	5^1
Poa nemoralis	–	–	–	–	–	–	–	5^1	+	–	–	–	–	–	10^1	–	+	5^1	20^1	10^1	30^1	50^1	–	–	–	5^1	5^1
Urtica dioica	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5^1	15^1	5^1	60^1	25^1	–	5^1	5^1
Stellaria nemorum ssp. gloch.	–	–	–	–	–	–	–	–	–	–	–	–	–	5^1	–	–	–	5^1	+	10^1	–	50^1	30^1	5^1	–	–	–
Galium aparine	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	70^1	5^1	–	–	5^1
Lamium galeobdolon	–	–	–	–	–	–	–	–	–	–	+	–	–	–	20^1	–	–	–	–	–	–	–	100^2	–	–	–	–
Milium effusum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	60^1	–	–	–	–	–
Melica uniflora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30^1	–	–	–	10^1	–	–	–	–	–
Mercurialis perennis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5^1	100^4	–	–	–	–
Shrub layer (%)																											
Sorbus aucuparia	–	–	–	–	–	–	–	–	<5	–	<5	10	10	<5	30	15	20	–	–	<5	<5	–	<5	<5	10	5	–
Sambucus racemosa	–	–	–	–	–	–	–	–	<5	–	5	<5	<5	<5	10	–	–	–	–	<5	<5	–	–	50	30	60	70
Sambucus nigra	–	–	–	–	–	–	–	–	–	–	<5	–	–	–	<5	–	–	–	–	<5	<5	–	<5	–	25	5	5
Area lacking field and bottom vegetation	100^1	100^3	100^1	100^2	100^4	100^3	100^5	100^4	100^1	100^3	100^1	100^1	100^3	100^4	100^1	100^1	100^2	100^2	100^3	100^3	100^2	100^3	100^1	100^1	100^3	100^5	100^5

Table 2. A—B. Vegetation survey tables showing the frequency (F) and characteristic degree of cover (C) as F^C of the bottom and field layers and percentage cover of the shrub layer in old planted spruce forests. Table A contains dominating and high frequency species (> 50 % at least in one column) while Table B contains low frequency species. (juv) = juvenile plants. *Quercus* spp. includes *Q. petraea* and *Q. robur*. *Plagiothecium* spp. includes *P. curvifolium*, *P. denticulatum* and *P. succulentum*. *Betula* spp. includes *B. pubescens* and *B. verrucosa*. *Sambucus* spp. includes *S. nigra* and *S. racemosa*. *Hypnum cupressiforme* may also include *H. ericetorum*.

Vegetation types / Species	I				II A		II B			III A			III B					III C		IV A	IV B		IV C	V A			V B
B. Low frequency species																											
Field and bottom layers (F^c)																											
Barbilophazia barbata	–	–	40'	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cladonia sp.	–	–	10'	10'	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Polytrichum juniperinum	–	–	–	5'	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhodobryum roseum	–	–	–	5'	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Aulacomnium androgynum	–	–	–	5'	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Monotropa hypopitys	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pteridium aquilinum	–	–	–	5^2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Rhytidiadelphus loreus	–	40'	–	–	–	–	–	–	–	–	–	–	40'	–	30'	–	–	–	–	–	–	–	–	–	–	–	–
Rhytidiadelphus squarrosus	–	15'	–	–	–	–	–	–	–	–	–	–	–	–	30'	–	–	10'	–	–	–	–	–	–	–	–	–
Polygonatum multiflorum	–	5'	–	–	–	–	–	–	5'	–	+	–	–	–	–	–	–	5'	–	5'	–	–	30'	–	–	–	–
Rumex acetosella	–	+	–	5	–	–	5'	–	5'	–	15	–	–	–	–	–	5'	–	–	–	5'	–	–	–	–	5'	–
Stellaria holostea	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–
Lophocolea bidentata	–	–	20'	15'	–	–	–	–	15'	–	–	60'	–	–	–	–	10'	–	–	5'	5'	–	–	–	–	–	–
Rhamnus frangula (juv)	–	–	–	5'	–	30'	–	30'	10'	–	–	–	–	–	30'	–	25'	35'	–	–	+	–	–	10'	–	–	–
Lycopodium annotinum	–	–	–	5'	–	–	–	–	–	–	–	–	5'	–	–	–	5'		–	–	–	–	–	–	–	–	–
Sphagnum sp.	–	–	–	+	–	–	–	–	–	–	–	–	–	5'	10'	–	–	–	–	–	–	–	–	–	–	–	–
Melampyrum sylvaticum	–	–	–	–	5'	–	–	–	–	–	–	–	40'	–	–	20^2	–	–	–	–	–	–	–	–	–	–	–
Melampyrum pratense	–	–	–	–	35'	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–	–	–	–
Dicranella heteromalla	–	–	–	–	25	–	–	10'	5'	–	–	–	20'	10	–	5'	–	–	20'	10'	10'	–	–	–	–	–	20'
Galeopsis tetrahit	–	–	–	–	25'	10'	–	–	–	20'	–	–	–	–	–	–	20'	–	–	5	5	25'	–	–	–	5'	–
Polypodium vulgare	–	–	–	–	–	10'	–	–	+	–	–	–	10'		10'	5'	–	–	–	5'	–	–	–	–	–	–	–
Solidago virgaurea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Scleropodium purum	–	–	–	–	–	–	–	–	10	–	–	–	–	–	–	–	–	–	–	5'	5'	–	–	–	–	–	–
Convallaria majalis	–	–	–	–	–	–	–	–	5'	–	5	–	–	–	–	–	–	–	–	5'	5'	–	–	–	–	–	–
Potentilla erecta	–	–	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–	–	–
Anemone nemorosa	–	–	–	–	–	–	–	–	–	–	+	–	–	–	40	–	–	–	–	10'	–	10'	–	15'	–	–	–
Lastrea dryopteris	–	–	–	–	–	–	–	–	–	–	+	–	–	5'	–	–	–	–	–	–	–	5'	10'	–	–	–	–
Galeopsis bifida	–	–	–	–	–	–	–	–	–	–	5'	–	–	25	–	20	–	–	–	5'	–	–	–	–	–	10'	–
Stellaria media	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–	–	5'	–	–	–	5'	–	–	10'	–	–
Brachythecium curtum	–	–	–	–	–	–	–	–	–	–	30	–	–	–	–	–	20'	–	–	–	15'	–	–	–	5'	–	–
Veronica officinalis	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–	–	–	–	5'	5'	5'	–	–	–	–	–
Fagus sylvatica (juv)	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	30'	–	5'	5'	15'	–	10'	–	–	–
Deschampsia caespitosa	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	5'	5'	–	10'	15'	–	+	–	–	–
Hieracium vulgatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	5'	–	–	–	–	–
Athyrium filix-femina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5^2	–	–	–	–	10'	–	10'	–	–	20'	–
Eurynchium stokesii	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	5'	–	–	–	–	20'	5'	–	–
Plagiochila asplenioides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–	–	–	–	–	–
Prunus sp. (juv)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	5'	–	+	–	–	–
Viola riviniana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	15'	–	10'	–	15	–	–	–
Hypnum imponens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10'	–	–	–	–	–	–	–	–
Salix sp. (juv)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	5'	–	5'	–	–	–
Calypogeia neesiana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	5'	–	–	–	–	–
Lepidozia reptans	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–	–	–
Corylus avellana (juv)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–	–	–
Campanula rotundifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	5'	5'	–	–	–	–	–
Dryopteris filix-mas	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	5'	–	10'	–	–	–	–
Phegopteris polypodioides	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	–	–	–	–	–	–
Ranunculus repens	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	+	–	30'	–	–	–
Epilobium montanum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	20'	25'	–	–	–
Brachythecium reflexum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	10'	–	–	–	–	–
Fragaria vesca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	5'	–	5'	–	–	–
Geranium robertianum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	40'	25'	–	–	–
Isothecium myurum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–	–
Dactylis glom. ssp. aschers.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10'	–	–	–	–	–
Festuca gigantea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–
Rubus fruticosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	–	+	–	–	–
Schrophularia nodosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5'	–	–	–	–	–
Galium odoratum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10	–	–	–	–	–
Pulmonaria officinalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20'	–	–	–	–
Melandrium rubrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20'	+	–	–	–
Campanula latifolia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30'	–	–	–	–
Actaea spicata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	40'	–	–	–	–
Dentaria bulbifera	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10'	–	–	–	–
Eurynchium striatum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		5	–	–	–
Adoxa moschatellina	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20'	–	–	–
Tussilago farfara	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15'	–	–	–
Lathyrus montanus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10'	–	–	–
Shrub layer (<5%)																											
Rhamnus frangula	–	–	–	–	–	–	–	–	–	–	<5	–	–	–	<5	<5	<5	–	–	–	–	–	–	<5	–	–	–
Fagus sylvatica	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	–	–	5	–	–	–	–	–	–	–	–	–	–
Quercus petrea	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	–	–	–	–	–	–	–	–	–	–	–
Corylus avellana	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	–	–	–	–	–	–	–	–	–	–	–
Betula verrucosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	–	–	–	–	–	–	–	–	–
Ribes rubrum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	–	–	–
Ulmus glabra	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	<5	–	–	–
Viburnum opulus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	<5	–	–
Lonicera xylosteum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	–	–
Ribes alpinum	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	–	–
Euonymus europaeus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	<5	–	–	–

Figs. 3 and 4.

thinnings and better light conditions and grows over a primary moss carpet. In some forests, however, the moss carpet is more or less absent and then *Deschampsia flexuosa* starts as small green plots over the whole area as in the first column of II B and remains as the only dominating species in later stages.

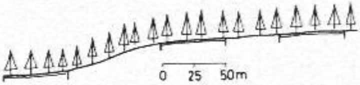
III. The *Deschampsia — Oxalis* types embrace some slightly different subtypes, A—C. They have in common dominating *Deschampsia flexuosa* and *Oxalis acetosella.* Apparently, they always occur on more moist soils than type II. This statement is established in Fig. 5. At the top of the slope (plot no. 3) the forest was slightly more thinned and consequently lighter than in plots no. 1 and no. 2, where the light conditions were estimated to be uniform. Plot no. 3 shows a pure *Deschampsia flexuosa* community where *Deschampsia* covers almost the whole area. In plot no. 2 the soil conditions were similar with an obvious mor horizon, but due to lower light intensities a *Deschampsia flexuosa* layer was not yet fully developed. However, in plot no. 1 situated at the bottom of the slope and facing north, the groundwater was wetting the soil surface and the humus layer was intermediate between mor and mull. The vegetation was an *Oxalis acetosella* variant, probably developing towards a *Deschampsia — Oxalis — Dryopteris* subtype (III B).

As the light conditions were similar in plots 1 and 2, this also illustrates, besides the floristic changes, a better development of the ground vegetation with improved soil conditions.

In subtype III A *Deschampsia flexuosa* and *Oxalis acetosella* are the only dominating species. *Oxalis* can be regarded as the primary species. *Deschampsia* is the secondary species, and has expanded over *Oxalis* when light intensities have increased. However, this vegetation will hardly become a pure *Deschampsia flexuosa* community, since after thinning shrubs such as *Sorbus aucuparia* and *Sambucus racemosa,* will appear. The shading influence of the shrubs will retain a *Deschampsia — Oxalis* community.

Fig. 3. A moss dominated vegetation with *Dicranum majus, Hypnum cupressiforme* and *Pleurozium schreberi* as the most prominent species. NE Vedby. — Photo: B. N. Sept. 1969.

Fig. 4. A subtype of the *Deschampsia — Oxalis* vegetation dominated by *Dryopteris austriaca, Oxalis acetosella, Deschampsia flexuosa, Polytrichum formosum, Mnium hornum, Luzula pilosa,* and *Vaccinium myrtillus.* Shrubs of *Sorbus aucuparia* are prominent. Sjunnerup. — Photo: B. N. Sept. 1969.

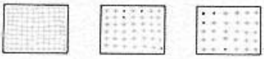


Main species	1.	2.	3.
Viola riviniana	80^{1}	—	—
Rubus idaeus	70^{1}	—	10^{1}
Thuidium thamariscinum	100^{1}	—	10^{1}
Galium saxatile	70^{1}	20^{1}	40^{1}
Dryopteris austriaca	100^{1}	50^{1}	60^{1}
Oxalis acetosella	$\underline{100}^{5}$	+	20^{1}
Lophocolea heterophylla	100^{1}	100^{1}	50^{1}
Hypnum cupressiforme	90^{1}	90^{1}	80^{1}
Plagiothecium spp.	100^{1}	100^{1}	100^{1}
Sorbus aucuparia (juv)	60^{1}	60^{1}	70^{1}
Vaccinium myrtillus	20^{1}	20^{1}	20^{1}
Dicranum scoparium	10^{1}	90^{1}	40^{1}
Deschampsia flexuosa	100^{1}	$\underline{100}^{3}$	$\underline{100}^{5}$
Calluna vulgaris	—	10^{1}	20^{1}

Fig 5

Fig. 5. The main results of vegetation analyses from a transect of a slope in the Crown forest of Dalby.

	1.	2.	3.
Number of trees / $100 m^2$	14	5-6	3-4
Cover of the tree crowns	80%	70%	50%



Main species	1.	2.	3.
Moerhingia trinervia	40^{1}	50^{1}	—
Rubus idaeus	90^{1}	90^{1}	—
Oxalis acetosella	$\underline{100}^{5}$	$\underline{100}^{5}$	30^{2}
Dryopteris austriaca	100^{1}	90^{1}	50^{1}
Chamaenerion angustifolium	100^{1}	100^{1}	—
Plagiothecium spp.	100^{1}	100^{1}	100^{1}
Lophocolea heterophylla	100^{1}	100^{1}	70^{1}
Deschampsia flexuosa	100^{1}	$\underline{100}^{3}$	$\underline{100}^{5}$
Dryopteris spinulosa	60^{1}	50^{1}	80^{1}
Galium saxatile	60^{1}	50^{1}	90^{1}
Sorbus aucuparia (juv)	50^{1}	50^{1}	60^{1}
Vaccinium myrtillus	—	10^{1}	90^{1}
Polytrichum formosum	—	30^{1}	80^{1}
Scleropodium purum	—	—	50^{1}

Fig 6

Fig. 6. Vegetation analyses from different thinned stands, situated side by side on the same soil in the Crown forest of Dalby. Stand number 1 and 3 belong to some experimental plots managed by the Forest Research Institute of Sweden.

On more moist soils, *Deschampsia flexuosa* is superseded by tall ferns, especially *Dryopteris austriaca*, and by *Rubus idaeus* (III B and III C). The *Dryopteris* variant is often found on stony moraine in slopes or hollows with a good supply of ground water (Fig. 4). More moist conditions are also indicated by species such as *Deschampsia caespitosa*, *Athyrium filix-femina* and *Plagiochila asplenioides*. Also, shrubs of *Sorbus aucuparia* and *Sambucus racemosa* can grow tall. The subtype III C with both *Deschampsia*, *Oxalis*, and *Rubus idaeus* can be regarded as an intermediate stage between III and IV.

IV. The *Rubus* — *Oxalis* types can be divided into three subtypes, A—C. In these *Deschampsia flexuosa* is rare or scattered and *Oxalis acetosella* and *Rubus idaeus* are usually co-dominating. In IV A *Oxalis* dominates alone, covering more than 50 % of the area. However, this community is not a fully developed vegetation type but must be regarded as an immigration stage in a vegetation succession of planted spruce forests on moist soils with good humification properties. *Oxalis acetosella* is a very shade tolerant species and the community is often found in very dense, middle-aged (about 45 years old) spruce forests. With increased thinnings the vegetation does not have to develop into a *Rubus* — *Oxalis* type, but might as well become a *Deschampsia* — *Oxalis* variant of type III. Such a succession is clearly demonstrated in some thinning plots for forestry production measurements in the Crown forest of Dalby (Fig. 6). The three stands in this example are situated side by side on the same stony moraine and are equal in age. In the densest stand, where no thinning has been done, *Oxalis acetosella* is dominating alone, while in the heaviest thinned plot, no. 3, *Deschampsia flexuosa* is the most important species. Plot no. 2 is intermediate.

In subtype IV B the vegetation has developed into a *Rubus idaeus* — *Oxalis acetosella* community. This is, in fact, not a clearing vegetation as it is found in relatively close stands, where it covers the whole area (Fig. 7). As with *Deschampsia flexuosa*, *Rubus idaeus* also rarely flowers inside the forests. This happens only in glades or clearings.

Subtype IV B always grows on soils with an astonishingly good humus condition, and podsolizing effects are almost lacking. It is frequently found on slopes where it has been planted on former meadows. It also occurs on level ground, especially when the spruce forest is planted as the first generation on former beech forest areas (cf. p. 333). Then some typical beech forest species, e.g. *Stellaria nemorum* ssp. *glochidosperma*, *Lamium galeobdolon*, *Dactylis glomerata* ssp. *aschersoniana*, *Festuca gigantea*, and *Galium odoratum* can also occur in the spruce forest.

Subtype IV C is a spruce forest vegetation found in one locality only. The spruce is planted on a former beech forest area, probably having a *Mercurialis perennis* community. The soil is extremely rich in lime, has a high pH value (cf. Fig. 11) and a good supply of water. *Lamium galeobdolon*, *Mercurialis perennis*, *Oxalis acetosella*, and *Rubus idaeus* are co-dominants in the field layer. Several other species indicating a good supply of water and mineral nutrients are found, e.g. *Actaea spicata*, *Campanula latifolia*, *Dentaria bulbifera*, *Melandrium rubrum*, and *Pulmonaria officinalis*.

V. The *Sambucus* — *Oxalis* type is separated because of a great dominance ($> 50\ \%$) of 1—3 m high *Sambucus* shrubs (Fig. 8). In the field layer *Oxalis acetosella* and sometimes *Dryopteris austriaca* are

Figs. 7 and 8.

dominating, while the bottom layer is poorly developed. This vegetation is found on similar soil types to the *Rubus* — *Oxalis* types, i.e. soils with a good water supply and probably a good nutrient status, especially concerning nitrate and ammonia. Fertilizing experiments on small plots made by BECHER (1963) indicate that *Sambucus racemosa,* as well as *Rubus idaeus* and *Chamaenerion angustifolium,* is favoured by a good nitrogen supply. The *Sambucus* type was never found on poor stony moraine with a mor humus.

An extreme variant is subtype V B with dominating *Sambucus* shrubs almost lacking field and bottom layers. This variant is usually found in isolated plantations on former arable land. The lack of ordinary forest vegetation can be explained by absence of suitable spreading agents. *Sambucus racemosa* and *S. nigra* are spread mainly by birds.

There is an ecologic difference between the occurence of *Sambucus racemosa* and *S. nigra.* Although they sometimes grow together, *Sambucus nigra* seems to have high demands of water and nutrients and prefers silt or clay rich soils with mull, while *Sambucus racemosa* can also grow on sandy soils where real mull structures are lacking. However the humus layer is very porous and loose, which is a common feature of all the *Sambucus* vegetation types.

A porous humus layer with mull structures can be created artificially by liming or by fertilizing with nitrogen (cf. the nitrogen experiments by BECHER 1963). The most striking effect of liming is the marked increase of the shrub layer (Fig. 9). Shrubs of *Sambucus racemosa* about 2 m tall have grown up in the limed plots. Moreover an increase of *Rubus idaeus* and *Oxalis acetosella* is noticeable. A great number of new species have invaded the limed ground, e.g. *Adoxa moschatellina, Lactuca muralis, Ranunculus repens, Viola riviniana.* Other species have disappeared or decreased, e.g. *Dicranum scoparium, Hypnum cupressiforme, Deschampsia flexuosa, Galium saxatile.*

Besides this qualitative floristic difference it can be noted that the cover of the vegetation is doubled in the limed stands. This demonstrates that it is not only low light intensities that prevent the development of the vegetation, but also the humus condition (cf. NIHLGÅRD 1969).

Fig. 7. Vegetation type dominated by *Rubus idaeus* and *Oxalis acetosella.* N. Rörum. — Photo: B. N. Sept. 1969.

Fig. 8. Vegetation type with 1—3 m high *Sambucus nigra* and *Sambucus racemosa* in the shrub layer. *Oxalis acetosella* is dominating the field layer. S. Djurup. — Photo: B. N. Sept. 1969.

Main species	Unlimed plots		Limed plots	
Dicranum scoparium	70^1	60^1	—	—
Galium saxatile	60^1	50^1	—	—
Hypnum cupressiforme	100^1	70^1	50^1	—
Deschampsia flexuosa	$\underline{80}^2$	80^1	40^1	—
Dryopteris austriaca	$\underline{100}^2$	$\underline{100}^2$	100^1	$\underline{100}^2$
Vaccinium myrtillus	60^1	80^1	40^1	20^1
Plagiothecium spp.	100^1	100^1	100^1	100^1
Oxalis acetosella	80^1	$\underline{100}^4$	$\underline{100}^5$	$\underline{100}^5$
Rubus idaeus	100^1	70^1	100^1	$\underline{100}^2$
Moerhingia trinervia	30^1	—	90^1	100^1
Lactuca muralis	—	—	100^1	100^1
Adoxa moschatellina	—	—	20^1	20^1
Ranunculus repens	—	—	40^1	20^1
Viola riviniana	—	—	30^1	30^1
Shrubs (%)				
Sorbus aucuparia	10%	<5%	< 5%	< 5%
Sambucus racemosa	<5%	< 5%	$\underline{50\%}$	$\underline{50\%}$
Cover of the vegetation, m^2/m^2	Σ 0.63	Σ 0.80	Σ 1.41	Σ 1.48
Humus conditions	Mor, 3–5 cm	Mor, 5–7 cm	Mull, 5–10 cm	Mull, 4–8 cm
pH in 0.2 M KCl	2.90	3.00	6.85	6.50
" " water	3.85	3.85	7.25	6.80

Fig. 9. Vegetation analyses showing the effects of liming on spruce forest vegetation. The sites belong to production experiments of the Forest Research Institute of Sweden in the Crown forest of Dalby.

b. Comparisons with Other Spruce Forest Vegetation

It is difficult to compare the described types of vegetation with the vegetation in natural spruce forests in Scandinavia or Central Europe. In natural stands the vegetation and soil have developed into ecosystems in equilibrium or with changes occurring very slowly. In the planted spruce forests, however, the thinnings have a great influence upon the vegetation and when planted on soils formerly used for other purposes, the soil conditions are in no way in ecologic equilibrium with the influence from spruce. Swift changes concerning the soil conditions can be observed (cf. GENSSLER 1959, NOIRFALISE 1964). These changes must be considered to proceed slowly throughout several generations of planted spruce forests and certainly will also influence the development of the bottom, field and shrub layers. It is probable that the vegetation types of these planted spruce forests in future generations will develop into vegetation types more like those of the naturally occurring forests.

It can be noted that real wet growing vegetation types are lacking in the planted Scanian forest. This mainly depends on the fact that plantation has not been done on such areas, and when wet vegetation does occur, the areas are too small to be included in my investigation as a different vegetation type.

The moss dominated forests of type I are those which are most closely related to the moss rich *Vaccinium myrtillus* or *Vaccinium vitis-idaea* forest types, which are common further north in Scandinavia and in Central Europe (CAJANDER 1909, 1922, HARTMANN 1932, REINHOLD 1939, MALMSTRÖM 1949, TAMM & HOLMEN 1961, ARNBORG 1964). However, the *Vaccinium* species are rarely dominating in the planted

Scanian spruce forest, probably due to the low light intensities. It is also notable that for example *Hylocomium splendens*, a moss species commonly found in natural spruce forests both in Scandinavia and Central Europe, plays a very small role in the Scanian forests.

Similar moss vegetation in planted spruce forests is described by KØIE (1938) from Denmark, MALMSTRÖM (1937) from Halland, RHEINHEIMER (1957) from the surroundings of Hamburg, and ELLENBERG (1968) from Ostfriesland.

Deschampsia flexuosa types (II) are reported by ALMQVIST (1929) from Uppland and is also found in investigations from Denmark (KØIE 1938) and from BRD (GENSSLER 1959). LINDQVIST (1932) mentioned a *Deschampsia flexuosa* community in the planted Scanian spruce forest.

The vegetation types III—V are all to be regarded as herb-forests with low or tall herbs (cf. TAMM & HOLMEN 1961).

With different composition of the non-dominating species the *Deschampsia — Oxalis* types (III) are found in several variants especially in vegetation analyses from Central Europe (CAJANDER 1909, HARTMANN 1932, REINHOLD 1939). KOIE (1938) distinguished a special *Deschampsia — Oxalis* sociation in Danish conifer plantations.

The *Dryopteris austriaca* subtype (III B) is reported as a fern spruce forest by ELLENBERG (1968) from Ostfriesland. Fern types with several *Dryopteris* species, particularly *Dryopteris filix-mas*, are common in Scandinavian spruce forests (cf. ALMQVIST 1929, ARNBORG 1964).

Rubus — Oxalis types (IV) are described both from Germany by CAJANDER (1909) and in planted forests from Denmark (KOIE 1938) as preferring soils with a mull or mor/mull structure.

The pure *Oxalis acetosella* subtype (IV A), considered as a primary stage of the types III—IV, is reported from Central Europe (CAJANDER 1909, LANGER 1960), from Denmark (KØIE 1938), and from Central Sweden (ALMQVIST 1929, HOLMEN 1964). HOLMEN found this community, including e.g. *Lophocolea heterophylla*, in dense spruce forest stands on drained peat land. LINDQVIST (1932) mentioned an *Oxalis* community which developed towards a *Deschampsia flexuosa* or a *Rubus idaeus* community.

The *Mercurialis* subtype (IV C) is reported both from natural spruce forests in Sweden (HEDBERG 1949), from the Alps (LANGER 1960) and from planted European forests (recognizable in investigations from AICHINGER 1952).

The *Sambucus* — *Oxalis* types (V) are perhaps more connected to Southern Sweden and to Central Europe than to the remaining part of Scandinavia. *Sambucus* shrubs in spruce forests, especially when planted on former arable land, can certainly be found inside the whole distribution area of *Sambucus racemosa* and *S. nigra*.

c. Soil Profiles and pH-values

Before discussing the results (Fig. 10) some remarks must be made on the terminology used, which essentially follows LINNERMARK (1960).

A podzol (P) is characterized as a soil with an obvious mor horizon containing different decomposition stages (F + H layers) and with a grey or ash-white leaching horizon (A_2), above a brown or red-brown precipitation horizon (B_2).

A podzoloid (Pd) is a soil with a mor horizon but with indistinct A_2 and B_2 horizons. Though it is possible to distinguish an A_2-horizon this is not ash-white but greyish-black from a high humus content. They often occur in spruce forests planted on former grasslands or heaths, or on soils with relatively good water conditions. The podzoloids can be regarded as degenerative soil types when occurring under spruce. Depending on the thickness of the A_2 horizon the podzols (P) and the podzoloids (Pd) can be divided into three groups: strong (SP, SPd) with $A_2 > 10$ cm, medium (MP, MPd) where A_2 is 10—4 cm and weak (WP, WPd) with $A_2 < 4$ cm. Often it is difficult to distinguish between podzoloids and weak podzols as there may be a successive transition from a grey colour immediately below the mor, to a more greyish-black colour further down, indicating a development into a humus podzol. However, these transitional stages have been classified as podzoloids.

Among the brown earths LINNERMARK distinguishes between oligotrophic brown earths (OBr) with the thickness of the mull horizon < 4 cm, mesotrophic brown earths (MBr) with 4—10 cm mull and eutrophic brown earths (EBr) with the mull horizon more than 10 cm thick. The mull horizon is denoted A_1. The term brown earth is used in a wide sense, and comprises brown and acid brown forest soils.

Strong podzols occur mainly in the moss rich forests (I) and in the *Deschampsia flexuosa* types (II) (Fig. 10 A). Of the *Deschampsia* — *Oxalis* variants (III) most profiles can be characterized as podzoloids but strong podzols and oligotrophic brown earths also appear. The *Rubus* — *Oxalis* type (IV) is most often found on podzoloids or brown earths, while the *Sambucus*-type (V) in its extreme form occurs only on different brown earths.

The mor or mull horizon under the litter layer acts very selectively on species and must be regarded as the most important soil horizon for the development of the shrub and ground vegetation. Obviously mor is the dominating soil surface horizon in the vegetation types I—III

A. Soil types

Vegetation type	Podzols			Podzoloides			Brown earths		
	SP	MP	WP	SPd	MPd	WPd	OBr	MBr	EBr
I	5	2	1	–	–	–	–	–	–
II	4	4	–	2	2	–	–	–	–
III	3	1	–	6	6	2	2	–	–
IV	–	1	–	1	2	3	4	7	–
V	–	–	–	–	–	–	6	2	1

B. Thickness of the humus layer (cm)

Mor			Mor/Mull		Mull	
>10	5–10	0–5	0–5	5–10	0–5	5–10
–	7	1	–	–	–	–
1	10	1	–	–	–	–
–	14	1	1	4	–	–
–	4	–	5	7	1	1
–	–	–	2	5	1	1

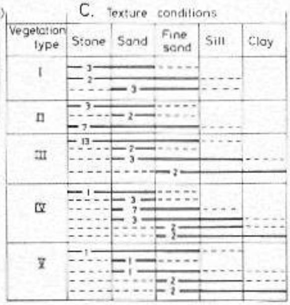


Fig. 10. Distribution of vegetation types on: A: Soil types. — B: Humus types. — C: Soil texture conditions, where the main fractions are indicated with thick lines, the other with broken lines.

(Fig. 10 B). However, in type III it is also possible to find many intermediate stages between mor and mull, designated mor/mull. — A real mor horizon can be characterized as a purely organic horizon, while a mull is an intimate mixture of both organic and inorganic compounds. In the mor/mull horizon one can find a very morlike structure above or sometimes slightly mixed with a more mull-like structure. — In the vegetation types IV and V usually this mor/mull horizon is found, but obvious mull horizons also appear.

The investigation of the texture conditions (Fig. 10 C) is founded solely on observations from the field and deals only with the main fractions of the soil. There is no great difference between the vegetation types, but on the whole stony and sandy soils are dominating in sites with the vegetation types I—III, while more silt and clay rich soils are found in sites with types IV and V. The fine sand and silt fractions are especially important for maintaining a good water supply.

For the correct interpretation of the pH-measurements (Fig. 11) the principal difference between a pH measured in extracts of distilled water and potassium chloride, must be realized. In water extract a pH essentially gives the acidity of the easily moving soil water, while in the potassium chloride extract the pH is an expression of the total exchangeable fraction of acid ions, since the potassium ions are exchanged e.g. for the hydronium ions. With increasing content of acid ions on the colloids the pH in potassium chloride extracts is lowered and will diverge more and more from those in water extracts. As can be seen from Fig. 11 this difference is distinctly marked in the mor or mull horizons, and especially in the vegetation types I—III where real mor horizons are dominating. The difference is at least one pH-unit. In the B/C horizons the differences between the measurements obtained from the two different methods are much less, only about 0.3—0.4 pH

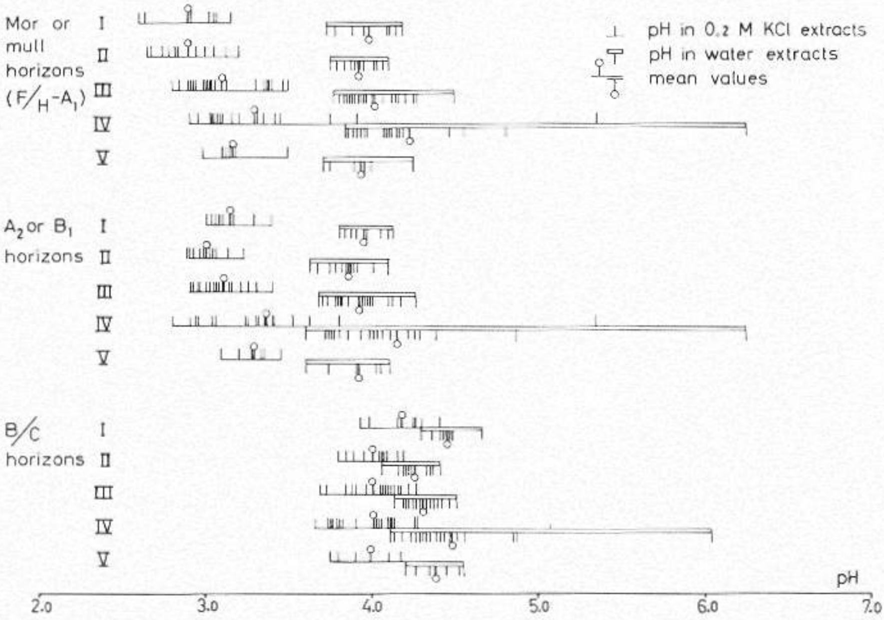


Fig. 11. pH-values on soil samples from three horizons of the different vegetation types.

units. Moreover, all these pH values are markedly higher than those of the soil surface. The A_2—B_1 horizon values have an intermediate position.

Significant differences concerning the pH values between the vegetation types are found neither in the water extracts from any horizon, nor in the potassium chloride extracts from A_2 or B/C horizons. It is only in the mor or mull horizon that differences are notable in the latter extracts. Thus the soils of types I and II are more acid than the other. Type IV shows a large variation, reflecting the great variation in vegetation. Values from the limed plots described on p. 326 are not included in type V.

The unimportant differences of pH in water extracts suggest that other ecological conditions, e.g. the supply of water and available nutrients, are of greater importance for the floristic differentiation of the vegetation.

The pH values of the water extracts are in good agreement with those of Køie (1938) of corresponding plant communities.

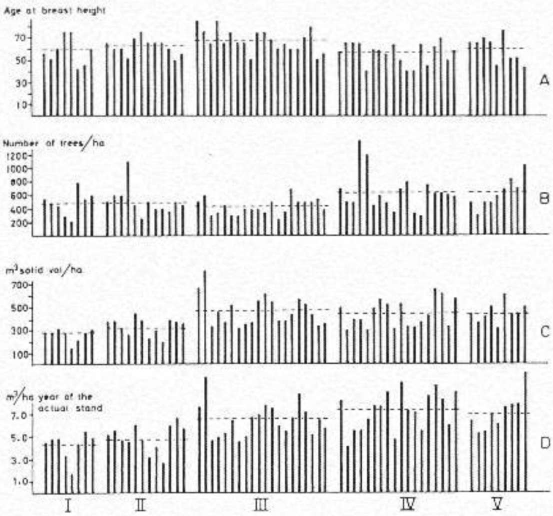


Fig. 12. Bar graphs on tree layer data of the investigated old planted spruce forests. Average values for the vegetation types are indicated by horizontal dashed lines. — A: The age of the trees at breast height. — B: The stand density expressed as trees per hectare. — C: The wood content (=the growing stock volume), expressed as cubic metre solid volume over bark per hectare. The values are based upon the estimations of tree height, tree diameter and number of trees/ha and are calculated from the volume tables of Näslund & Hagberg (1950). — D: The production calculated as the mean production of wood per hectare and year of the present remaining stand, i.e. earlier thinnings are overlooked.

d. Notes on the Tree Layer

In Fig. 12 A—D some notes on the tree layer of the investigated stands are given. The age at breast height (Fig. 12 A) varies from 40 to 85 years, but the average age of the different vegetation types differs only slightly. The number of trees per hectare (Fig. 12 B) varies from 250 to 1400. The average values are lowest in types I—III and highest in IV and V. The absolute values of the growing stock volume indicated in Fig. 12 C are founded on estimations, and must be very rough. *t*-tests on the given values in Fig. 12 C, reveal that solid volume over bark in types I and II differ with a probability of 99 or 99.9 % from the other types. A difference in the solid volume could of course be due to different thinning procedures but the average values of the tree density do not advocate this, as in fact types I and II have a slightly higher tree density than e.g. III, but still a lower solid volume.

In calculating the production of solid volume per hectare and year, the values of the growing stock volume were divided by an estimation of the total age, obtained after adding six years to the age at breast height of the vegetation types I and II, five years to the others. Also in productivity the vegetation types I and II differed with a probability of 99 or 99.9 % from the remaining types. There is an indication of lower productivity in the *Sambucus* type (V), but this can equally be due to different management of the forests. It is, for instance, impossible to know how much timber has been removed earlier by thinnings.

CHANGES IN VEGETATION WHEN BEECH FORESTS HAVE BEEN REPLACED BY PLANTED SPRUCE FORESTS

The beech forests included in this study (Table 3) represent the most important types viz. the "heath beech forests", on podsolized soils with mor, and the "meadow beech forests" on brown earth with mull (LINDGREN 1968).

The most prominent changes are that species typical for the meadow beech forests decrease while species typical for the heath forests increase in the spruce forests. Thus e.g. *Deschampsia flexuosa* and *Maianthemum bifolium* increase but *Allium ursinum, Deschampsia caespitosa, Galium odoratum, Lamium galeobdolon, Mercurialis perennis, Stellaria holostea, S. nemorum* ssp. *glochidosperma,* and *Viola riviniana* decrease. *Stellaria nemorum* ssp. *glochidosperma,* known as a fairly acidophilic species, manages better in the spruce forest than e.g. *Galium odoratum* or *Lamium galeobdolon.* Among other species, e.g. the nitrophilic species *Rubus idaeus* increases greatly. Also *Oxalis acetosella* is favoured in the spruce forests, but *Anemone nemorosa* decreases. Several other species are favoured and are often found to be frequent in the spruce forests but rarely or never in the beech forests. To these belong most of the species in the second half of Table 3 (p. 333). In particular several mosses and plants such as *Dryopteris austriaca* and *Sambucus racemosa* appear. Similar changes are found by THILL in the Ardennes (in NOIRFALISE 1964). He points out a drift towards a shrub land flora on mor in the planted spruce forests. LOHMEYER (1964), in a report to NOIRFALISE, mentions *Stellaria holostea* as a species that will disappear, *Oxalis acetosella* as one that will remain unchanged, while e.g. *Chamaenerion angustifolium, Mnium hornum, Moehringia trinervia, Rubus idaeus,* and *Sambucus nigra* will increase.

Table 3. Vegetation survey table showing the vegetation of some beech forests and corresponding spruce forests situated side by side on the same soil. Typical beech forest species are found in the upper half of the table. Below these the high frequency species left from the spruce forest vegetation in Table 2 A are added.

Stand No.	Beech forests											Spruce forests										
	4	19	22	7	8	5	14	16	12	10	15	4	19	22	7	8	5	14	16	12	10	15
Cover of the tree crowns,%	75	70	90	80	80	70	90	70	90	60	90	60	60	60	60	65	75	65	60	75	60	60
Number of trees / 1000 m²	16	22	25	14	17	11	14	30	21	14	36	70	50	50	50	50	85	65	60	120	80	65
Diameter at breast height, cm	30	32	27	45	35	40	47	40	40	35	30	27	30	30	30	33	23	35	24	20	25	30
Height of the trees, m	23	23	27	29	28	29	31	24	27	27	26	25	30	25	30	28	24	29	24	21	23	27
Species / Total number of species	45	27	12	28	30	34	24	15	21	34	30	30	44	22	31	27	25	26	31	20	32	35
Vaccinium myrtillus	–	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–	–
Trientalis europaea	100^1	–	70^2	–	–	–	–	–	–	–	–	20^1	–	30^1	20^1	10^1	–	10^1	–	–	–	–
Carex pilulifera	50^1	80^1	10^1	90^1	40^1	–	–	–	–	–	–	100^1	90^1	–	–	20^1	–	–	–	–	–	–
Deschampsia flexuosa	100^5	40^1	30^1	40^1	70^1	–	–	–	–	–	–	40^1	50^1	100^5	100^2	100^4	–	60^1	90^1	–	10^1	70^2
Luzula pilosa	100^1	90^1	50^1	90^1	20^1	10^1	–	–	10^1	–	–	30^1	90^1	40^1	–	50^1	–	–	–	–	–	10^1
Maianthemum bifolium	60^1	0^1	70^2	10^2	–	10^1	30^1	20^1	70^1	10^1	–	80^1	30^1	60^3	10^1	–	10^1	50^1	90^1	50^1	–	30^2
Oxalis acetosella	70^1	100^1	100^3	90^2	100^2	100^4	100^2	100^3	90^3	100^2	100^1	100^2	100^3	100^2	100^4	100^4	60^1	100^3	100^5	100^4	90^3	100^4
Anemone nemorosa	10^1	100^1	100^1	10^1	10^1	100^4	100^3	100^2	100^1	100^2	60^1	–	–	–	70^1	–	–	10^1	30^1	40^2	10^1	–
Poa nemoralis	50^1	30^1	10^1	30^1	80^1	20^1	20^1	20^1	–	80^1	10^1	–	90^1	–	20^1	–	–	20^1	60^1	+	40^1	10^1
Dryopteris spinulosa	20^1	–	–	10^1	–	10^1	30^1	–	60^1	–	–	100^1	80^1	10^1	70^1	40^1	60^1	100^1	60^1	50^1	90^1	20^2
Milium effusum	–	+	–	–	20^1	–	50^1	+	20^1	100^3	70^1	–	30^1	–	–	30^1	–	20^1	80^1	–	30^1	100^2
Dryopteris filix-mas	–	–	–	–	–	–	–	–	+	–	30^1	–	+	–	–	–	–	–	–	+	–	–
Rubus idaeus	+	20^1	–	30^1	40^1	–	20^1	+	20^1	80^2	20^1	100^1	100^4	100^2	100^3	90^2	60^1	100^3	100^4	70^1	100^3	100^3
Deschampsia caespitosa	40^1	10^1	–	20^2	50^1	+	20^1	–	–	60^1	10^1	–	30^1	–	–	–	–	20^1	–	–	50^1	10^1
Viola riviniana	–	20^1	–	20^1	90^1	70^1	20^1	100^1	50^1	90^1	40^1	–	–	–	10^1	–	–	–	30^1	–	10^1	–
Stellaria holostea	20^1	–	–	70^1	10^1	+	40^1	–	–	100^2	60^1	–	–	–	+	60^1	–	–	–	–	–	–
Melica uniflora	–	20^1	–	30^1	100^2	–	–	–	–	100^1	90^1	–	–	–	70^1	10^1	–	–	20^1	–	–	10^1
Lamium galeobdolon	–	40^1	–	–	30^1	100^3	30^3	–	–	90^2	90^4	–	–	–	–	–	–	–	–	–	–	–
Galium odoratum	–	–	–	–	–	–	20^2	100^4	100^3	100^3	100^3	–	–	–	–	–	–	–	20^1	–	–	10^1
Stellaria nemorum ssp. gloch	–	–	–	–	–	–	80^3	50^4	100^4	100^2	100^4	–	–	–	–	–	–	40^1	20^1	30^1	30^1	100^2
Urtica dioica	–	–	–	–	–	10^1	–	10^1	+	40^1	40^1	–	10^1	–	–	–	–	10^1	–	–	20^1	–
Dactylis glomerata ssp aschers.	–	–	–	10^1	–	–	–	–	–	90^1	30^1	–	–	–	–	–	–	–	–	–	40^1	+
Mercurialis perennis	–	–	–	–	–	20^3	–	–	–	20^2	90^4	–	–	–	–	–	–	–	–	–	–	10^1
Hordelymus europaeus	–	–	–	–	–	–	–	–	–	–	40^1	–	–	–	–	–	–	–	–	–	–	10^1
Aegopodium podograria	–	–	–	–	–	–	–	–	–	–	30^1	–	–	–	–	–	–	–	–	–	–	–
Allium ursinum	–	–	–	–	–	–	–	–	–	–	10^3	–	–	–	–	–	–	–	–	–	–	–
Pleurozium schreberi	20^1	–	–	–	–	–	–	–	–	–	–	–	–	80^1	–	–	–	–	–	–	–	–
Quercus spp (juv)	20^1	–	–	–	–	–	–	–	–	–	–	10^1	20^1	–	30^1	10^1	10^1	–	–	20^1	20^1	10^1
Galium saxatile	40^1	–	–	–	–	–	–	–	–	–	–	–	90^1	–	50^1	30^1	–	–	20^1	–	–	–
Mnium hornum	40^1	–	–	10^1	10^1	–	–	–	–	–	–	90^1	70^1	–	10^1	10^1	10^1	20^1	–	–	10^1	40^1
Sorbus aucuparia (juv)	10^1	10^1	30^1	30^1	–	–	–	10^1	10^1	–	–	20^1	20^1	10^1	60^1	50^1	50^1	+	80^1	30^1	–	+
Picea abies (juv)	100^1	70^1	–	60^1	10^1	–	–	–	–	–	–	80^1	80^1	40^2	60^1	80^1	20^1	–	50^1	–	90^1	30^1
Pohlia nutans	10^1	10^1	–	–	–	–	–	–	–	10^1	–	50^1	–	–	–	10^1	30^1	+	–	–	–	10^1
Dicranum scoparium	70^1	40^1	–	20^1	40^1	10^1	–	–	–	–	–	90^1	90^1	50^1	30^1	10^1	10^1	10^1	–	–	–	–
Polytrichum formosum	90^1	30^1	10^1	–	20^1	–	10^1	–	+	–	10^1	100^1	100^1	+	20^1	30^1	10^1	+	–	30^1	10^1	10^1
Hypnum cupressiforme	40^1	60^1	–	60^1	–	10^1	10^1	–	–	–	–	40^1	20^1	–	10^1	80^1	10^1	30^1	–	–	–	–
Plagiothecium spp	20^1	40^1	–	40^1	40^1	20^1	40^1	–	30^1	10^1	10^1	90^1	100^1	100^1	100^1	90^1	100^1	100^1	100^1	100^2	100^1	90^1
Lophocolea heterophylla	20^1	–	–	20^1	20^1	20^1	20^1	–	30^1	10^1	–	100^1	100^1	100^1	20^1	70^1	100^1	100^1	100^1	100^1	100^1	40^1
Lactuca muralis	–	10^1	–	–	10^1	–	–	–	–	–	–	–	+	–	10^1	20^1	–	–	50^1	–	20^1	90^1
Moerhingia trinervia	–	10^1	20^1	10^1	10^1	30^1	–	10^1	–	–	–	10^1	10^1	10^1	40^1	50^1	–	–	10^1	–	90^1	40^1
Atrichum undulatum	–	10^1	–	–	20^1	70^1	–	–	–	20^1	–	20^1	50^1	–	20	–	70^1	+	10^1	10^1	50^1	–
Sambucus spp	–	–	–	–	–	30^1	20^1	–	–	–	–	10^1	+	–	–	–	100^2	10^1	10^1	–	10^1	10^1
Chamaenerion angustifolium	–	–	–	–	–	–	–	–	–	–	–	60^1	20^1	30^1	20^1	–	80^1	40^1	50^1	+	100^1	50^1
Betula spp. (juv)	–	–	–	–	–	–	–	–	–	–	–	30^1	–	–	30^1	–	20^1	–	–	–	–	–
Hylocomium splendens	–	–	–	–	–	–	–	–	–	–	–	10^1	50^1	–	–	10^1	–	–	–	–	–	–
Plagiothecium undulatum	–	–	–	–	–	–	–	–	–	–	–	40^1	–	–	–	–	–	–	–	–	–	–
Mnium affine	–	–	–	–	–	–	–	–	–	–	–	–	80^1	–	10^1	–	–	–	40^1	10^1	–	–
Dryopteris austriaca	–	–	–	–	–	–	–	–	–	–	–	–	20^1	–	–	100^2	–	–	–	–	–	–
Calluna vulgaris	–	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–	–
Dicranum majus	–	–	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–
Ptilium crista-castrensis	–	–	–	–	–	–	–	–	–	–	–	–	–	10^1	–	–	–	–	–	–	–	–
Shrub layer (%)																						
Sambucus racemosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	50%	–	–	–	–	5%
Sorbus aucuparia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	10%

Deschampsia flexuosa, Galium saxatile and *Mnium affine* are regarded as new species in the spruce forest.

CONCLUDING REMARKS

The development of the vegetation in planted spruce forests in Scania is strongly dependent on the direct effects of thinnings. The light must be regarded as the limiting growth factor for the bottom field and shrub layers (cf. NIHLGÅRD 1969). The first species to invade the naked forest ground after the first thinnings are very shade tolerant species. Many of them will stay at a germinating stage. With increased thinnings and at 45—50 years of age the light intensities are high enough to permit an active growth of the bottom, field and shrub layers. Species which can withstand or prefer an acid milieu — probably often rich in soluble nitrogen — on a thick layer of spruce needles, are favoured. Certainly the vegetation of the surrounding forests is of importance as a source of immigration.

Most of the mature forest vegetation can be regarded as a mixture of unstable plant communities, but it is possible to establish some types, due to the dominance of species in the bottom, field or shrub layers. Such a "type" of vegetation is usually found in connexion with particular ecological conditions what concerns the soil, soil-water and light. See Fig. 13, which is founded on earlier discussions and thus derives mainly from my own field observations.

Considering the dry—moist gradient the *Deschampsia flexuosa* type and the moss types belong to the driest, though the species have a very wide ecologic range. *Rubus idaeus,* often characterized as a nitrophilic species, is dominating on more moist soils with good humification properties. The *Sambucus — Oxalis* type appears on a similar soil type as the *Rubus idaeus* community, but often on soils with a higher content of clay which are slightly wetter. However, the *Sambucus* subtype V B occurs on former cultivated soils which could be fairly dry, but there is still a porous humus layer, apparently with good nitrification and characterized as a mor/mull.

The *Dryopteris austriaca* community is obviously linked to soils which are influenced by high but drainable ground water, and moreover it is found mainly on stony and sandy moraine.

The dark—light gradient especially illustrates that a primary *Oxalis acetosella* vegetation can develop into many of the other separated types. Moreover, this gradient indicates that vegetation occurs and

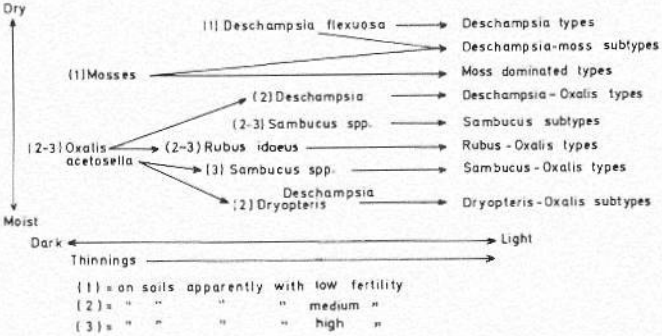


Fig. 13. Schematic ecological interpretation of the vegetation types in planted Scanian spruce forests.

covers larger areas at an earlier stage on soils with good humification properties or with a good water supply, than on drier soils with a mor horizon.

Thus the different vegetation types are linked to certain ecological conditions and these differences obviously also affect the production of the tree layer. It is possible to separate the vegetation types I and II as more low-productive than the others, which show higher and equal production, in spite of apparently better soil conditions in types IV and V compared with type III. This suggests that the optimum cultivating conditions for spruce in Scania have already been reached in type III, and it further suggests that the ground water is the limiting growth factor (cf. TROEDSSON 1955 p. 183). Changes in vegetation when spruce forests have replaced beech forests, indicate that species which can withstand a more acid milieu are favoured.

The studied vegetation types are found in the first generation of planted spruce forests in Scania. It is very probable that with further generations the soil conditions will change in an acidifying and mor developing way, which will favour the development of vegetation types I—III. The *Sambucus* and the *Rubus idaeus* variants, indicating a good nitrification status, are likely to disappear with future generations, as mor formation with a delayed nitrification can be expected.

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On the Typification of Papaver radicatum Rottb. and its Nomenclatural Consequences

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ABSTRACT

KNABEN, G. & HYLANDER, N.: On the Typification of Papaver radicatum Rottb. and its Nomenclatural Consequences. — Bot. Notiser 123: 338—345, Lund.

Papaver radicatum ROTTB. 1770 should be typified by the main figure of the plate in ROTTBÖLL's original publication, not by a fragmentary specimen in herb. EGEDE (C) as proposed by LÖVE (1962 a). This figure was evidently based on an Icelandic specimen and corresponds so well with the race described by LÖVE (1955) as *P. nordhagenianum* ssp. *islandicum*, that this should be considered the typical race of *P. radicatum*. The last-mentioned name should thus not be used in the sense of *P. lapponicum* A. TOLM. coll., i.e. the 56-chromosomic taxa, as in LÖVE 1962 a and b, but for the 70-chromosomic taxa, excl. *P. dahlianum* NORDH., in the same way as in KNABEN 1958. The name *P. nordhagenianum* LÖVE 1955 becomes a superfluous synonym. By the wide concept used by LÖVE (1962 b), which includes *P. relictum*, the latter name should, by the way, have been used as collective species name, not the 24 years younger *P. nordhagenianum*.

Papaver radicatum was described as a new species by ROTTBÖLL 1770 in a treatise on some collections of plants from Iceland and Greenland. As shown by LÖVE (1962 a), the name was later more or less neglected until it was taken up again by MURBECK (1894) as designation for a group of arctic poppies with more or less sulphureous yellow (rarely white) petals, low growth and short stamens, occurring in Greenland, the Faeroes, and Scandinavia.

NORDHAGEN (1931), in his study of the Scandinavian representatives of this group, split it into four species, *P. dahlianum*, *P. lapponicum* (based on *P. radicatum* ssp. *lapponicum* A. TOLM.), *P. relictum* (based on *P. nudicaule* ssp. *relictum* E. LUNDSTR.), and *P. radicatum*, the latter including four subspecies, namely ssp. *dovrense* (correctly: ssp. *ovatilobum* A. TOLM.), ssp. *subglobosum*, ssp. *hyperboreum*, and ssp. *laestadianum*, to which he later (1940) added ssp. *macrostigma* (in 1931 a var. of ssp. *hyperboreum*).

The chromosome numbers of these taxa were published by HORN (1938). He found the somatic number to be 56 in *P. lapponicum* and *P. radicatum* ssp. *laestadianum* (which was, partly for that reason, raised to specific rank by NORDHAGEN 1939), but 70 in *P. dahlianum*, *P. relictum* and in the *P. radicatum* subspecies *ovatilobum*, *hyperboreum*, *macrostigma* and *subglobosum*. Later LÖVE & LÖVE (1948) published the number 2n=70 for the Icelandic races they then called *P. radicatum* ssp. *faeroense* (also in the Faeroes), ssp. *islandicum* (n. nud.) and ssp. *Stefansonii*.

In 1955, LÖVE united in one collective species all the Scandinavian taxa with 2n=70, except *P. relictum* and *P. dahlianum*, which were kept as independent species (as also the two Icelandic taxa now called *P. stefanssonianum* and *P. steindorssonianum*, the latter corresponding to the Icelandic plants included in ssp. *faeroense* in 1948). The two taxa with 2n=56 were kept as *P. laestadianum* and *P. lapponicum*. On the assumption that ROTTBÖLL's *P. radicatum* should be typified by a Greenland plant, this name was restricted to a group of 56-chromosomic forms from Greenland and arctic Canada. For *P. radicatum* s. NORDHAGEN, thus left without a specific name, he created the new name *P. nordhagenianum*; as the typical subspecies, ssp. *nordhagenianum*, LÖVE chose *P. radicatum* ssp. *hyperboreum*. Under *P. nordhagenianum* new combinations were made for ssp. *macrostigma*, ssp. *ovatilobum*, ssp. *subglobosum*, ssp. *faeroense*, and the now validly published ssp. *islandicum*.

Still using the same typification, LÖVE 7 years later (1962 b) reduced the species number and placed under *P. radicatum* as subspecies *P. laestadianum* and *P. lapponicum* (into which he put as vars. two species described in the meantime by SEMENOVA-TIAN-SCHANSKAIA from the Kola Peninsula). At the same time *P. relictum* was reduced to a subspecies under *P. nordhagenianum*, the taxonomy of which was widely rearranged into 5 subspecies, 3 of which including (except the type race) several varieties, *inter alia* the subspecies described from Norway by KNABEN in 1959. When doing so, LÖVE did not observe that all these 11 new combinations (as well as two made by him in 1955) were illegitimate, since with such a specific circumscription the name *P.*

nordhagenianum must be replaced by *P. relictum,* which antedates the former by 24 years. This was later pointed out by NANNFELDT (1963), who made, however, no new combinations.

By acceptance of LÖVE's typification of *P. radicatum* ROTTB., a correct nomenclature for the taxa placed by him in *P. nordhagenianum,* would, however, imply a corresponding number of new combinations under *P. relictum.*

Is such a step necessary? That depends, of course, on the typification of *P. radicatum.* Should this name be used in the sense of NORDHAGEN (and later by KNABEN and other Scandinavian authors), or in the sense of LÖVE — or should it not be used at all as having become a *nomen ambiguum*? Although LÖVE has been, unfortunately, followed by BÖCHER, HOLMEN & JAKOBSEN in their Greenland flora (1966), the name *P. radicatum* should, in our opinion, not be abolished but should be used in the sense proposed by KNABEN in 1958, for the 70-chromosomic complex (excluding *P. dahlianum*) because in our opinion LÖVE is wrong both in his choice of type and in the interpretation of ROTTBÖLL's plate of *P. radicatum.*

In 1955, LÖVE still based his typification on that plate. This, he says, shows "a plant with a small capsule, subcylindrical to oblong with a flat stigmatic disc the rays of which run almost to the middle of the capsule. The plant must have been from Greenland, and there is little doubt as to its identity with *P. radicatum* ssp. *occidentale* described by LUNDSTRÖM (1923) from Sabine Island and Pendulum Island in eastern Greenland . .". KNABEN already in her paper of 1958 pointed out that the organ shown as a detail in ROTTBÖLL's plate and interpreted as a capsule by LÖVE is rather a young gynoecium than a ripe capsule, and after further study of a very large material (many thousands of specimens) in cultivation of this group she will now stress this point and also point out that the form of the gynoecium in ROTTBÖLL's figure is that shown at the same stage of flowering in Scandinavian and Icelandic forms of "*P. nordhagenianum*". In his diagnosis ROTTBÖLL describes the "germen", i.e. the ovarium, as "oblongum", and the figure of the plate does not contradict this description. Nor is there any reason for LÖVE's assumption that "ROTTBÖLL, in drawing his plant, idealized his species on the basis of specimens from both Greenland and Iceland".

On the other hand, too much importance should not be ascribed to the gynoecium detail in the plate, since we do not know from which specimen it was taken; in fact, remembering the stage of flowering shown by the main figure in the plate, it is at least most probable that it emanated from another specimen in ROTTBÖLL's collections. The important thing is the identification of the main figure and its relation to ROTTBÖLL's diagnosis, since this figure must in our opinion be selected as the type of *P. radicatum*.

In his "Nomenclatural Detective Story" (LÖVE 1962 a) on the typification of *P. radicatum,* LÖVE gave, however, another motivation for his emendation of the concept *P. radicatum* and chose as type a fragmentary specimen in the EGEDE herbarium in the Botanical Museum of Copenhagen (C). In comparison with the picture in ROTTBÖLL's work this is very poor, consisting of a single flowering stem and five, partly incomplete rosette leaves, all in a very bad state of preservation. It is, therefore, only possible to guess that it belongs — as LÖVE holds — to the 56-chromosomic Greenland poppies, but to which race within that it is impossible to decide. It may be, that this specimen was among those seen by ROTTBÖLL, still one may ask why this should be chosen as the type of *P. radicatum.*

ROTTBÖLL, in the introduction to his work, says that, had it not been for the collections made by Professor EGEDE, he would not have included any Greenland plants at all in his treatise. According to LÖVE (1962 a p. 118) "this indicates that although a substantial number of the plants he discussed were recent collections from Iceland the main purpose of his paper was to describe the plants from western Greenland found in this herbarium". To us it means just the opposite.

As mentioned by LÖVE, ROTTBÖLL says that he had a very large material of his new poppy from Iceland. When he selected a specimen for the plate figure which should represent the species, he took of course one which was well developed so that it would show the details he considered as important in his new species, in other words, one which he himself considered typical of this. The first of these characteristics, pointed out just by the epithet *radicatum,* was the nature of the roots being unusually long and thick. These are present in ROTTBÖLL's plate, but not in the fragmentary EGEDE specimen. Further, the seven-lobed type of leaves stressed by ROTTBÖLL, accords with that of his figure, not with that in EGEDE's specimen.

In the choice between the good figure in the original plate of a well developed specimen showing the roots, the organ that caused the specific epithet, and a leaf type in accordance with that of the original description, and a fragmentary herbarium specimen without roots and with a leaf type disagreeing with that described by ROTTBÖLL, there

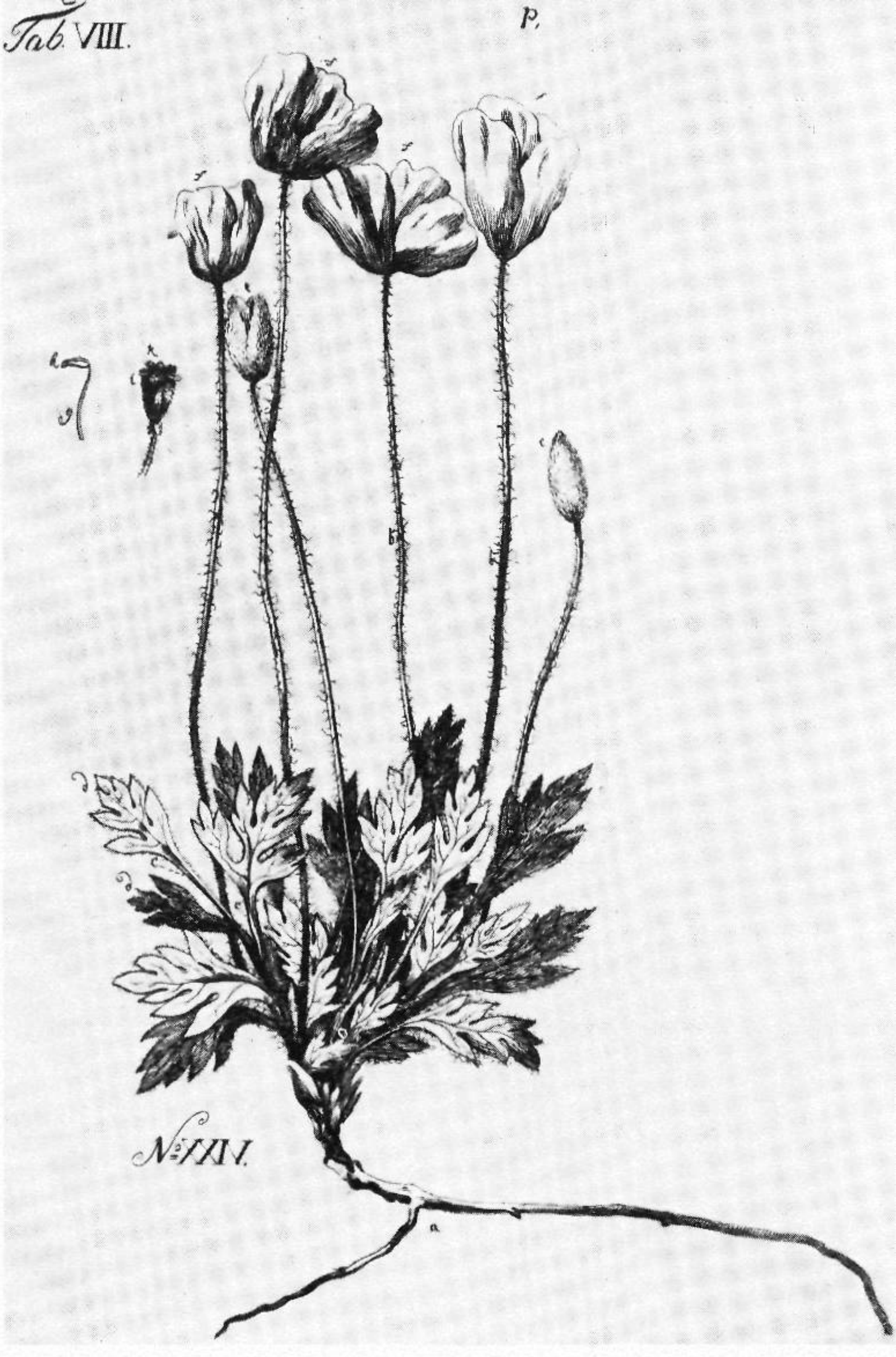

Fig. 1. ROTTBÖLL's (1770) original figure of *Papaver radicatum* ROTTB. Lectotype of the species. Original size of the plate.

Fig. 2. *Papaver radicatum* Rottb. var. *radicatum* (=*P. nordhagenianum* Löve ssp. *islandicum* Löve). — Iceland. Barðastrandasýsla: Brjánslækur, 23.VII. 1962, leg. J. A. Nannfeldt, no. 17564 (UPS). — Photo: F. Hellström.

should be no doubt that the former — not, as LÖVE urged the latter — should be chosen as the type of *P. radicatum* ROTTB.

Then the important question arises, to what taxon the plant of this picture did belong. In our opinion there can be no doubt that it belongs to the group called *P. nordhagenianum* by LÖVE, in fact, as shown by KNABEN 1958, the form of the rosette leaves matches extremely well that in some races of the latter species but differs decidedly from that in LUNDSTRÖM's *P. radicatum* ssp. *occidentale*, with which LÖVE identified ROTTBÖLL's plant. Contrary to the opinion of LÖVE that the depicted specimen emanated from Greenland, it was certainly collected in Iceland, and in all characteristics that can be judged from the plate, it coincides closely with the taxon described by LÖVE as *P. nordhagenianum* ssp. *islandicum*. This should, therefore, be considered the type race of the species and, according to the IR, be called var. *radicatum*, in accordance with the systematic rank KNABEN considers to be the more adequate and which will be discussed by her in a following paper.

It may be mentioned that there is in Copenhagen (C) a herbarium sheet labelled "Hb. ROTTBÖLL" with a well developed flowering specimen of a *Papaver* which clearly belongs to *P. radicatum* in our sense (*P. nordhagenianum* of LÖVE) and most probably emanating from Iceland, since it agrees very well with specimens from there. It also comes close to the specimen in ROTTBÖLL's plate, although it cannot have been the "model" of that. Since there is, as also pointed out by LÖVE, no information about its provenance, this specimen cannot, however, be chosen as the type for ROTTBÖLL's species — this must be typified by the main figure of his plate.

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Studies in Galápagos Plants IX[1]

New Taxonomical and Distributional Records

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ABSTRACT

ELIASSON, U.: Studies in Galápagos Plants IX. New Taxonomical and Distributional Records. — Bot. Notiser 123: 346—357, Lund.

Xiphopteris serrulata (SWARTZ) KAULFUSS (*Polypodiaceae*), *Sida rupo* ULBRICH (*Malvaceae*), and *Bowlesia palmata* RUIZ & PAVÓN (*Umbelliferae*) are reported as new to Galápagos. New distributional records are given for *Urocarpidium insulare* (KEARNEY) KRAPOVICKAS (*Malvaceae*), *Pernettya howellii* SLEUMER (*Ericaceae*), *Nama dichotomum* (RUIZ & PAVÓN) CHOISY (*Hydrophyllaceae*), and *Nolana galapagensis* (CHRISTOPHERSEN) JOHNSTON (*Nolanaceae*).

The species are treated in systematic order. All specimens examined are deposited at the Riksmuseum, Stockholm (S).

Xiphopteris serrulata (SWARTZ) KAULFUSS. Fig. 1

Xiphopteris serrulata (SWARTZ) KAULFUSS 1824 p. 85. *Acrostichum serrulatum* SWARTZ 1788 p. 128. *Polypodium serrulatum* METTENIUS 1856 p. 30, non SWARTZ 1801 p. 25. *P. duale* MAXON 1912 p. 61.

This small and inconspicuous fern has not previously been recorded from the Galápagos Islands. Here it has been collected on San Salvador and Santa Cruz. On both islands it has been found growing epiphytically among mosses in moist regions. The species has a wide distribution and ranges from the West Indies to Peru. It is known also from Africa (MAXON 1914, COPELAND 1947).

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[1] Contribution No. 123 from the Charles Darwin Foundation for the Galápagos.

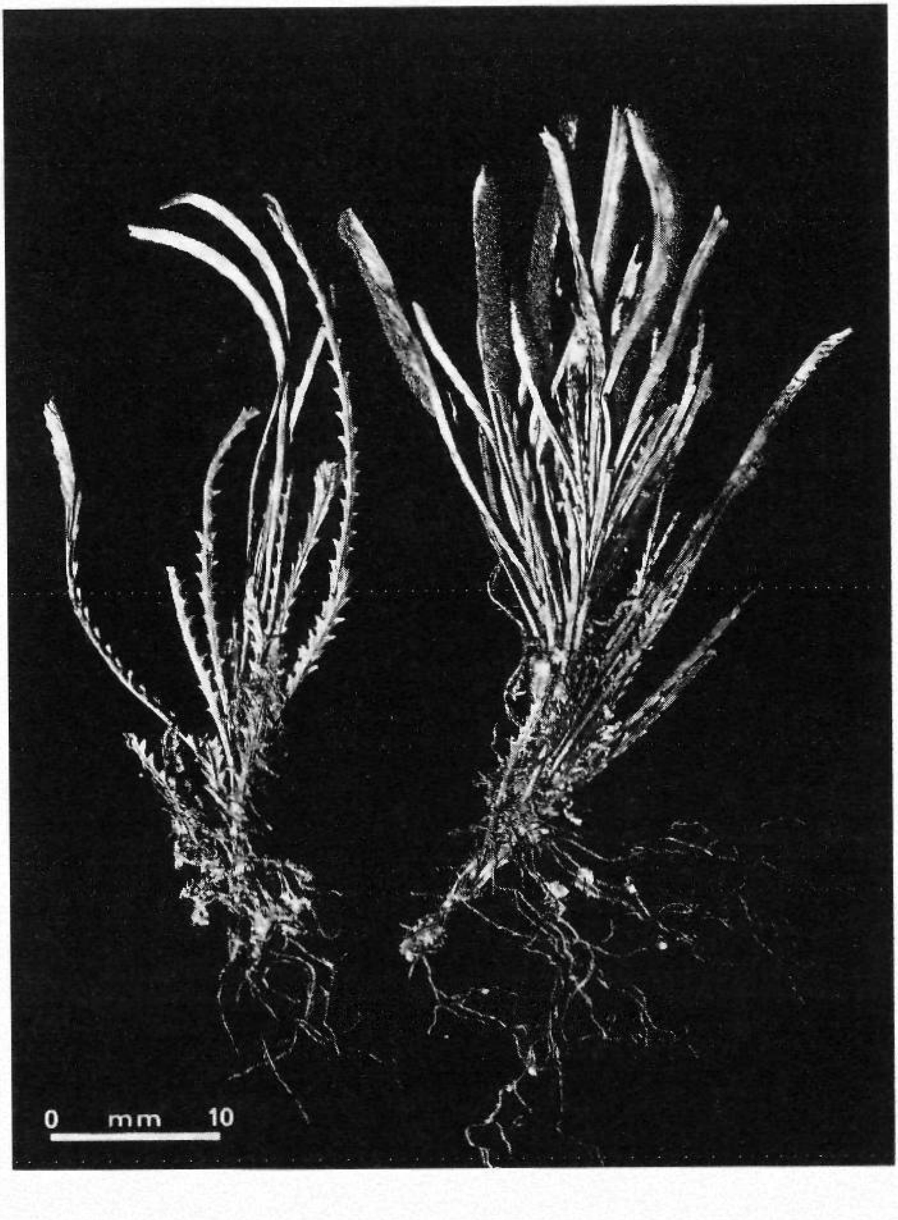

Fig. 1. *Xiphopteris serrulata* (SWARTZ) KAULF. Specimen from Santa Cruz (left, ELIASSON 362) and San Salvador (right, ELIASSON 1131). Note the dense sporangia agglomerations on the right specimen.

Collections studied: San Salvador. ELIASSON 1131, the highland in the north-western part of the island, alt. 850 m, January 26, 1967. Epiphytic on *Zanthoxylum fagara* (L.) SARG. — Santa Cruz. ELIASSON 362, between Bella Vista and Mt. Crocker, alt. 480 m, October 19, 1966. Epiphytic on *Miconia robinsoniana* COGN.

Urocarpidium insulare (KEARNEY) KRAPOVICKAS. Fig. 2

Urocarpidium insulare (KEARNEY) KRAPOVICKAS 1954 p. 631. *Malvastrum insulare* KEARNEY 1952 p. 167.

Since the collections cited below diverge in several respects from KEARNEY's original description, a complete description, based on the specimens examined, is given.

Annual. Stem ascending, up to 12 cm in length, richly stellate-pubescent. Leaves sparse; the lower leaves on stellate-hairy petioles to 15 mm long, the upper petioles c. 2 mm long; stipules subulate, pilose, c. 2 mm in length; leaf-blades ovate or subovate to suborbicular, generally truncate at base, more or less rounded at apex, irregularly serrate-dentate, often slightly lobed, 5—15 mm long, 5—12 mm wide, stellate-pilose on both sides. Flowers axillary and solitary, generally agglomerated towards the branch apices. Pedicels (1—) 2—4 (—10) mm long, stellate-pilose, with subulate, very caducous bractlets c. 1 mm in length. Calyx campanulate, (3—) 4-lobed, richly stellate-pubescent (Fig. 2 A, D), the lobes triangular, 2—3 mm long. Petals 3 in number, adnate to the stamen column, the free part obovate or subspathulate (Fig. 2 B, C), c. 2 mm long. Stamen tube (Fig. 2 F) 1.5—2 mm long, strongly dilated at base, with a few simple trichomes; stamens 5 in number; the free filaments 0.3—0.8 mm long; anthers c. 0.3 mm long. Style branches 7 in number (Fig. 2 E), c. 0.7 mm long, at apex subcapitate. Mericarps (Fig. 2 G) 7—10 in number, subreniform, c. 1.5 mm long, muricate on the back, prominently radially ridged on the sides, slightly stellate-pubescent but becoming subglabrous, black when mature with the basal part beak-like and slightly notched, the upper apex obtuse and prominently notched.

The genus *Urocarpidium* was established by ULBRICH (1916 p. 63) on *U. albiflorum* ULBR. from Peru [treated as synonymous with *Sphaeralcea arequipensis* (JOHNST.) KRAPOVICKAS by MACBRIDE (1956 p. 506)]. The characters on which ULBRICH (1916 pp. 63—66) referred his species to a new genus were the single apical awn of the mericarps, the close connection of the corolla with the stamen-tube, making them

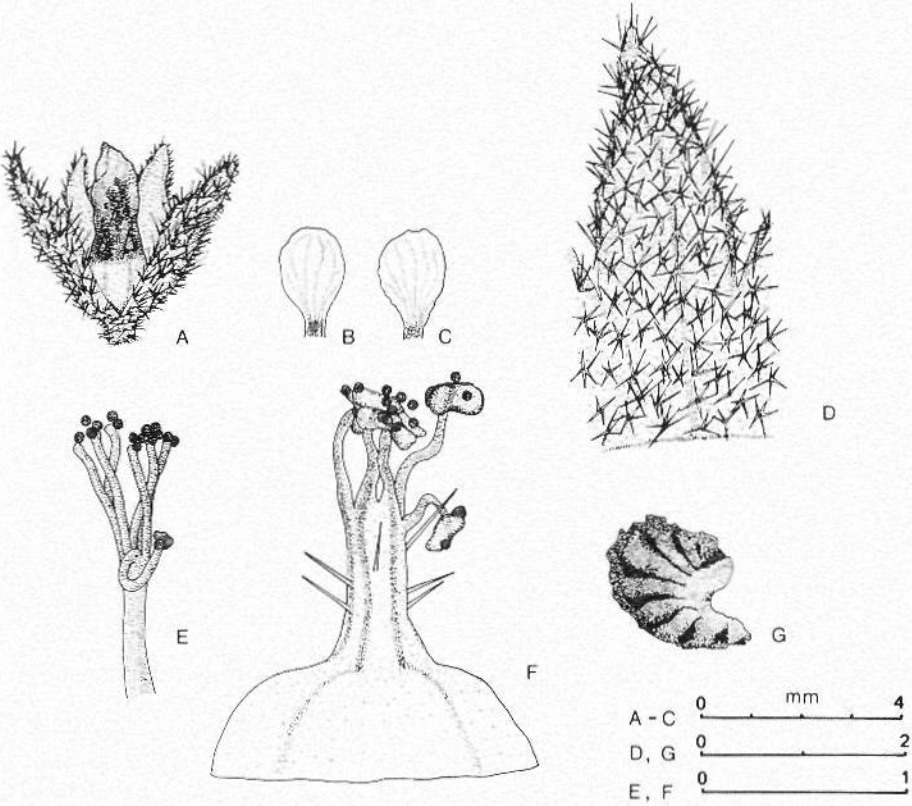

Fig. 2. *Urocarpidium insulare* (KEARNEY) KRAPOV. (ELIASSON 2040). — A: Calyx slightly cut up. The petals, basally adnate to the staminal column, have not yet separated. — B—C: Petals. Note the symmetrical shape. Most other species of the genus have asymmetrical petals. — D: Calyx-lobe. Note the rich stellate pubescence. — E: Upper part of style with its seven branches. Pollen grains are attached to the subcapitate branch apices. — F: Staminal column. The anthers are emptied.

fall off as a unit, and the attachment of the filaments to the summit of the stamen tube. The genus belongs to the tribe *Malveae*, having the carpels borne in a single verticil, and shows affinity to the genera *Sphaeralcea* ST. HIL., *Malvastrum* A. GRAY and *Eremalche* GREENE (KRAPOVICKAS 1954 pp. 607—610).

Ten species, most of which had previously been included in *Malvastrum*, were referred to *Urocarpidium* by KRAPOVICKAS (1954, 1965, 1967) and were referred to a new section, *Anurum*. This section, to which *U. insulare* of the Galápagos Islands belongs, differs from the section *Urocarpidium* (=*U. albiflorum*) in the lack of the long apical awn of the mericarps.

The delimitation of the genus *Malvastrum* has for long been a source of confusion. According to a re-definition by KEARNEY (1955) the genus would comprise perennial species of tropical and subtropical America having a persistent, triphyllous involucel, yellow corollas and nearly indehiscent carpels, which are smooth dorsally and smooth or rugose laterally. The somatic chromosome number has been found to be 12, 24, 32, 36, or 48 (SKOVSTED 1935, KRAPOVICKAS 1954, 1967), with one exception indicating the basic number to be 6 (cf. SKOVSTED 1935, pp. 268, 276, KRAPOVICKAS 1954 pp. 611—613, 1967 pp. 30—31). The somatic number of *Urocarpidium* has been found to be 10, 20 or 30 (KRAPOVICKAS 1954 pp. 612—613, 1967 pp. 29, 34), indicating the basic number of this genus to be 5.

Urocarpidium is a genus of annual herbs, distributed in mountainous and semi-arid regions of Mexico and South America, occupying two areas separated by the tropical zone of Central America (KRAPOVICKAS 1954 p. 613). The Galápagos species differs from the mainland species in having only 5 stamens (10 or more in the mainland species), 4 calyx-lobes and 3 petals (in most cases 5 calyx-lobes and 5 petals in the mainland species) and symmetrically shaped petals (most, but not all, species on the mainland have asymmetrical petals). The endemic Galápagos species has been collected on the crater rims of Volcán Wolf, Volcán Darwin and Cerro Azul on the island of Isabela. Previously it was known only from the type collection from Volcán Darwin ("Tagus Cove Mountain").

Collections studied: Isabela. ELIASSON 2040, Cerro Azul, on the south-western part of the crater rim, alt. 1530 m, April 26, 1967. ELIASSON 2213, Volcán Wolf, on the north-eastern part of the crater rim, alt. 1600 m, May 20, 1967.

Sida rupo ULBRICH. Fig. 3

Sida rupo ULBRICH 1916 p. 75.

Since this species is very poorly known and has often been misinterpreted, a complete description, based on the specimens examined, is given.

Annual, 50—60 cm tall. Stem erect, the lower half unbranched, the upper part with inflorescence-bearing branches; the lowest part glabrous, the upper part more or less densely pilose with simple trichomes. Leaves alternate, successively smaller towards the top of the plant; petioles (2—)3—5 cm long, those of the lowest leaves thinly pilose,

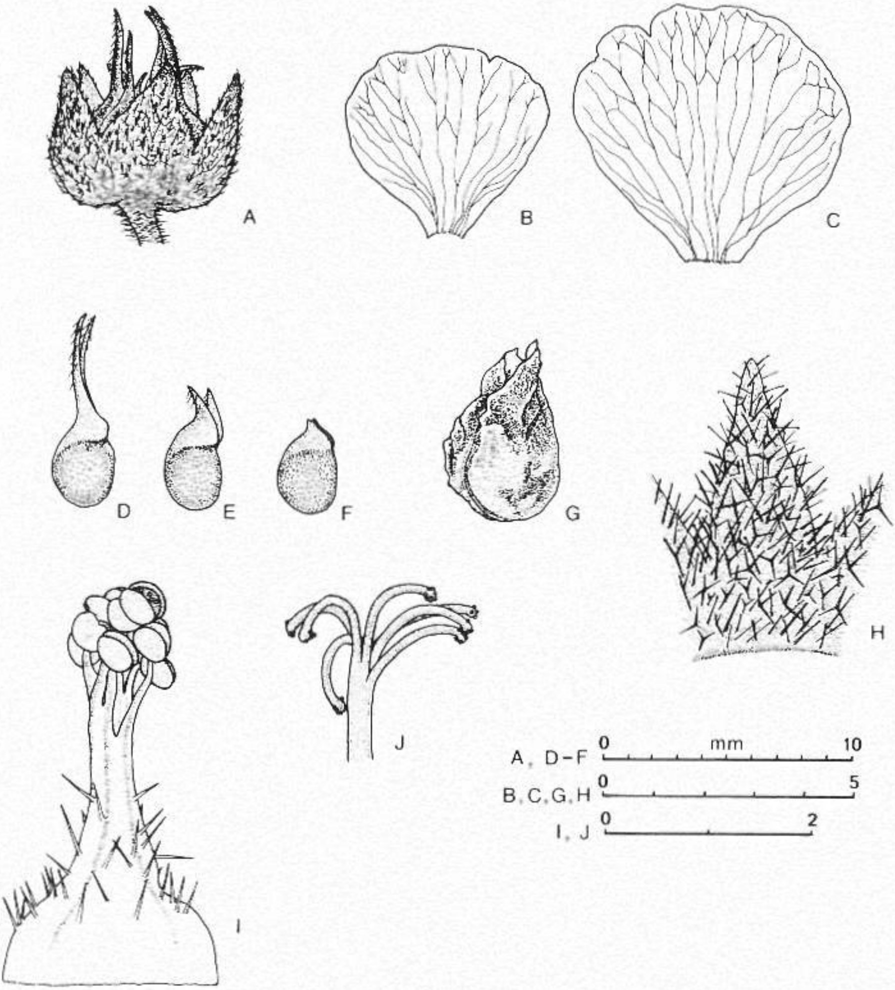

Fig. 3. *Sida rupo* ULBRICH. (ELIASSON 2017). — A: Calyx with mature mericarps. — B—C: Petals from two separate buds. — D—F: Mericarps from the calyx shown in A. Note the different length of the apical awns. — G: Mature mericarp. — H: Calyx-lobe. The calyx is stellate-pubescent with interspersed simple trichomes. — I: Staminal column. — J: Upper part of style with branches. Pollen grains are attached to the branch apices.

those of the upper leaves densely pilose or velutinous; leaf-blade palmately 5—7-lobed; the lowest leaves c. 5 cm long and 6 cm wide, the lobes subovate to subelliptical, acuminate, irregularly serrate; the upper and smaller leaves with narrowly elliptical lobes; leaf-blades on both sides with 3-rayed (2—4-rayed) stellate hairs, above also with interspersed simple trichomes; especially the lowest leaves conspicuously bluish when dried. Inflorescence paniculate; the axis and pedicels velutinous; pedicels 0.5—5 mm long. Calyx (Fig. 3 A) 5-lobed, c. 5 mm long, with 3-rayed stellate hairs (Fig. 3 H) but with interspersed simple trichomes; the lobes triangular. Petals (Fig. 3 B, C) 5 in number, roundly obovate to suborbicular, in mature flowers c. 5 mm long, very thin, easily caducous, violet. Staminal column (Fig. 3 I) 3—4 mm in length, at base strongly dilated, the lower half with straight simple trichomes, free filaments only in the uppermost part, 0.5—1 mm long (Fig. 3 I); anthers 10 in number, c. 0.5 mm long. Style branches (Fig. 3 J) 5—7, recurved, minutely dilated at apex. Carpels as many as the style branches, arranged in a single verticil about a central columella; each carpel with a single pendulous ovule. Mericarps when mature 5—6 mm long, glabrous, irregularly wrinkled (Fig. 3 G), at apex prominently notched and partially dehiscent along the midnerve; the apices of varying length (Fig. 3 D—F), sometimes beak-like or lance-like, retrorsely barbed; differently armed mericarps often present in the same flower.

The species group *Oligandrae*, to which this species belongs, is characterized by palmately lobed leaves and small red-violet flowers. It seems restricted to Ecuador, Peru and Bolivia. MACBRIDE (1956 p. 579) treated *S. rupo* as synonymous with *S. jatrophoides* L'HÉRITIER (1789 p. 117, pl. 56),[1] but ULBRICH's description of the first-named species does not match L'HERITIER's description and plate of the last-named plant. Both species have palmately lobed leaves, but the lobes of *S. jatrophoides* are again irregularly but deeply lobed and serrate, while the lobes of *S. rupo* are merely serrate. *S. rupo* has 10 anthers, while *S. jatrophoides* has twice this number (FRIES 1947 p. 19, cf. MACBRIDE loc. cit.). To me these two plants are definitely distinct species.

S. rupo is new to Galápagos. Previously it has been reported only from Peru.

Collection studied: Isabela. ELIASSON 2047, Cerro Azul, on the south-western part of the rim of the caldera, alt. 1590 m, April 26, 1967.

Bowlesia palmata RUIZ & PAVÓN

Bowlesia palmata RUIZ & PAVÓN 1802 p. 28.

For a complete description of this species, the reader is referred to MATHIAS & CONSTANCE (1965 p. 52).

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[1] The date of this work is 1789, not 1785 as printed (GARCKE 1891 p. 463).

The distribution of this species ranges from southern Ecuador to southern Peru (MATHIAS & CONSTANCE 1965). The genus is new to Galápagos. The occurrence here is no doubt the result of a successful long-distance dispersal, most probably by birds. The fruit of this as well as of most other species of the genus is well adapted to synzooic dispersal through the presence of coprinoid glochids.

Collection studied: Fernandina. ELIASSON 1647, on the upper part of the inner north-eastern wall of the caldera, alt. 1350 m, March 24, 1967.

Pernettya howellii SLEUMER

Pernettya howellii SLEUMER 1935 p. 649.

The type locality of this endemic Galápagos species is Mt. Crocker, the highest part of Santa Cruz. I have collected this plant also on the rim and the floor of the caldera of Volcán Santo Tomás on Isabela. According to SLEUMER (1935 p. 632) this species shows more affinity to the Chilean *P. mucronata* (L. f.) GAUD. than to the species of the Ecuadorian mainland.

Collections studied: Isabela. ELIASSON 1478, 1479, Volcán Santo Tomás, on the eastern part of the rim of the caldera, alt. 1000—1030 m, March 3, 1967. ELIASSON 1570, Volcán Santo Tomás, on the floor of the caldera, alt. 870 m, March 6, 1967. — Santa Cruz. FAGERLIND & WIBOM 2867, 3254, 3255, April—May 1953. HARLING 5162, Mt. Crocker (type locality), alt. 860 m, May 23, 1959. ELIASSON 276, near Mt. Crocker, among *Sphagnum* in a wet depression, alt. 760 m, October 17, 1966. ELIASSON 1606, vicinity of Mt. Crocker, alt. 780 m, March 14, 1967.

Nama dichotomum (RUIZ & PAVÓN) CHOISY

Nama dichotomum (RUIZ & PAVÓN) CHOISY 1833 p. 113. *Hydrolea dichotoma* RUIZ & PAVÓN 1802 p. 22.

This is a species of western South America, known from Ecuador, Peru, Bolivia, Chile, and Argentina (GIBSON 1967 p. 106). In Galápagos it has been found at high elevations on the island of Isabela. Here I have collected it on Volcán Alcedo, Volcán Darwin and Cerro Azul. Previously the species was known only from Volcán Darwin ("Tagus Cove, occasional in lava crevices at 4000 ft.", STEWART 1911 p. 126).

Collections studied: Isabela. ELIASSON 1281, Volcán Alcedo, on the south-eastern part of the rim of the caldera, alt. 1100 m, February 12, 1967. ELIASSON 1752, Volcán Darwin, on the plateau in the south-western part of the caldera, alt. 1180 m, March 28, 1967. ELIASSON 2044, Cerro Azul, on the south-western part of the rim of the caldera, alt. 1530 m, April 26, 1967.

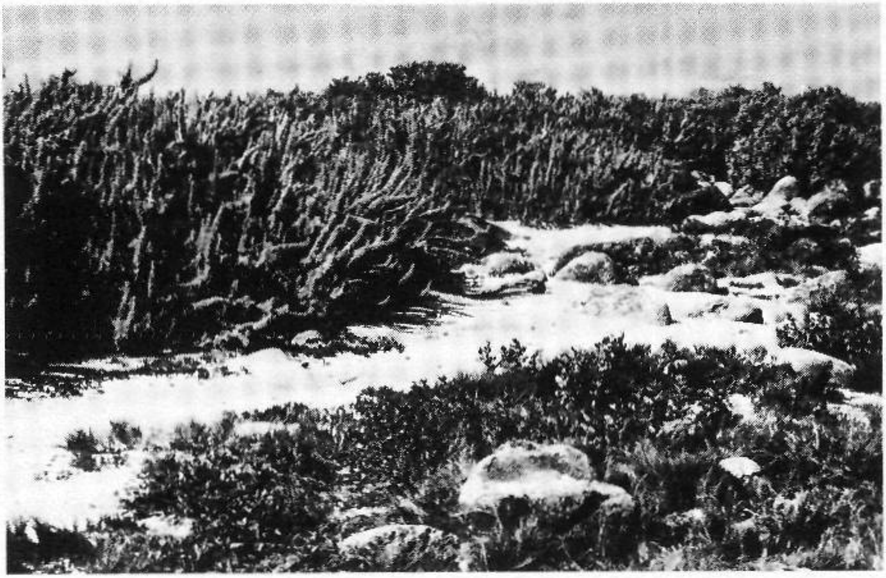

Fig. 4. Dense stands of *Nolana galapagensis* (CHRISTOPH.) JOHNST. on the Caamaño islet (Jensen Island) in Academy Bay on the south side of Santa Cruz. In the foreground *Amaranthus scleranthoides* ANDERSS., *Sesuvium portulacastrum* L., *Trianthema portulacastrum* L., *Heliotropium curassavicum* L., and *Sporobolus virginicus* (L.) KUNTH. — Photo: U. E. 18.3. 1967.

Nolana galapagensis (CHRISTOPH.) JOHNSTON. Figs. 4—5

Nolana galapagensis (CHRISTOPH.) JOHNSTON 1936 p. 32. *Periloba galapagensis* CHRISTOPHERSEN 1932 p. 89.

For a complete description of this species, the reader is referred to JOHNSTON (loc. cit.).

The species is endemic to Galápagos. It grows on sea-shores, preferably on shell sand on scattered localities in the archipelago (Fig. 5). It flowers during January—March. During nine months in the archipelago in 1966 and 1967 I found this plant on seven widely scattered localities. It had not previously been collected on the islands of Isabela and San Cristóbal. The type locality is Turtle Bay on the south side of Santa Cruz. Ten or fifteen shrubs were seen here, growing on shell sand between 50 m and 100 m from the sea. The largest occurrence of this species is on the islet of Caamaño (Jensen Island), a low, flat islet, possibly 200 metres across, in the mouth of Academy Bay on the south

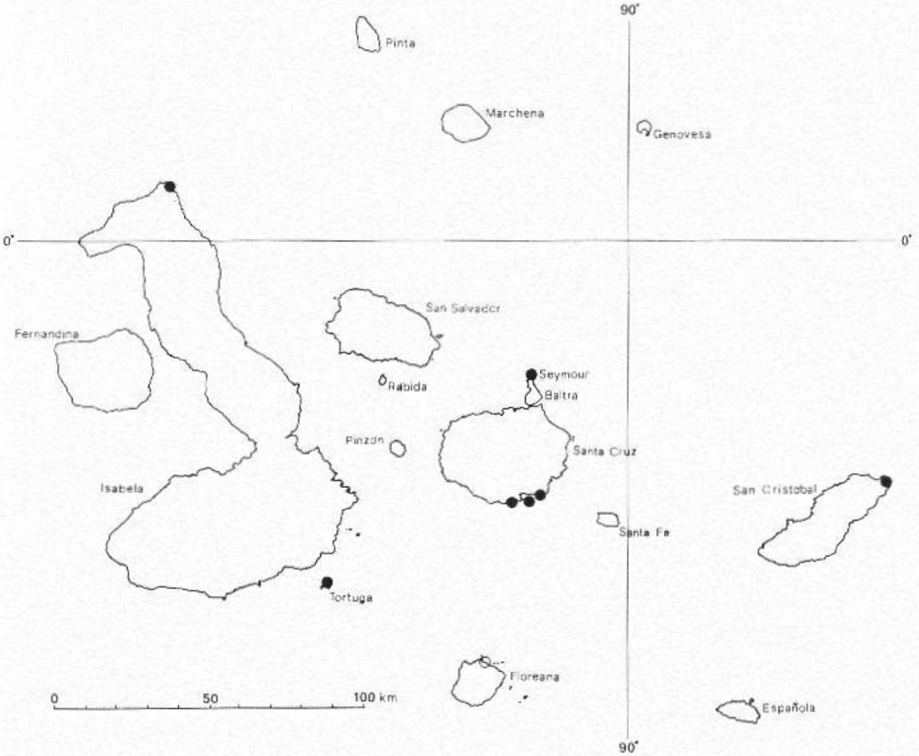

Fig. 5. Distribution of *Nolana galapagensis* (CHRISTOPH.) JOHNST., as hitherto recorded. Filled circles represent records made by me in 1966—1967. The open circle on Floreana is a record made by STEWART (1911 p. 65) as "*Aizoacea* (?) sp.". The western-most circle on Santa Cruz represents the type locality.

side of Santa Cruz. *Nolana* is extremely abundant here (Fig. 4), forming pure stands over large surfaces and being the most important plant on the islet. The other species noted here are *Amaranthus scleranthoides* ANDERSS., *Cryptocarpus pyriformis* H. B. K., *Sesuvium portulacastrum* L., *Trianthema portulacastrum* L., *Portulaca oleracea* L., *Parkinsonia aculeata* L. (a few trees), *Coldenia* sp., *Heliotropium curassavicum* L., *Lycium minimum* HITCHC., *Eragrostis cilianensis* (ALL.) LUTATI, and *Sporobolus virginicus* (L.) KUNTH.

N. galapagensis sets the northern limit for the genus, the main distributional area of which is the coastal regions of Chile and southern Peru. The species seems more closely related to Chilean species than to those of Peru, in spite of the less geographical distance of the latter (JOHNSTON loc. cit.).

Collections studied: Isabela. ELIASSON 2176, Punta Albemarle, alt. 0—5 m, May 19, 1967. — San Cristóbal. ELIASSON 2245, Cerro Pitt, alt. 5—10 m, May 26, 1967. — Santa Cruz. ELIASSON 266, Turtle Bay, alt. 5—10 m, about 50 m from the sea. ELIASSON 1206, Turtle Bay, alt. 5—10 m, February 3, 1967. ELIASSON 1614, 1621, 1623, Isla Caamaño (Academy Bay), alt. 0—5 m, March 18, 1967. — Seymour. ELIASSON 1835, south side, alt. c. 15 m, April 7, 1967. — Tortuga. ELIASSON 1805, 1808, alt. 20—50 m, March 31, 1967.

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Botanical Literature

Botanisk litteratur

Swanson, C. P., Merz, T. und Young, W. J.: Zytogenetik. — Gustav Fischer Verlag, Stuttgart 1970. 179 Seiten, 93 Abbildungen, flexibler Kunststoffband. DM 19,80.

Dieses Buch gehört zu einer Reihe von ähnlichen Schriften (Grundlage der modernen Genetik), von denen bereits fünf Bände erschienen sind. Die Autoren sind Professoren bzw. der Biologie, Radiologie und Biophysik an der John Hopkins Universität, Baltimore. Das Buch kann als eine abgekürzte und modernisierte Fassung von Swansons angesehenem „Cytology and Cytogenetics" (2nd ed., London 1960) betrachtet werden. Es beschäftigt sich hauptsächlich mit Zytogenetik im klassischen Sinne, d.h. auf dem Niveau des Lichtmikroskops. Gewisse elektronmikroskopische Beobachtungen und biochemisch-genetische Verhältnisse, z.B. die Ultrastruktur der Lampenbürstenchromosomen und die Replikation des DNS-Moleküls von Bakterien- und Phagenchromosomen werden doch erwähnt. Es mangelt doch an einer einleitenden Beschreibung des Baues und der Funktion des DNS, der vielleicht als bekannt voraussetzt wird und allerdings in Band 5 dieser Reihe (Hartman und Suskind: Die Wirkungsweise der Gene) ausführlich behandelt wird.

Die Zytogenetik ist historish gesehen eine Mischwissenschaft. Die im Beginn dieses Jahrhunderts aufgestellte Chromosomentheorie der Vererbung wurde erst mit der Arbeit der klassischen amerikanischen *Drosophila*-Schule endgültig bewiesen. Swanson, Merz und Young erstatten einen gründlichen Bericht über den Verlauf der Meiose und die chromosomale Grundlage der Kopplung und des Crossing-over. Der Mechanismus der Chiasma-Bildung wird besonders ausführlich behandelt und verschiedene neuere Theorien von Uhl, Whitehouse, Grell u.a. werden diskutiert.

In zwei von den sieben Kapiteln werden strukturelle Veränderungen der Chromosomen bzw. Variation ihrer Anzahl konzis und überblickbar besprochen. Das Vererbungsmuster von Komplex-Heterozygoten und die Wirkungsweise des Renner-Effektes werden durch gute Abbildungen erklärt. Polyploidie ist doch etwas stiefmütterlich behandelt und Abb. 86 (S. 131), die die Beziehungen zwischen Autopolyploidie, Allopolyploidie und segmentaler Allopolyploidie darstellt, ist schwer zu deuten.

Wie im Schlusskapitel erwähnt sind viele zytogenetische und zytochemische

Verhältnisse noch nicht befriedigend erforscht. Die Natur der chemischen oder physikalischen Kräfte der meiotischen Paarung ist z.B. noch unbekannt. Praktisch unerklärt ist auch die interessante Tatsache, dass gewisse verhältnismässig primitive Organismen (z.B. das Lungenfisch) viel mehr DNS pro Chromosomensatz haben als Tiere von grösserer struktureller und funktioneller Komplexität. Vielleicht enthalten besondere Chromosomen grosse Mengen von dupliziertem DNS-Material, das durch anomale Replikation entstanden ist.

Am Ende von jedem Kapitel ist eine z.T. kommentierte Literaturauswahl hinzugefügt. Wahrscheinlich ist das Buch als Lehrbuch für Universitätsstudenten der Genetik abgesehen aber kann auch für Biosystematiker empfohlen werden. Gewisse genetische Vorkenntnisse sind doch wünschenswert, da der Text oft ziemlich konzentriert ist.

ARNE STRID

STILES, W. & COCKING, E. C.: An Introduction to the Principles of Plant Physiology. — Methuen & Co., London 1969. VIII + 633 pp., 53 figs. Price £8.80.

The first thing that strikes the reader of this text when he glances through the table of contents is the appearance of completeness. The book at least touches upon all the different topics that by tradition have been included in the discipline of plant physiology. In comparison with almost every other modern text, it is most comforting that the irritability and the movements of plants have not been forgotten. In fact, 126 of the 564 text pages have been allotted to this subject.

The present edition is the third one, completed by Dr. COCKING after the death of Professor STILES. STILES started writing the original work in 1925. Making new editions of old textbooks, a way of renewing the literature appropriately called "the Strasburger method" certainly has its drawbacks. It must be admitted that Dr. COCKING has made great attempts to update the material, and references have been included up to the time of printing. Still the treatment of the subject, at least in many instances, must be regarded as old-fashioned. This is obvious already in the first chapter, where old views about the nature of the "protoplasm" are accounted for in rather great detail, while the treatment of the endoplasmatic reticulum seems to be limited to two sentences and the abbreviation e.r. in a figure. The median year in the reference list at the end of the book seems to be near 1936.

Although there are 39 pages on respiration, the hexose monophosphate shunt is not mentioned. In the section about fixation and reduction of carbon dioxide, the CALVIN cycle is fortunately treated. There is no mention, however, of the HATCH and SLACK pathway, which would certainly be more worth a few words than WARBURG's theory about photolysis of a chlorophyll-CO_2 complex.

The chapter on heterotrophic plants, apart from the lack of all figures, is put on the positive side of my account. Such a chapter is often lacking altogether in textbooks of plant physiology. At first I was shocked to find *Monotropa* and several orchids listed under the heading "Saprophytes". However, the mykorrhiza of these plants and others are later accounted for in a correct way. It could have been mentioned that *Monotropa* develops best when the same mycelium associates both with the herb and with trees. It has also been shown that phosphate and organic carbon are transferred from trees to *Monotropa* plants. The relationship should therefore probably be described as symbiosis between *Monotropa*, fungus and tree (on the borderline to parasitism by *Monotropa*).

The heading "Periodicity" arose my interest, but I became somewhat disappointed when reading it. After a short introduction there is a sub-heading "Annual periodicity", and this seems to be all that the chapter deals with. In the introduction it is said that »most plants exhibit a daily periodicity in their activities. Generally it is obvious that this is directly traceable to daily rhytmic alternations of temperature and illumination». Although in a later chapter there is a section on autonomic movements (called automatic movements on p. 459), the treatise seems to completely disregard the circadian rhytms, the "biological clocks" which are important not only for movements. The authors manage to get through the chapter on photoperiodism with only two sentences touching on this aspect of the phenomenon: "As suggested by Bünning, other endogenous time-measuring systems" (i.e. other than the P730 to P660 conversion) »probably also function in photoperiodic responses. The operation of biological 'clocks' is evident in the daily movement of leaves and often leaf-movements parallel the photoperiodic responses of the plant." This certainly is to compress unduly the knowledge of to-day, considering the size of the book.

The text would have been easier to follow and to remember if there had been more simple little figures and diagrams in it. However, there is also something very positive to say about the illustrations: The photographs that occur are excellently reproduced.

To sum up: There is much positive to say about the book. It gives what the title promises, "An introduction to the principles of plant physiology", a firm foundation in the past research and the old ideas which belong to a perfect education. If it could be followed up a similar volume on "Recent developments in plant physiology" it might be O.K., if a student could be found who is willing to swallow two volumes of this size in his introductory course. In real life compromizes must be made. I think this compromizing must start with a trimming down of obsolete ideas. Some knowledge of the history of science, of the great steps forward and of the great mistakes, hurts nobody.

L. O. Björn.

Schmithüsen, J.: Allgemeine Vegetationsgeographie. — Lehrbuch der allgemeinen Geographie. IV. 3. uppl. — Walter de Gruyter & Co. Berlin 1968. XXIII+463 sid., 275 figurer. Klotband. DM 48: —.

När andra upplagan av denna bok, som ingår i en serie geografiska läroböcker, kom ut hade jag tillfälle att ge några allmänna synpunkter på boken ur botanisk synpunkt (Bot. Notiser 113: 122—123). Den nu utgivna upplagan är i första hand en kraftig utvidgning jämfört med de båda tidigare men också en omfattande nyarbetning. Textmaterialet har ökat med ungefär 50 % och antalet bilder fördubblats jämfört med 2. upplagan samtidigt som dispositionen i stort sett är oförändrad.

Avsikten med boken är uppenbarligen att ge en allsidig växtgeografisk beskrivning av jorden. Bokens första del ägnas i huvudsak åt floristisk växtgeografi. Där finns en traditionell översikt över jordens florariken, olika livsformtyper etc. hos växterna samt utvecklingshistoriska och ekologiska orsaker till växternas olika utbredning. Den största utvidgningen av boken faller på den andra huvuddelen, där framförallt översikten av jordens olika växtformationer fått ett väsentligt ökat utrymme. I detta avsnitt behandlas också växtsociologin och dess arbetsmetoder, vegetationsdynamik och vegetationens plats i landskapet med utgångspunkt från gängse mellaneuropeiska synpunkter. Ett teoretiskt avsnitt om vegetationskartering och därmed förknippade problem samt en jämfört med tidigare upplaga något utvidgad framställning om de klimatiska vegetationszonerna ingår i bokens tredje och sista del. Typografi och bildmaterial är genomgående tilltalande och av betydligt bättre kvalité än i förra upplagan.

Urvalet av läro- och handböcker i allmän växtgeografi är mycket litet. De som finns behandlar dessutom vanligen endast delar av växtgeografien, som regel antingen enbart den floristiska och historiskt-genetiska växtgeografin eller enbart den ekologiska växtgeografin och de klimatiskt betingade högre vegetationsenheterna. Så tillvida är denna lärobok bra som den behandlar växtgeografin relativt allsidigt och inte heller inriktar sig på någon speciell världsdel eller region vilket gör många amerikanska läroböcker relativt ointressanta i Europa. Detta medför emellertid också att den i åtskilliga delar ur botanisk synpunkt trots den betydande utökningen är rätt ytlig, exempelvis beträffande den historiskt-genetiska delen. Boken har som så många andra tyska läroböcker sin styrka i terminologin och de beskrivande momenten. Just då det gäller beskrivningen av vegetationen och sambandet mellan vegetationens fysionomi och makroklimat jämte därmed sammanhängande förhållanden har boken betydande förtjänster. Man saknar dock mera ingående ekologiska diskussioner, exempelvis kring temat vegetation—mark. Författarens disposition av stoffet gör att tonvikten ligger på den terrestra vegetation som karakteriserar de olika vegetationsregionerna. Sådana landskapsekologiska element som myrarna, vilka ju är betydelsefulla både på norra och södra halvkloten, får därigenom en jämförelsevis styvmoderlig behandling.

Med beklagande måste man alltså konstatera att den nya upplagan liksom den tidigare innehållsmässigt inte uppfyller de önskemål man ur botanisk synpunkt skulle vilja ställa på en växtgeografisk lärobok och behovet av en modern, botanisk lärobok i allmän växtgeografi är alltjämt lika trängande.

NILS MALMER

SINGH, AMAS: Plant Physiology. — Asia Publishing House. London 1968. XI+615 pp., 201 figs. Price 60 s.

The author opens with the following statement with which the reviewer completely agrees: "Progress concerning an inquiery into the facts relating to the domain of Plant Physiology has been appreciable in the recent past." A little further down the following is found: "This text book does cite in quite an extensive manner the relevant literature on the subject." The more surprising is it to find that the author has almost completely neglected the scientific progress during the past ten years. Out of about 1260 references listed at the end of the book, I have found only about 30 from the 1960's (several of them refer to the Encyclopedia of Plant Physiology and thus to older research). I will mention only one example of what this neglect of the modern literature has led to. On 2 1/2 pages the author discusses the effect of light on respiration. He divides his discussion in a "I. View" and a "II. View". "According to the second view there is no effect of light on respiration", while according to the first there is. The reader must get the impression that nothing is really known on the subject. The author refers to chloroplasts as "normal dark respiratory centres" which is, to say the least, misleading. But he touches on the truth when he states that "Very recently (sic!) Thimann and others (1958) found an induced additional respiration in light". In fact, ten years later a special session of a large scientific congress was devoted to photorespiration. I consider it meaningless to mention anything at all about light effects on respiration if the modern findings are disregarded.

The book is specifically written for use at Indian universities. Therefore some of the critizism I would deliver if it were planned to be used in Europe is rather irrelevant. Like the author I do think that a book for Indian universities is best written by somebody thoroughly aquainted with the specific needs of Indian students, and of India. This country can, however, even less than any other, afford to disregard the last ten years of research in plant physiology.

Chapter 2 is entitled "Physiology of the cell" but deals entirely with osmotic conditions. I do not consider the two synonymous. Some technicalities, although of minor importance, are irritating. The printing errors are frequent. Upper and lower case letters are used inconsistently. Hand-written letters are used in many formulae and figures, which makes them tiring to follow, even if the writing in most cases is perfectly legible. Phosphate groups are written either as OPO_3H_2, as P or as Ph. The way of writing chemical formulae often effectively hides the true nature of the compounds. One example is $CH_2=CO \sim PO_3H_2COOH$ (p. 270). Who would understand that the second and third carbon atom are directly united by a covalent bond, if he did not know it already? Many such examples could be cited. The use of the abbreviations DPN and TPN and the corresponding chemical names instead of NAD etc, must also be considered obsolete by now.

L. O. Björn

OPERA BOTANICA

is edited by the Lund Botanical Society in cooperation with the Institute of Systematic Botany, University of Lund. It consists of larger treatises issued at indefinite times. After vol. 12 the series is published in separate numbers, each with an individual price. The reduced prices for members of the Lund Botanical Society are indicated.

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