Drawings of Scandinavian Plants 9–10

Eleocharis R. Br.

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"Squamae undique imbricatae, conformes: vix ullae steriles.
Setae hypogynae (4—12) denticulatae, raro nullae.
Stylus 2—3-fidus, basi dilatata cum ovario articulata.
Nux saepius lenticularis, basi dilatata indurata styli coronata.
Plantae paludosae (unde nomen).
Culmi simplices, aphylli, basi vaginati.
Spica unica, terminalis, erecta, nuda."

R. Brown (1810)

The genus *Eleocharis* R. Br. includes more than 150 species which were arranged in 9 series by H. K. Svenson (1929—1939). The taxa are found in large numbers especially in the New World. *Eleocharis* is, however, floristically difficult and critical in Scandinavia, where only ten species and subspecies are native.

All Scandinavian taxa within *Eleocharis* are perennial. The stem is sympodial and each adult shoot generation normally includes three vegetative nodes. The next shoot generation is formed axillary from the leaf of the first node. The stem may be short, as in *E. multicaulis*, but most often forms a rhizome, which is composed of the first two internodes of each shoot generation. The first internode of a shoot generation is accreted to the second internode of the former generation.

No foliage leaves are produced, but only sheath-like structures along the rhizomes and around the culm bases. The culm is nodeless and assimilating. It has a ± well developed aerenchyma. Anatomical and epidermal structures of the culm afford useful taxonomical characters in several species.

The inflorescence is a solitary, terminal and ebracteate spike. The flowers are arranged in a ± dense spiral and imbricately covered by

[1] Strandhede is responsible for the text and Dahlgren for the drawings.

glumes. The receptacle density (number of flowers per cm of spike) and the glumes (the basal, often "sterile" glumes as well as the other, "fertile" glumes) afford taxonomically useful characters.

The stigmatal branches are three in some series, but two in others. The fruit is a nutlet (achene), crowned by the ± prominent style base (stylopodium), the texture of which is different from the remainder of the achene. The achene is surrounded by 0—8 hypogyneous and sometimes branched setae. Fruit characters are of great diagnostic value.

The morphological differentiations between the species of *Eleocharis* are only in a few cases suitable to illustrate by drawings. Several attempts have been made, but many of them have only been of limited value for the identification of the taxa. The main reason for this is the small, often quantitative rather than qualitative morphological differences between several taxa in combination with a considerable variation within the taxa. The morphological differences between *E. palustris* ssp. *palustris* and ssp. *vulgaris* form a good example of these conditions.

Several of the macroscopic characters used in floras, such as the style bases and the total culm length, are easily modified by environmental factors such as humidity, but also by the ripeness of the plant when dried. Nevertheless, the style bases are of high diagnostic value for distinguishing certain taxa such as *E. mamillata* ssp. *mamillata* and ssp. *austriaca*, but not for others such as *E. palustris* ssp. *vulgaris* and *E. uniglumis* ssp. *uniglumis*. The same may be said about such a character as the bristles, which are rather indifferent for distinguishing *E. mamillata* ssp. *mamillata* and ssp. *austriaca*, but of a certain value for distinguishing *E. palustris* ssp. *vulgaris* and *E. uniglumis* ssp. *uniglumis*.

Literature: Bibliographies are given in STRANDHEDE, S.-O. 1965. Chromosome studies in *Eleocharis*, subser. *Palustres*. III. Opera Bot. 9(2). — 1966. Morphologic variation and taxonomy in European *Eleocharis*, subser. *Palustres*. Ibid. 10(2).

E. mamillata LINDB. FIL.

[*Scirpus mamillatus* LINDB. FIL. nom. alt., *Scirpus palustris* L. sensu ampl. p.p., *E. palustris* (L.) R. & S. sensu ampl. p.p.]

Rhizomes weak and slender; the second internode of the shoot generations normally much shorter than the first internode of the next axillary shoot generation accreted to it. Basal sheaths of the culms

yellowish-brown to pale reddish (rarely carmine) or pale green to lightly greyish-brown; orifice straight or somewhat oblique, often with a marked margin.

Culms usually 10—60 cm, soft and *easily compressed*; *collenchyma strands weak and few*, (3—) 6—11 (—21) epidermal cell rows between them; *single layers of palisade cells and parenchyma cells* in the interspaces between the vascular bundles resulting in a *semi-translucent, brightly green* appearance of the culms. Cell walls markedly thin; *stomatal guard cells longer than the subsidiary cells and protruding* at the ends of the stomata, resulting in *convex short ends of the stomata*; stomatal length (38—) 42—52 (—65) µ.

Basal glumes of the spike semi-amplexicaul rarely ± amplexicaul, 1—2, sterile. Fertile glumes 3—3.5 mm, commonly dull and greyish-brown, with a distinct, green midrib and hyaline margins during prefloral and floral stages, when older increasingly membranaceous. Receptacle density great but different in the two subspecies.

Thecae whitish-yellow and shorter than 1.8 mm. Shape of pollen grains rounded; length 29—42 µ, width 25—37 µ.

Achene shape subrotund or obovoid, more rarely pyriform; colour *yellowish to brownish*; *surface rather smooth. Style base* prominently developed, *sessile*; shape extremely different in the two subspecies. *Bristles* (4—) *5—6* (—8), longer than or as long as the achenes; *barbs coarse, spreading.*

Chromosome number 2n=16 (heteroploid chromosome numbers occur).

E. mamillata is often rather *ephemeral* in nature as well as in culture. It occurs in cleared ponds and ditches or in other shallow water ± free from other vegetation and with *soft, organogenic or fine sedimentary bottoms.*

The species forms two interfertile subspecies distinguished in morphology, ecology, and geographical distribution.

E. mamillata LINDB. FIL. ssp. mamillata

[*E. palustris* ssp. *mamillata* (LINDB. FIL.) BEAUV., *S. palustris* ssp. *mamillatus* (LINDB. FIL.) MELA & CAJ.]

This subspecies is distinguished from the next one in the following characters:

Receptacle density (30—) *36—48* (—56) *fruits per cm of the rachis.*

Achene shape often subrotund; length 1.2—1.4 mm, width 1.0—1.3 mm; colour often *yellowish* to greyish-brown. *Style base mamillate, broader than long*; length 0.3—0.5 (—0.6) mm, width (0.4—) 0.5—0.7 (—0.8) mm. Bristles often more than 5 in number.

This subspecies is rather common in suitable localities (small stagnant ponds etc. without competing vegetation) in ± *oligotrophic, non-calcareous areas.*

Rather common in the lowlands except in the northernmost parts of Scandinavia and Finland, further eastward through the Soviet Union and Asia. Rarer in Central Europe and unknown west of the Rhine and from S. Europe and Iceland.

E. mamillata LINDB. FIL. ssp. **austriaca** (HAYEK) STRANDH.

[*E. austriaca* HAYEK, *E. benedicta* BEAUV., *E. palustris* ssp. *austriaca* (HAYEK) PODP., *E. leptostylopodiata* ZINSERL., *E. ussuriensis* ZINSERL.]

This subspecies is distinguished from ssp. *mamillata* in the following characters.

Receptacle density (40—) *50—75* (—95) *fruits per cm of the rachis. Achene shape often obovoid*; length 1.2—1.5 mm, width 0.9—1.3 mm; colour more often *brown* to dark brown, rarely reddish-brown. *Style base narrowly conical, longer than broad*; length 0.5—0.8 mm, width 0.3—0.5 mm. Bristles (4—) 5 (—6).

Ssp. *austriaca* occurs in *mountainous, often calcareous areas* where it grows in shallow back waters and oxbows in streams, rarely along shores of lakes.

In Scandinavia, it is only known in Norway (Sör-Tröndelag, Nord-Tröndelag, and Nordland). During the last 10 years, it has also been found in a few localities in Britain. It is common in the Alps (Austria, Switzerland, France and Italy), and in S. Germany. It is known also in other mountainous areas such as the Pyrenees, Jura, Tatra, and Ukraine. The synonym *E. leptostylopodiata* is reported as disjunct in European Russia to the Middle Volga region, Urals, Siberia, Altai, and Amur, from where it was also described as *E. ussuriensis*.

E. palustris (L.) R. & S.

[*Scirpus palustris* L.]

Rhizomes stout and tough: the second internode of the shoot generations normally of about the same length as the first internode of the

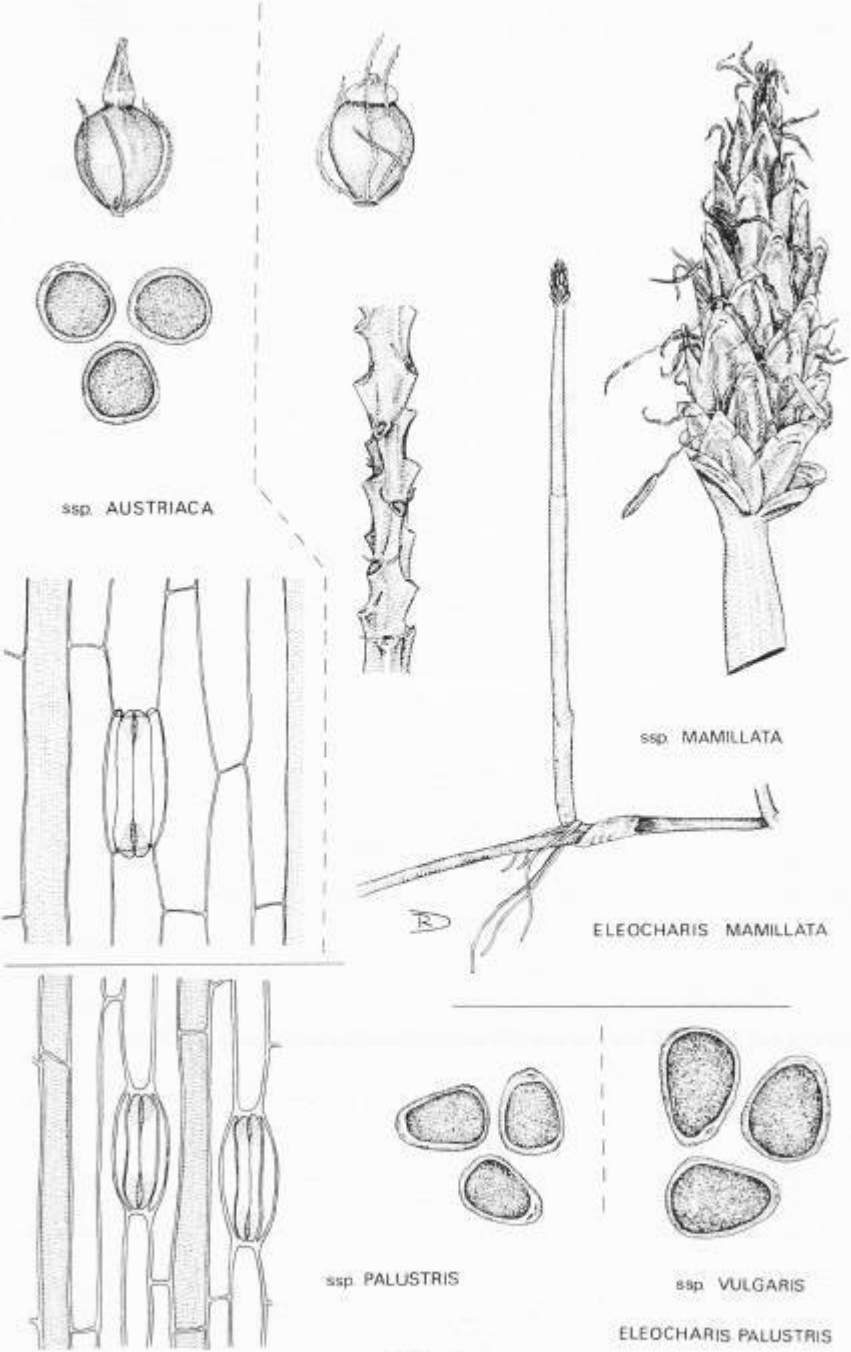
ssp. AUSTRIACA
ssp. MAMILLATA
ELEOCHARIS MAMILLATA
ssp. PALUSTRIS
ssp. VULGARIS
ELEOCHARIS PALUSTRIS

Fig. 1.

next axillary shoot generation accreted to it. Basal sheaths of the culms ± *red to blackish-red* or greenish (especially in the northern parts of Scandinavia); orifice straight or somewhat oblique, often with a marked margin.

Culms extremely variable in length from a few cm to more than one metre, normally *not easily compressed* (with the exception of extreme water modifications); *collenchyma strands stout and numerous,* normally less than 5 epidermal cell rows between them; normally *two palisade layers and more than two parenchyma layers* in the interspaces between the vascular bundles resulting in *dark, not translucent,* commonly olive-green to green culms. Cell walls rather thick; *stomatal guard cells shorter than the subsidiary cells and not protruding* at the ends of the stomata, resulting in *concave short ends of the stomata*; stomatal length different in the two subspecies.

Basal glumes of the spike semi-amplexicaul, rarely ± amplexicaul, 2 (sometimes 1 in ssp. *vulgaris*) *sterile.* Fertile glumes variable but normally somewhat different in the two subspecies, commonly brown to blackish-red, with (in certain strains without) a distinct green midrib and in certain infraspecific taxa and subpopulations ± hyaline margins during prefloral and floral stages, when older increasingly membranaceous. Receptacle density different in the infraspecific taxa.

Thecae pure yellow and longer than 1.6 mm. Shape of *pollen grains markedly sector- and sack-shaped*; size different in the two subspecies.

Achene shape variable with a certain difference between the subspecies; colour *lustrously brown to dark reddish-brown; surface punctate. Style base* prominently developed, *necked*; shape variable but normally different in the two subspecies. *Bristles 4,* of various shape and longer than half the achene, *or* ± *lacking* in ssp. *palustris*; barbs ± retrorse, of varying lengths.

Chromosome number different in the two subspecies.

E. palustris is common in shallow water such as along shores of lakes, but also in wet meadows. It is little competitive in dense and tall vegetation. It is often favoured by the influence of fertilizing substances and cultural activities such as clearing operations.

The species forms two, partly interfertile subspecies distinguished in chromosome number, morphology (mainly quantitative and microscopic characters), ecology and geographical distribution.

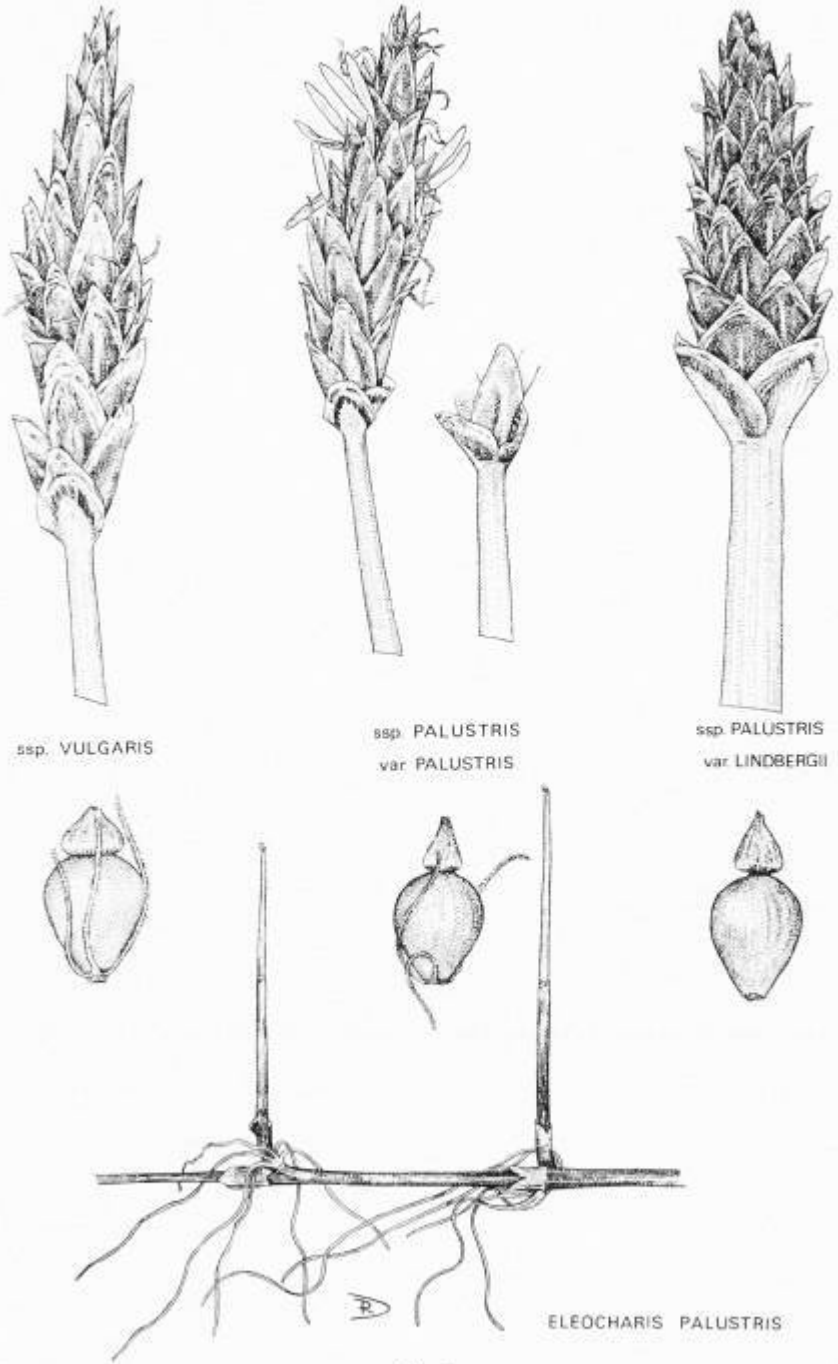
ssp. VULGARIS
ssp. PALUSTRIS
var PALUSTRIS
ssp. PALUSTRIS
var LINDBERGII
ELEOCHARIS PALUSTRIS

Fig. 2.

E. palustris (L.) R. & S. ssp. **palustris**

[*E. palustris* ssp. *microcarpa* WALTERS, see also Opera Bot. 10(2) p. 146]

This subspecies is distinguished from the next one in the following characters:

Stomatal length (35—) *39—49* (—56) µ.

Sterile basal glumes 2. *Fertile glumes commonly shorter than 3.5 mm*, midrib distinct or none-existent, *hyaline margins normally narrow* or none-existent during prefloral and floral stages. *Receptacle density more than 40 fruits per cm of the rachis.*

Pollen length (30—) *34—42* (—46) µ, *width* (23—) *27—30* (—34) µ.

Achene shape commonly pyriform in N. Scandinavia and Finland but in the southern parts more often obovoid or intermediate; *length* (1.1—) *1.2—1.5* (—1.6) *mm* (cf. var. *lindbergii*), *width* (0.8—) *0.9—1.1* (—1.2) *mm* (cf. var. *lindbergii*). *Style base variable, often conical and longer than broad*; length (0.3—) 0.4—0.8 (—1.0) mm, width (0.4—) 0.5—0.6 (—0.7) mm. *Bristles 4 or absent*, normally *rather thin*; barbs retrorse, often ± thin and of variable length.

Chromosome number 2n=16 (heteroploid chromosome numbers occur).

The ecological preferences are somewhat different in S. Scandinavia and northwards. *In S. Scandinavia*, where ssp. *palustris* and ssp. *vulgaris* are sympatric, ssp. *palustris* prefers *fine sedimentary substrates*, ± *rich in humus and nutriments*. The distribution there coincides closely with the sedimentary plains. *In N. Scandinavia and Finland*, where ssp. *vulgaris* does not occur, ssp. *palustris* is *common also on sandy*, ± *oligotrophic shores*, but the distribution here coincides closely with human settlements along the shores of rivers and lakes.

The distribution pattern may be characterized as Euroasiatic in the sense of HULTÉN. It is common in large parts of Scandinavia below the timber-line but is ± lacking in the S. Scandinavian highlands. It is rather common in Iceland but is not known from the Faroe Islands. In the British Isles, ssp. *palustris* is restricted to the southern parts. It is rather common in Central Europe but ± rare in the Mediterranean area.

A morphologically and ecologically distinct subpopulation along the shores of the Bothnian Sea, has been described as var. *lindbergii* STRANDH.

E. palustris (L.) R. & S. ssp. **palustris** var. **lindbergii** STRANDH.

This variety is distinguished from the main population of the subspecies in the following characters:

Culm stout, olive-green to brown or yellowish, rarely pure green in the basal two-thirds of the culm.

Spike large and stout. Fertile glumes dark, generally without midrib during prefloral and floral stages, later ± hyaline. *Receptacle density* (44—) *52—65* (—75) *fruits per cm of the rachis.* [In the main Scandinavian population of ssp. *palustris* (30—) 37—47 (—57) fruits per cm of the rachis.]

Achene shape commonly *pyriform*; *length* (1.3—) *1.4—1.7* (—1.9) *mm, width* (0.9—) *1.0—1.3* (—1.4) *mm.* Style base ± conical; length (0.4—) 0.5—0.8 (—0.9) mm, width 0.5—0.7 mm. *Bristles lacking, rarely 4.*

This variety is very common in a zone outside *E. uniglumis* (LK.) SCHULT. ssp. *uniglumis along the shallow shores of the Gulf of Finland and the Gulf of Bothnia*, where it often forms broad and distinct belts.

E. palustris (L.) R. & S. ssp. **vulgaris** WALTERS

[*S. intermedius* THUILL., *E. palustris* s. str. sensu Á. LÖVE (as an incorrect proposal 1951, see Opera Bot. 10(2) p. 111)]

This subspecies is distinguished from ssp. *palustris* in the following characters:

Stomatal length (50—) *54—70* (—77) µ.

Sterile basal glumes 2 or 1—2. *Fertile glumes normally more than 3.5 mm long* midrib normally distinct, *hyaline margins rather broad and silvery* during prefloral and floral stages. *Receptacle density 20—38* (—45) *fruits per cm of the rachis.*

Pollen length (35—) *41—53* (—59) µ, *width* (27—) *31—38* µ.

Achene shape often intermediate between pyriform and obovoid; *length* (1.3—) *1.4—1.8* (—1.9) *mm, width* (1.0—) *1.1—1.3* (—1.5) *mm. Style base convex or conical* (rarely concave), *often somewhat broader than long*; length (0.4—) 0.5—0.7 (—0.9) mm, width (0.5—) 0.6—0.8 (—0.9) mm. *Bristles 4 and always present, rather coarse and about as long as the achenes*; barbs retrorse, coarser than in ssp. *palustris.*

Chromosome number 2n=38, 39 (heteroploid chromosome numbers occur).

This subspecies makes no special demands upon substrates and nutriments, but prefers localities influenced by human activities.

The distribution is "Euroatlantic" in the sense of HULTÉN. *In Scandinavia, the northern limit mainly follows that of Quercus.* In Finland,

it is restricted to Åland (Alandia) and to the southwesternmost part of the Finnish mainland. It is only known from a warm spring in Iceland, but is common on the Faroe Islands and in the British Isles. It is common in Central Europe eastwards to the Baltic Soviet Republics, Poland and Czechoslovakia; southwards to northern Jugoslavia, Switzerland and through S. France to the western parts of the Iberian Peninsula.

Embryological Studies on the Haloragidaceae. I.

Haloragis colensoi Skottsb.

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ABSTRACT

In *Haloragis colensoi* the anther wall consists of 4 or 5 layers. The tapetum is of the secretory type. Its cells become binucleate (rarely bicelled). The middle layers begin to degenerate at the time of tetrad formation. The cells of the endothecium develop fibrous thickenings. The epidermis persists though its cells become flattened. Cytokinesis is simultaneous. The pollen grains have 4 germ pores and are shed at the 3-celled stage.

The ovules are anatropous, bitegminal and crassinucellar. In the chalazal region, a few cells of the nucellus become conspicuous after fertilization and organize into a hypostase. The development of the embryo sac is of the Polygonum Type. Fertilization is porogamous. The remnants of the pollen tube persist up to the 10- or 12-celled stage of the proembryo. The endosperm is Cellular. The embryogeny conforms to the Caryophyllad Type. A feature of special interest is the occurrence of a conspicuous suspensor haustorium derived from the basal cell. The seed coat comprises 1 or 2 layers of flattened cells contributed by the outer integument whereas the inner integument and nucellus disorganize excepting a few cells at the tip. The pericarp is hard due to the presence of an inner zone of sclerenchymatous tissue.

INTRODUCTION

The *Haloragidaceae* is a cosmopolitan family consisting of 8 genera and about 160 species (MELCHIOR 1964). Its members are herbaceous and grow on land, marsh or in water. The leaves are opposite, alternate, or sometimes whorled. Some species display heterophylly. The plants are monoecious and bear unisexual or bisexual flowers with 4 or 8 stamens and an inferior ovary containing a single ovule in each locule.

Except for a couple of papers which deal with the life history of *Laurembergia* and *Myriophyllum*, most of the published work refers to the floral morphology, anatomy, and structure of the ovule. Besides, taxa of doubtful affinities (like *Callitriche*, *Hippuris* and *Gunnera*) have been grouped together in this family. In view of the divergent

opinions regarding the systematic position of some genera and lack of sufficient embryological literature, an investigation on the life history of *Haloragis, Laurembergia* and *Myriophyllum* was undertaken in 1962. The present paper is the first in the series and concerns the embryology of *Haloragis colensoi* and *H. asperrima*.

MATERIALS AND METHODS

Buds, flowers and fruits were collected by the late Professor P. MAHESHWARI from the Royal Botanic Gardens, Kew, England, during August, 1961. Formalin-acetic-alcohol was used for fixation. After dehydration in the alcohol-xylene series, the material was imbedded in paraffin wax of 56—58°C melting point. The fruits are hard and difficult to section. They were, therefore, treated with 20 per cent hydrofluoric acid (diluted in 70 per cent ethanol) for 15—20 days, and dehydrated through the tertiary butyl-ethyl alcohol series before infiltration. Sections were made at a thickness varying from 7 to 18 microns and stained with safranin and fast green.

EXTERNAL MORPHOLOGY

Haloragis colensoi is a small, terrestrial, branched and moisture-loving herb. The leaves are sub-opposite and have serrate margins. The inflorescence is a monochasial cyme (Fig. 1 A). The flowers are small, pedicellate, bracteate, bracteolate (bracteoles being opposite and hairy), bisexual, tetramerous, and actinomorphic (Fig. 1 B—D). The sepals are adnate to the ovary whereas the petals are free, and boat-shaped (Fig. 1 D). The stamens are arranged in two whorls and those of the outer whorl are opposite to the petals. The filament is short but the anther is long (Fig. 1 F). The ovary is inferior, tetracarpellary, syncarpous and tetralocular (Fig. 1 E) with each chamber having a single pendulous ovule (Fig. 1 I, J). There are as many styles and feathery stigmas as the number of carpels. The fruit is a 4-seeded nut surrounded by a persistent calyx (Fig. 1 G, H).

MICROSPORANGIUM

In a young anther (Fig. 2 A, D) the microspore mother cells are surrounded by glandular uninucleate tapetum, 2 middle layers, endothecium and epidermis. Some cells in the connective region show the presence of crystals. During tetrad formation, the outer wall of the epidermis becomes slightly thickened; middle layers begin to disorganize; and tapetal cells enlarge, become vacuolate and binucleate (Fig. 2 B,

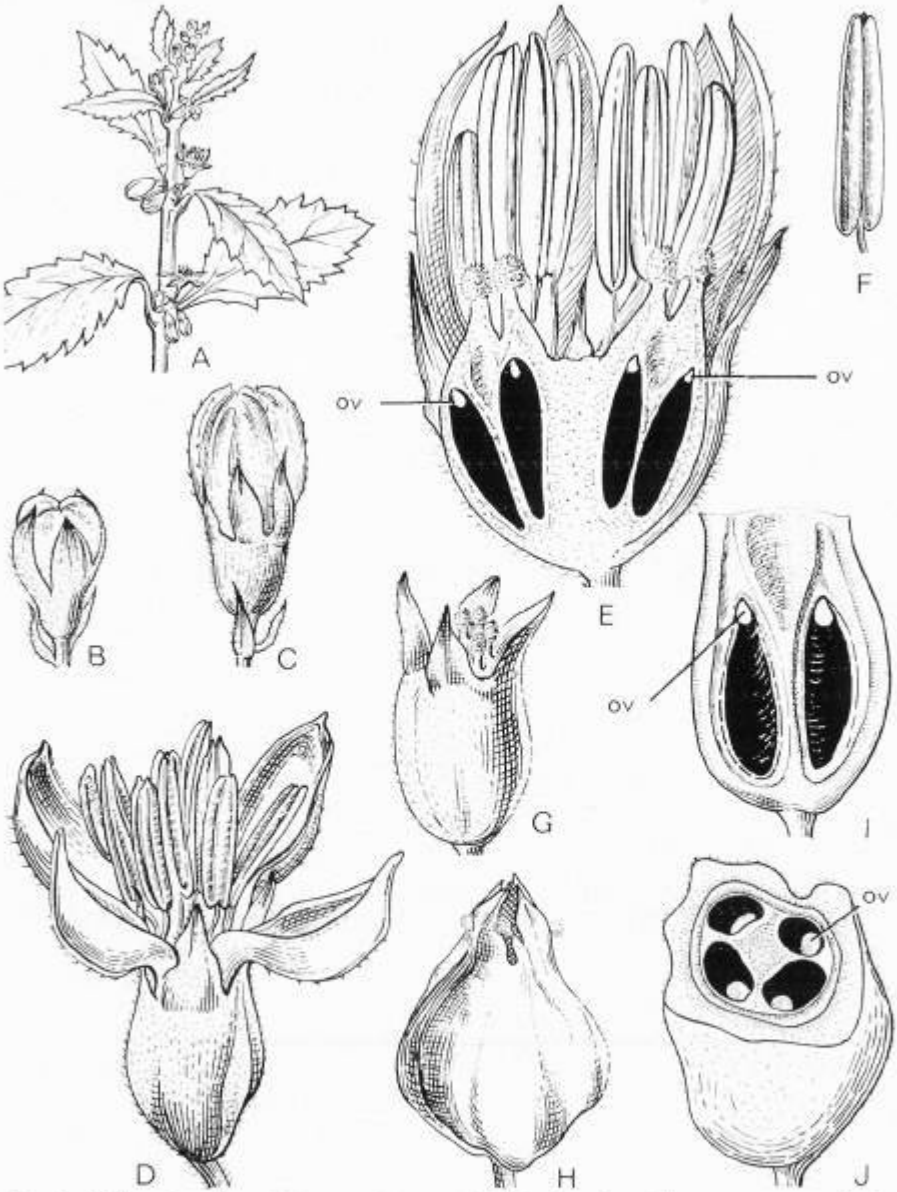

Fig. 1. *Haloragis colensoi*. (*ov*, ovule). — A. Twig bearing inflorescences. — B, C. Young and old flower buds. — D. Open flower; bracteoles have been removed. — E. Flower spread out to show androecium and tetralocular gynoecium. — F. Stamen showing short filament and long anther. — G, H. Young and mature fruits with persistent calyx. — I, J. Longitudinal and transverse sections of ovaries with each locule containing one ovule. — A ×1.5; B—E ×15; F ×25; G—J ×15.

E, F, G). Occasionally the nuclear division in tapetal cells is followed by wall formation (Fig. 2 H). At the time of anther dehiscence, the epidermal cells slightly protrude out at some places and lend a wavy contour to the wall. The cells of the endothecium elongate and develop fibrous thickenings. The middle layers and tapetum disorganize although their remnants persist for some time (Fig. 2 C). In a mature anther, the partition walls between the adjacent lobes break down and the dehiscence occurs by a longitudinal slit.

MICROSPOROGENESIS AND MALE GAMETOPHYTE

The cytokinesis in the microspore mother cells is of the simultaneous type (Fig. 2 I—K) and the microspores are arranged in tetrahedral or decussate fashion (Fig. 2 L, M). They are surrounded by a thick sheath of mucilage which dissolves before their separation. Soon after its release from the tetrad, the young microspore increases in size, becomes squarish and develops a thin intine and a thick exine. The mature pollen grains possess 4 germ pores (Fig. 2 N, O, Q, R) but occasionally they show 5 apertures (Fig. 2 P). The nucleus of the pollen grain moves to the wall before division (Fig. 2 N). A small generative cell is cut off (Fig. 2 O, P) but as a result of the dissolution of the separating membrane it comes to lie in the centre of the pollen grain and divides to produce 2 male gametes (Fig. 2 Q).

MEGASPORANGIUM

Initially each locule of the ovary contains 2 ovular primordia which appear as small, homogeneous masses of cells (Fig. 3 A). Soon, one of these aborts and has been designated as the sterile ovule (Fig. 3 A, *so*). The other primordium develops into a fertile ovule (*fo*). The initials of the inner integument appear slightly earlier than those of the outer. The young ovule continues to curve until it attains an anatropous condition (Fig. 3 B—G). It is bitegminal and crassinucellar. The funicular vascular supply terminates at the chalaza. At the time of fertilization some cells of the funicular epidermis elongate towards the micropyle and probably function as a feeble obturator.

At the megaspore mother cell stage the cells of the nucellar epidermis near the tip divide periclinally (Fig. 4 C) to produce 2 layers in the micropylar region. In the chalazal region, however, a few cells of the nucellus become conspicuous after fertilization due to the presence of

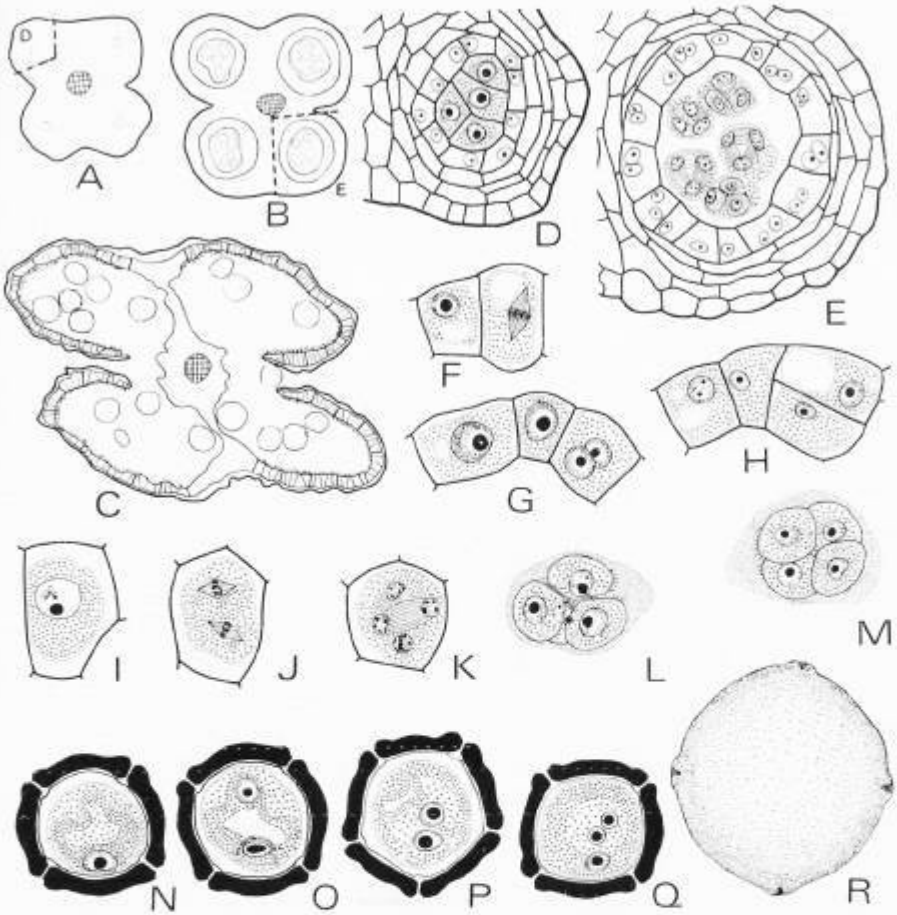

Fig. 2. *Haloragis colensoi*. — A—C. Cross sections of anthers at various stages of development (diagrammatic). — D. Enlarged view of portion marked "D" in A to show wall layers at microspore mother cell stage. — E. Magnified view of sector marked "E" in B; note the binucleate tapetal cells. — F—H. Uninucleate, binucleate and (rarely) 2-tiered tapetal cells. — I—K. Microspore mother cells undergoing reduction divisions. — L, M. Tetrahedral and decussate microspore tetrads. — N—Q. Stages leading to the development of 3-celled pollen grain. — R. Acetolyzed pollen grain. — A—C ×125; D, E ×450; F—R ×900.

some contents which take a deep red stain with safranin. These cells organize into a hypostase (Fig. 7 E, F). Usually all the fertile ovules in an ovary form seeds but sometimes 1 or 2 of them may degenerate.

A few abnormalities were also observed. In 1 ovule the curvature

stopped half-way so that the nucellus and the integuments were more or less at right angles to the funiculus; the nucellus projected out of the integuments and contained an embryo sac showing egg apparatus and 1 nucleus in the middle (Fig. 3 H). Another anomalous condition was the occurrence of 2 atropous ovules within the same locule, either one above the other (Fig. 3 I) or side by side (Fig. 3 J). In Fig. 3 H, I the ovules show a funicular outgrowth.

MEGASPOROGENESIS AND FEMALE GAMETOPHYTE

The female archesporium is hypodermal and single-celled. It divides transversely to form a parietal cell and a sporogenous cell (Fig. 4 A). Some ovules show 3 archesporial cells, each of which cuts off a parietal cell (Fig. 4 B), but only 1 develops further. The parietal cell divides periclinally to produce 2 superposed cells whereas the sporogenous cell enlarges and functions as the megaspore mother cell (Fig. 4 C). The latter divides to form two dyad cells which in turn produce a linear tetrad of megaspores (Fig. 4 D, E). Occasionally a T-shaped tetrad is organized (Fig. 4 F). The chalazal megaspore functions and the remaining 3 degenerate in basipetal order (Fig. 4 G, H). A delayed division of the upper dyad cell sometimes results in a triad (Fig. 4 I) where the chalazal megaspore functions and the other 2 degenerate (Fig. 4 J). A double triad was also observed (Fig. 4 K).

The functional megaspore divides to form a 2-nucleate embryo sac (Fig. 4 L). Its nuclei move to the poles (Fig. 4 M). Two successive mitoses result in 4 (Fig. 4 N) and 8 nuclei which organize into an egg apparatus, 2 polar nuclei and 3 antipodal cells (Fig. 4 O, P). The polar nuclei lie in the chalazal part of the embryo sac just above the antipodal cells (Fig. 4 P) where they fuse to produce a secondary nucleus (Fig. 4 Q). Frequently the antipodal cells contain starch. Fig. 4 R shows an embryo sac with laterally placed egg and 2 elongated antipodal cells.

FERTILIZATION

The pollen tube penetrates the embryo sac through the micropyle (Fig. 5 A). Both the synergids disorganize soon after fertilization. How-

Fig. 3. *Haloragis colensoi*. (*fo*, fertile ovular primordium; *so*, sterile ovular primordium). — A. Longitudinal section of carpel showing fertile and sterile ovular primordia. — B—G. Stages in the development and curvature of ovule which becomes anatropous at 2-nucleate stage of embryo sac. — H. Abnormal ovule with nucellus projecting out of the micropyle. — I, J. Twin ovules. — A ×39; B—G ×173; H ×86; I ×69; J ×86.

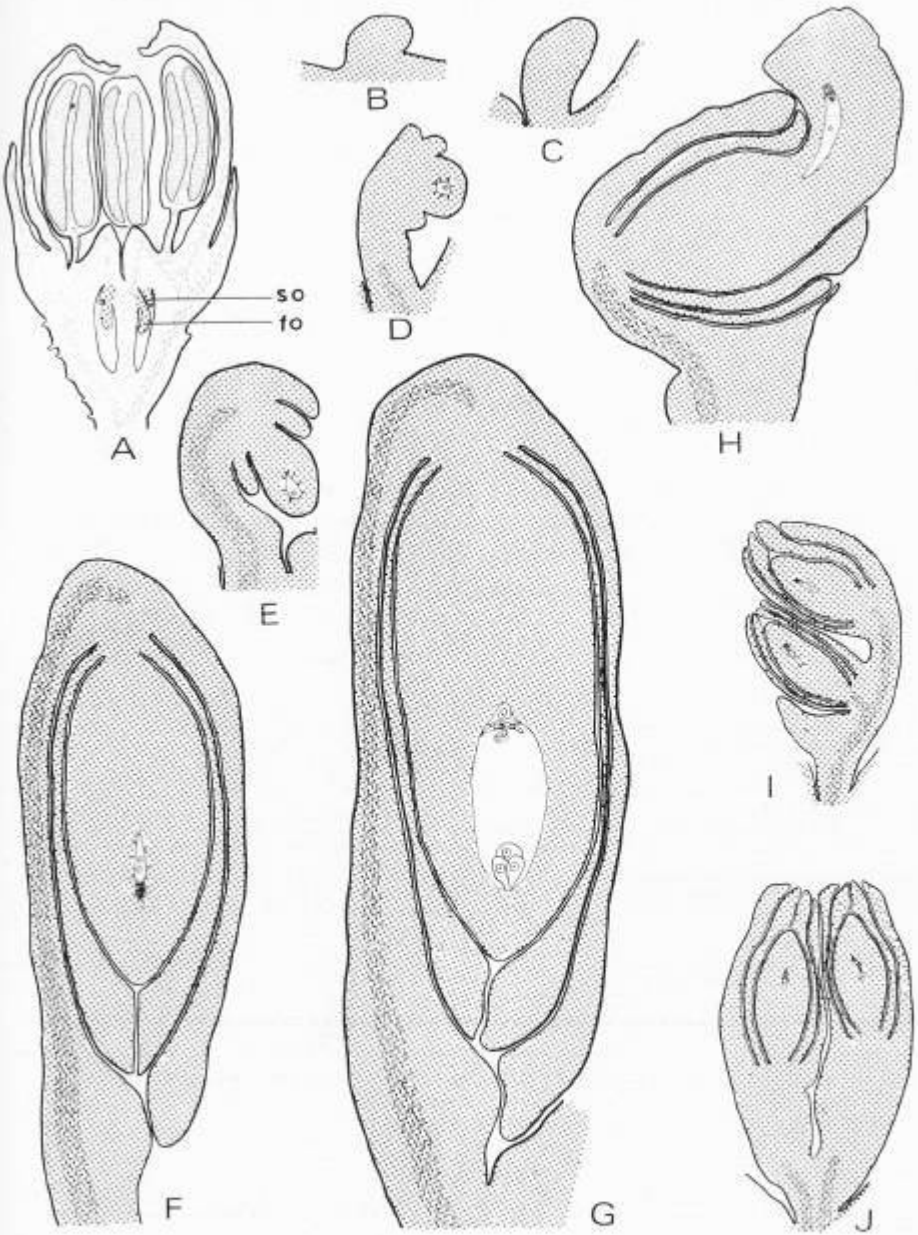

Fig. 3.

ever, the remnants of one of them persist for some time. The antipodal cells appear healthy up to the 5-celled stage of the proembryo (Fig. 5 G) but subsequently they degenerate and their identity is lost. Darkly stained remnants of the pollen tube are discernible up to the 10- or 12-celled stage of the proembryo (Fig. 5 I).

ENDOSPERM

The primary endosperm nucleus lies in the chalazal region of the embryo sac (Fig. 5 B) and divides *in situ*. Its first division is followed by a vertical wall (Fig. 5 C). On the other hand, in *H. asperrima*, a usually transverse (Fig. 5 D) wall (sometimes vertical) is laid down. The second division is transverse and results in 4 cells of which the upper 2 are larger than the lower 2 (Fig. 5 E). Subsequent divisions lead to the formation of a massive endosperm (Fig. 5 F—I). Its cells are thin-walled, vacuolate (Fig. 5 K), and contain starch. Although a few cells of endosperm around the embryo lose their contents and disintegrate, most of them persist in the mature seed (Fig. 5 J) and are filled with reserve food materials (Fig. 5 L).

EMBRYO

The first division of the zygote is transverse and results in a small terminal cell *ca*, and a large vesicular basal cell *cb* (Fig. 6 A, B). The latter divides vertically (Fig. 6 C), and the former transversely (Fig. 6 D) to give rise to the cells *cc* and *cd*. The cell *cc* is partitioned by a vertical wall whereas *cd* divides transversely to produce the cells *m* and *ci* (Fig. 6 E). Although conventionally *m* and *ci* are the derivatives of the tier *cb*, here they are derived from the tier *cd* and not *cb* (see SOUÈGES 1940).

Fig. 4. *Haloragis colensoi*. (*ant*, antipodal cells; *e*, egg; *ii*, inner integument; *nu*, nucellus; *oi*, outer integument; *pn*, polar nuclei; *s*, synergid; *sn*, secondary nucleus). — A. L.s. young nucellus showing megaspore mother cell and parietal cell. — B. Same showing 3 sporogenous and parietal cells. — C. Megaspore mother cell. — D. Dyad cells in division. — E, F. Linear and T-shaped tetrads. — G, H. Basipetal degeneration of megaspores of a tetrad. — I, J. 'Triads'. — K. Double 'triad'; the micropylar shows functioning megaspore whereas the upper dyad cell of the lower 'triad' is in division. — L—N. Two and 4-nucleate embryo sacs. — O. L.s. ovule at the mature embryo sac stage. — P. Embryo sac enlarged from O; the polar nuclei are lying above the antipodal cells. — Q. Mature embryo sac. — R. Embryo sac with laterally placed egg nucleus and 2 elongated antipodal cells. — A—C ×346; D—N ×692; O ×42; P—R ×692.

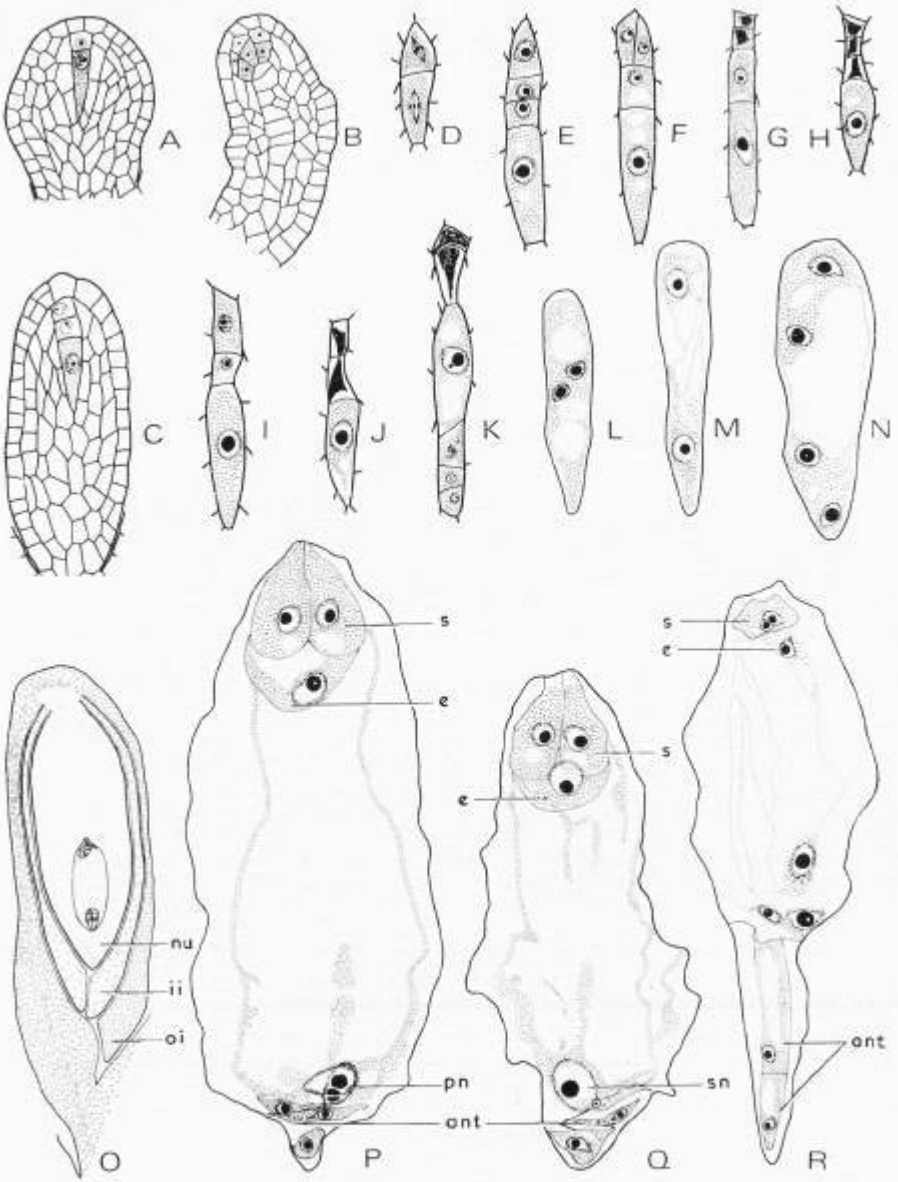

Fig. 4.

The 2 daughter cells formed by the vertical division of the cell *cc* (Fig. 6 F), now divide by another vertical wall, at right angles to the first, resulting in a quadrant (Fig. 6 G) which later engenders an octant (Fig. 6 H). Subsequent divisions in the tiers of the octant lead to the formation of a globular proembryo (Fig. 6 I, J) which differentiates into a heart-shaped (Fig. 6 K) and finally a mature dicotyledonous embryo (Fig. 6 L). The derivatives of *cd* close to *cb* organize into a short suspensor. The cells of the mature embryo contain starch.

The daughter cells of *cb* do not divide but enlarge considerably and their bases fit into the apical part of the embryo sac (Fig. 6 C—K). They show vacuolation and their nuclei become hypertrophied. These cells constitute a suspensor haustorium. Some of the proembryos showed accumulation of starch in the haustorial cells. As the embryo grows, this haustorium begins to degenerate and its remnants can be seen above the suspensor in a mature embryo (Fig. 6 L).

SEED COAT

At the megaspore mother cell stage, each integument consists of 2 layers of cells (Fig. 7 A, G). During the development of the gametophyte the integuments show more than 2 layers in the micropylar region (Fig. 7 B, H). With the maturation of the embryo sac, the outer integument may become 3-layered (Fig. 7 C, I) whereas the inner epidermis of the inner integument begins to degenerate. The latter disorganizes at the 2-celled stage of the proembryo (Fig. 7 D, J). This is followed by the degeneration of the outer epidermis of the inner

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Fig. 5. *Haloragis colensoi*. (*ant*, antipodal cells; *cot*, cotyledon; *ds*, degenerated synergid; *dsh*, degenerated suspensor haustorium; *emb*, embryo; *end*, endosperm; *hyp*, hypostase; *ii*, inner integument; *nu*, nucellus; *oi*, outer integument; *pemb*, proembryo; *pen*, primary endosperm nucleus; *pt*, pollen tube; *rc*, root cap; *s*, synergid; *sh*, suspensor haustorium; *sus*, suspensor; *vs*, vascular supply; *z*, zygote). — A. L.s. ovule after fertilization. — B. Fertilized embryo sac; primary endosperm nucleus is lying in the chalazal region. — C, D. Two-celled endosperm; first division of the primary endosperm nucleus is followed by a vertical wall in *H. colensoi* (C) and transverse wall in *H. asperrima* (D). — E. Four-celled endosperm. — F—H. Further stages in the development of endosperm; antipodal cells are also seen. — I. Young seed in l.s. showing nearly globular proembryo and persistent pollen tube. — J. L.s. mature seed (testa removed) at dicotyledonous stage of embryo. — K, L. Enlarged views of portions marked "K" and "L" in I and J to show vacuolate endosperm cells and reserve food material respectively. — A ×83; B—F ×366; G ×333; H, I ×53; J × 30; K, L ×600.

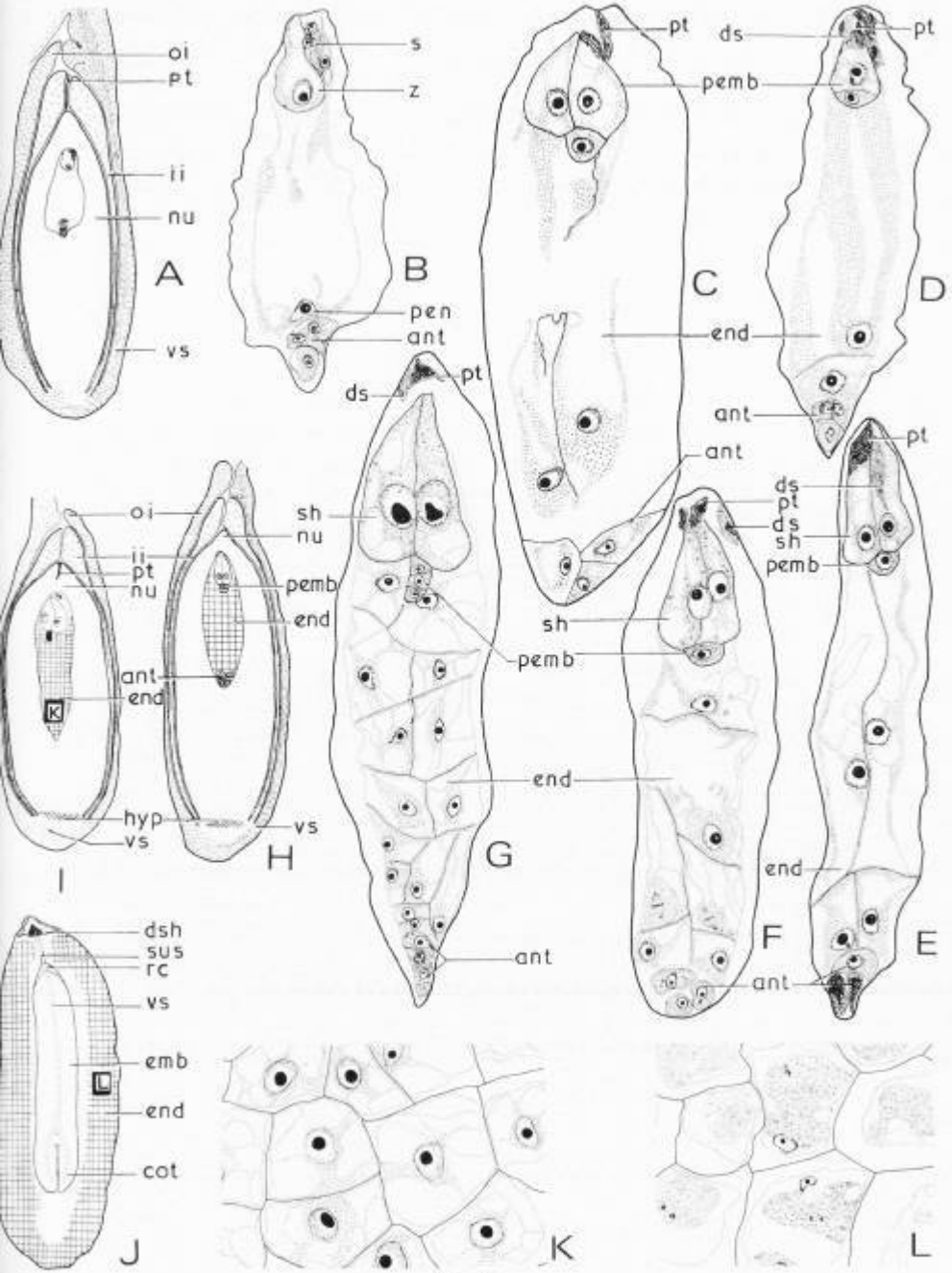
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Fig. 5.

integument as well (Fig. 7 E, K). By this time the cells of the nucellus increase in size considerably, show intense cavuolation and develop a thick cuticle on the epidermis. During further development these cells as well as those of the inner epidermis of the outer integument also start disintegrating, and the outer epidermis of the outer integument becomes stretched (Fig. 7 F, L). The mature seed is albuminous; it contains degenerated tips of the inner integument and nucellus in the micropylar region; a patch of thin-walled, tannin-filled cells in the chalazal part; and is covered with the remnants of the outer integument.

PERICARP

The ovary wall can be broadly divided into two distinct regions; an outer zone of large, thin-walled cells containing chloroplasts and an inner zone of small cells lacking chloroplasts (Fig. 8 A, E). These two regions are separated by a few layers of elongated, parenchymatous cells which do not undergo any significant change during further development.

Initially the cells of the outer epidermis are radially elongated and contain irregularly-shaped nuclei but at the 4-celled stage of the proembryo they enlarge laterally. The hypodermis is distinguishable from the adjacent layers by the presence of a lesser number of chloroplasts (Fig. 8 B, F).

At the young globular stage of the proembryo the cells of the inner zone develop uniform thickenings and become sclerenchymatous (Fig. 8 C, G). The inner epidermis consists of thin-walled elongate cells to begin with, but later acquires sclerenchymatous thickenings (Fig. 8 D, H). The sclerenchymatous shell, contributed by the inner zone of the pericarp, lends hardness to the mature nut.

SUMMARY AND CONCLUSIONS

In *Haloragis colensoi* the inflorescence is a monochasial cyme. The flowers are bracteate, bracteolate, bisexual, tetramerous and actinomorphic. The sepals are persistent and adnate to the ovary. There are 8 stamens in 2 whorls. The ovary is inferior and tetracarpellary, and the fruit is a 4-seeded nut.

The anther wall consists of 4 or 5 layers. The tapetum is of the secretory type. Its cells become binucleate (rarely bicelled). The middle

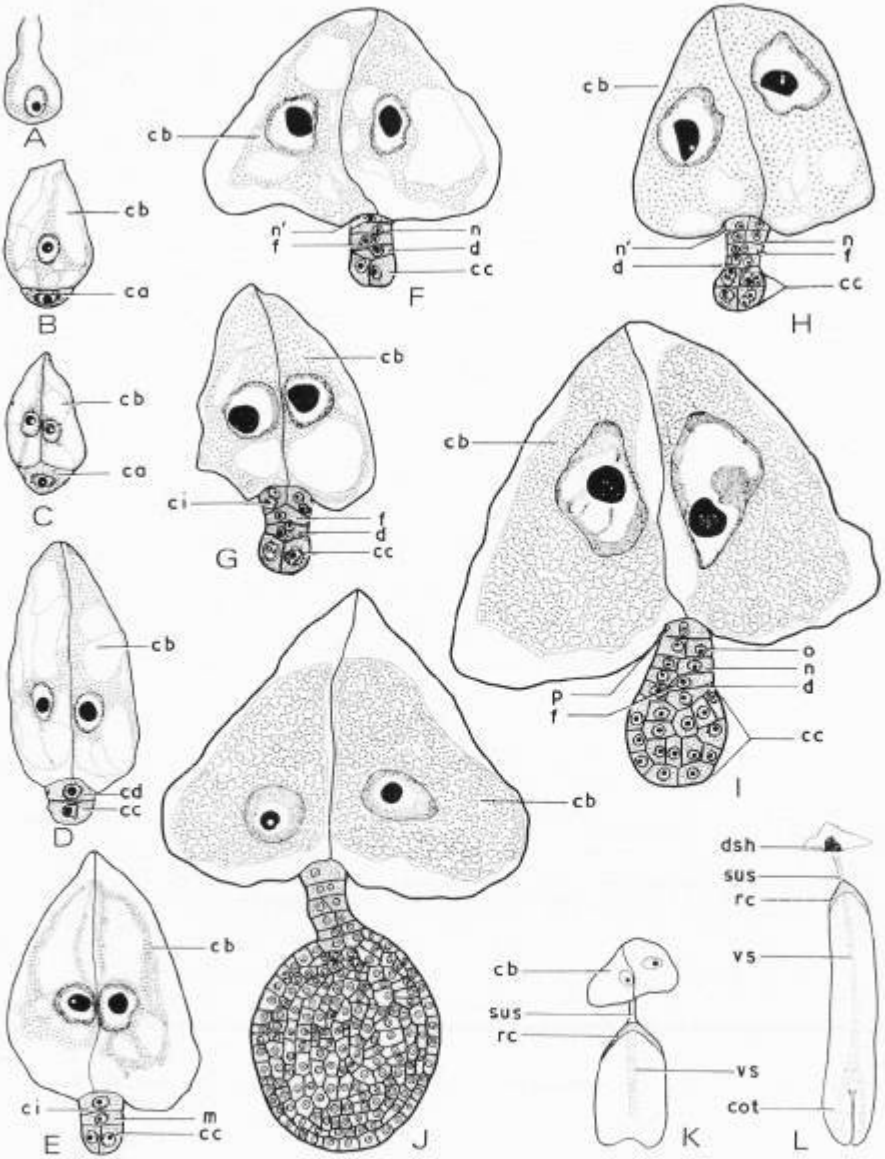

Fig. 6. *Haloragis colensoi*. (*cot*, cotyledon; *dsh*, degenerated suspensor haustorium; *rc*, root cap; *sus*, suspensor; *vs*, vascular supply). — A. Zygote. — B. Two-celled proembryo with a small apical cell. — C. Vertical division in basal cell. — D. Four-celled proembryo; basal cells have enlarged. — E—J. Stages leading to the formation of globular proembryo and hypertrophied basal cells. — K, L. Young and mature dicotyledonous embryos. — A—I ×360; J ×348; K ×64; L ×36.

layers begin to degenerate at the time of tetrad formation. The cells of the endothecium develop fibrous thickenings. The epidermis persists though its cells become flattened. The cytokinesis is simultaneous. The pollen grains are usually squarish and have 4 germ pores. They are shed at the 3-celled stage.

Although 2 ovular primordia are initiated in each locule of the tetralocular ovary, only 1 develops into an anatropous, bitegminal and crassinucellar ovule and the other aborts. VAN TIEGHEM (1898) stated that in *Haloragis* the 2 integuments are almost completely fused and this fusion extends up to the micropyle. However, in *H. colensoi* the 2 integuments are distinct throughout and never appear like a single integument. The funicular vascular supply terminates at the chalaza. A few cells of the nucellus, situated below the embryo sac, organize into a hypostase.

Usually a single hypodermal archesporial cell develops in the young nucellus. This cuts off a parietal cell. The megaspore tetrads are mostly linear but rarely T-shaped. Triads are also met with. The chalazal megaspore functions and the development of the embryo sac is of the Polygonum type. ERNST (1908), MODILEWSKI (1908) and SAMUELS (1912) recorded a 16-nucleate embryo sac in *Gunnera* (previously included in the *Haloragidaceae*). The synergids degenerate soon after fertilization. However, one of them may remain healthy for some time. The 3 antipodal cells persist after fertilization. The polar nuclei fuse in the chalazal part of the embryo sac just above the antipodal cells. Fertilization is porogamous. Darkly stained remnants of the pollen tube are discernible up to the 10- or 12-celled stage of the proembryo.

JØRGENSEN (1923) remarked that the endosperm in the *Haloragidaceae* is probably Nuclear and devoid of haustoria. While working on

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Fig. 7. *Haloragis colensoi*. (*ant*, antipodal cells; *emb*, embryo; *end*, endosperm; *hyp*, hypostase; *ii*, inner integument; *nu*, nucellus; *oi*, outer integument; *pemb*, proembryo; *sh*, suspensor haustorium; *vs*, vascular supply). — A—F. Outline diagrams of l.s. of ovules at various stages of development. — G, H. Enlarged views of portions of integuments and nucellus from A and B. Both integuments consist of 2 layers of parenchymatous cells in G but more than 2 layers near micropyle in H. — I, J. Magnified views of sectors marked "I" and "J" in C and D; outer integument is 3-layered; inner epidermis of the inner integument is degenerating in J. — K. Enlargement of portion marked "K" in E; outer epidermis of inner integument has started disorganizing whereas cells of nucellar epidermis have considerably enlarged. — L. Portion marked "L" magnified from F; nucellar epidermis shows cuticle; inner integument has disorganized whereas inner layer of outer integument is compressed and unhealthy. — A ×96; B—D ×61; E, F ×35; G—L ×692.

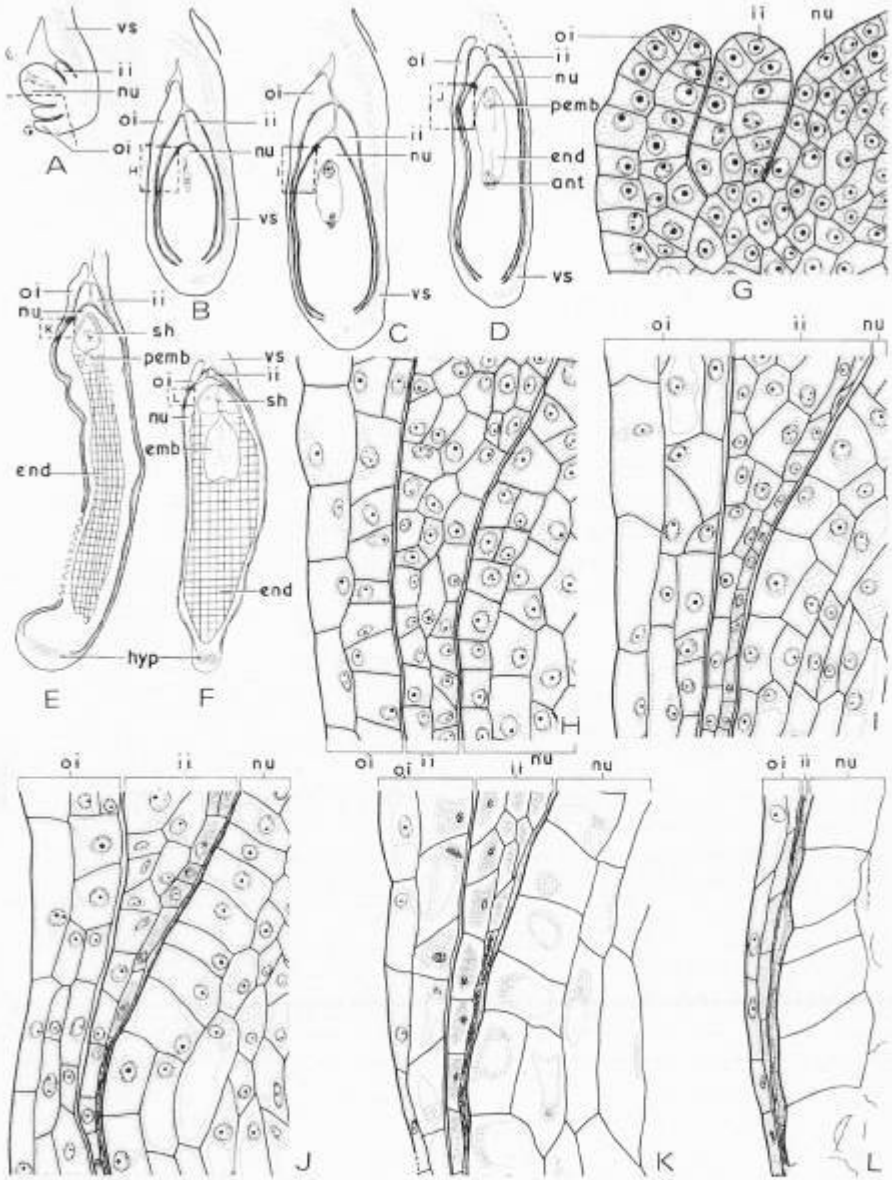

Fig. 7.

Myriophyllum alterniflorum STOLT (1928) also stated that the presence of Nuclear endosperm and suspensor haustorium may be regarded as general features of the family. However, in contrast to these statements our observations indicate that the endosperm is Cellular and the first division of the primary endosperm nucleus is followed by a vertical or a transverse wall.

The embryogeny conforms to the Caryophyllad Type. A feature of special interest is the occurrence of a conspicuous suspensor haustorium derived from the basal cell. It bears a remarkable resemblance with the synergids, and a 3-celled proembryo can be easily confused for an egg apparatus. Such an error was actually made in *Hypecoum* (*Papaveraceae*) in which HEGELMAIER (1878) interpreted the haustorial cells for synergids (see GUIGNARD 1903). The mature embryo is large, dicotyledonous and straight.

The seeds are small and albuminous. At maturity the testa comprises 1 or 2 layers of flattened cells contributed by the outer integument whereas the inner integument and nucellus disorganize excepting a few cells at the tip. The pericarp becomes hard due to the presence of an inner zone of sclerenchymatous tissue.

ACKNOWLEDGEMENTS

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Fig. 8. *Haloragis colensoi*. (*des*, degenerated embryo sac; *ii*, inner integument; *nu*, nucellus; *oi*, outer integument; *ow*, ovary wall; *pc*, pericarp; *scl*, sclerenchyma; *vs*, vascular supply). — A—D. L.s. developing fruits (diagrammatic). — E. Enlarged view of portion marked "E" in A; ovary wall consists of 24—28 layers of parenchyma of which 6 or 7 layers below outer epidermis contain chloroplasts. — F. Portion marked "F" in B enlarged to show pericarp at 4-celled stage of proembryo; cells of parenchymatous layers above inner epidermis have enlarged and become vacuolate. — G. L.s. pericarp at globular stage of proembryo magnified from C; 8—10 layers of cells above inner epidermis have conspicuously thickened walls. — H. Enlarged view of portion marked "H" in D showing an increase in the number of sclerenchymatous layers; cells of inner epidermis also develop thickenings. — A—D ×16; E—H ×243.

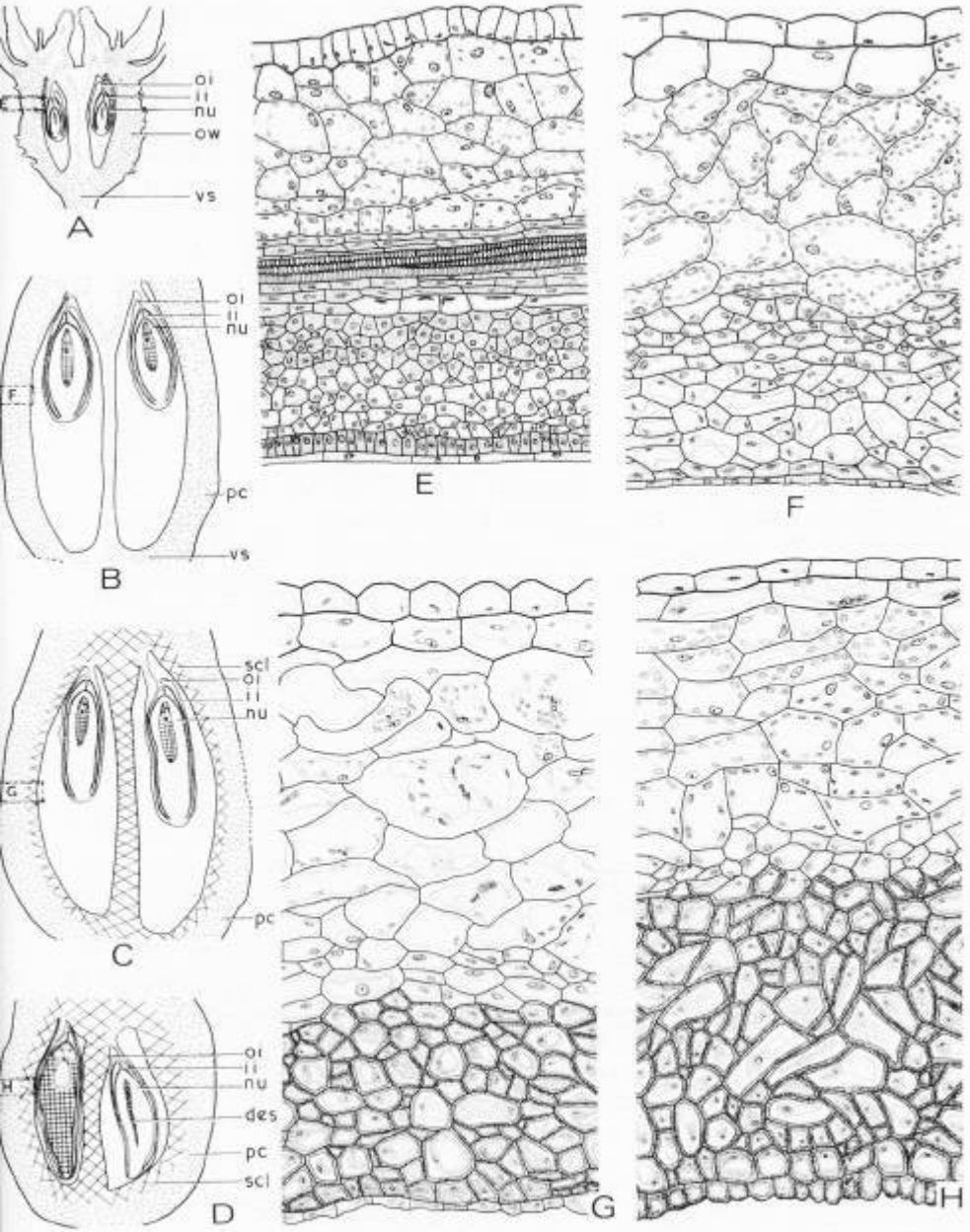
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Fig. 8.

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Critical Comments on the Use of Statistical Methods in Chemotaxonomy

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ABSTRACT

The investigations as yet published, dealing with comparisons of presence and absence of spots in chromatograms, have usually been restricted to a single (or a few) individuals of each taxon. Normally no statistical calculations have been made in connection with interpretations of resemblances or dissimilarities between chromatograms from different taxa. NYBOM & al. have recently introduced the use of data concerning the size of the individual spots in the comparisons. They have also recommended a statistical treatment in comparisons between different chromatograms in order to avoid subjective evaluations.

The following main objections to the statistical treatment of the data in chromatograms may be raised. — (1) The scanty data presented, which do not include any information about variation, make normal statistical calculations inadequate. — (2) Statistical treatment of quantitative features can hardly be relevant in this case, as relationships between the sizes of different spots in a chromatogram to a considerable extent depend on the solvent system used. Thus, a statistical treatment may lead to different interpretations about chemical similarity between the same taxa depending on the solvent system used. — (3) An unlimited number of coefficients of association can be used. Therefore almost any hypothesis held by the investigator can be supported, provided a suitable coefficient is selected. — (4) A numerical estimation of the similarity between different chromatograms may be defensible. However, the coefficients chosen by NYBOM & al. are either inadequate (the correlation coefficient) or presuppose conditions rarely fulfilled by data available (the coefficient of similarity, the matching coefficient, and the biochemical distance).

A better understanding and use of the data in chromatograms can only be achieved by analyses of quantitative and qualitative variation within and between populations in different taxa on a large scale.

INTRODUCTION

Data on chemical compounds, e.g. different amino acids and phenolic substances, have been used to an increasing extent in plant taxonomy during the last decades. In several cases the distribution of such com-

pounds has given valuable information about relationships between taxa, which could not have been obtained by using morphologic, cytologic, and experimental data alone (cf., e.g., the investigation on *Viola* by STEBBINS & al. 1963).

The increased use of chemical compounds in taxonomy depends mainly on the development of simple and rapid methods for tracing small amounts of substances, such as paper-chromatography (now usually replaced by the more sensitive and efficient thin-layer chromatography), and in special cases gas chromatography or electrophoresis.

Very efficient standard methods for thin-layer chromatography have recently been worked out (cf., e.g., NYBOM 1964). The compounds investigated, e.g. phenolic substances, are extracted from leaves, flowers, seeds, etc. by means of a suitable solvent. They are separated in thin-layer chromatograms usually processed in two directions. The different compounds, occurring as spots, are visualized by treatment with different reagents and are usually observed in ultraviolet light. The data obtained by such a method can be analysed in different ways.

(1) The compounds can be chemically identified, their chemical affinities can be discussed, and a hypothesis for their biogenesis may be presented. Such investigations have been made, e.g., on the mint oils in *Mentha* (REITSEMA 1958) and the depsides and depsidones in the lichen genus *Rhizocarpon* (RUNEMARK 1956). In these cases a number of related compounds occur as substitutes for each other in different taxa. Such compounds are apparently produced within the same metabolic system by minor alterations in the enzymatic processes. In *Mentha*, REITSEMA (l.c.) has shown that two allelic genes may be responsible for the production of a spearmint or a peppermint type of oil, respectively.

(2) Chromatograms from different taxa can be compared with respect to agreements and differences in the occurrence of spots, without any attempt to identify the substances. In order to make better use of the information in the chromatograms the amount of the compounds (i.e., the size of the spots) have also recently been included in comparisons (JAWORSKA & NYBOM 1967).

The method outlined under (1) gives the most valuable information from a biological point of view. However, such investigations are very laborious and require a good training and experience in chemistry rarely held by taxonomists, or a cooperation between a taxonomist and a specialist in organic chemistry or biochemistry.

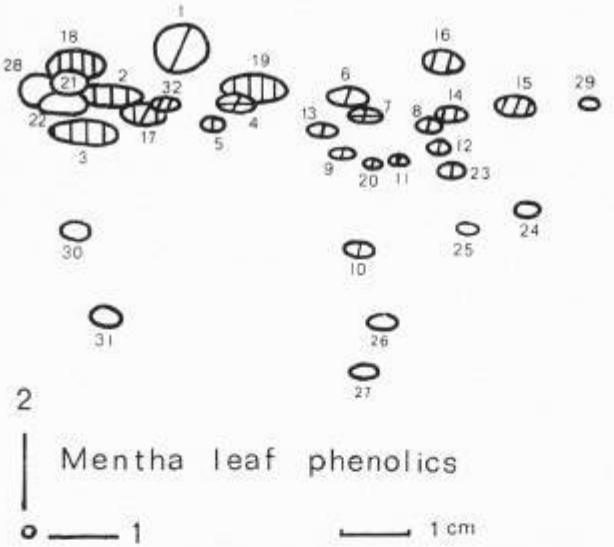

Fig. 1. Spots of phenolic compounds investigated in *Mentha arvensis* L., *aquatica* L., and their putative hybrid derivatives (from OLSSON 1967).

The other method, outlined under (2), gives much more restricted information. Its advantage lies in the simple and rapid technique, which also makes possible investigations on a large scale. The pattern of spots obtained in a chromatogram may be regarded as a "chemical fingerprint" of the actual group of compounds in a taxon (or individual). Different "fingerprints" may be compared, but considering the fact that the constitution of the substances causing the spots is unknown, resemblances and differences must be interpreted with much caution. The method, cautiously used, may in many cases give indications about relationships of considerable taxonomic interest. However, it can scarcely be recommended as a taxonomic standard method, but should be restricted to special problems, such as the origin of hybrids and allopolyploids or the effects in a certain material of geographical or ecological isolation.

In order to avoid subjective evaluations JAWORSKA & NYBOM (1967) have recommended a statistical treatment of comparisons between different chromatograms. For qualitative as well as quantitative comparisons they suggest a number of coefficients of association. These coefficients have been tested on phenolic compounds in leaves in some groups of taxa, the relationships of which are relatively well known, such as

Table 1. Occurrence of spots of phenolic compounds in *Mentha arvensis* L. (2n=72), *aquatica* L. (2n=96), and their putative hybrid derivatives (extracted from OLSSON 1967; cf. Tab. 4).

Spot no.	Polyploid levels (2n)						
	72	78	84	90	96	120	132
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	—	+	—	—	—	—	—
Number of spots	11	15	17	8	19	14	9

Saxifraga aizoides L., *caesia* L. and their putative hybrid (JAWORSKA & NYBOM 1967), *Brassica oleracea* L., *campestris* L., *nigra* (L.) KOCH, and their amphidiploids (DASS & NYBOM 1968), *Mentha arvensis* L., *aquatica* L., and their presumed hybrid derivatives (OLSSON 1967).

Two objections can be raised against the empiric method used in tests of the coefficients.

(1) There are reasons to postulate a rather wide variation within taxa both qualitatively and quantitatively concerning the phenolic compounds investigated. Therefore, the only adequate tests are those of the actual parental individuals and their primary hybrid derivative

or amphidiploid. As the production of phenolic substances certainly is influenced by the environment (cf. BALL & al. 1967) only material cultivated under uniform conditions may be taken into account. The first of these demands is not fulfilled in any of the three cases investigated. The second demand is apparently not fulfilled in the *Saxifraga* investigation as herbarium material has been used. Therefore the results of the tests as yet performed have little value for an empiric evaluation of different coefficients.

(2) An unlimited number of coefficients of association can be formed. Therefore if a suitable coefficient is chosen almost any theory held by the investigator can be supported. An empiric evaluation of the usefulness of different coefficients by tests in a number of plant groups with known relationships can scarcely be regarded as adequate, as there are reasons to believe, that the very complex biochemical conditions involved in the production of the substances causing spots, may be dissimilar in different plant groups.

STATISTICAL ANALYSIS OF QUALITATIVE FEATURES

The comparisons of chemical resemblances between taxa have as yet mostly been based on chromatograms from a single more or less "representative" individual of each taxon. The chromatographic data have usually been presented in tables (cf. Tab. 1), in which the presence of a spot is indicated by a + and the absence by a —. JAWORSKA & NYBOM (1967) suggested a numerical estimation of the biochemical similarities between different taxa. For comparisons between taxa the following features are of major interest from biological and statistical points of view.

(1) *The number of spots in each taxon.* The absolute number of spots in a taxon has a considerable influence on the size of the coefficient in most numerical calculations. From a biological point of view this feature seems to be of restricted value. A division of a taxonomic complex by means of their different numbers of spots will usually be inadequate.

(2) *Spots occurring in all taxa.* Spots occurring in all investigated taxa are of no interest in comparisons and have to be excluded in any numerical analysis. Such a treatment agrees with SOKAL & SNEATH (1963 p. 130), who state that "A similarly absurd procedure would be the introduction of positive matches for characters that are invariant over the group of study", but is contrary to JAWORSKA & NYBOM (1967).

(3) *Spots occurring in a single taxon.* The number of spots restricted to a single taxon are of considerable importance for the discussion of the degree of its isolation from other taxa.

(4) *Positive matches.* A positive match, i.e., a spot occurring in two taxa compared, is a very strong indication of the occurrence of an identical metabolic system. A spot restricted to two taxa only, may be of special interest in comparisons including more than three taxa. Such "qualified" matches are generally of greater biological importance than "normal" ones, especially if the number of taxa compared is large.

(5) *Negative matches.* A negative match, i.e., the absence of a spot in two taxa compared, may be caused by different features: (a) both taxa wholly lack the biogenetic system necessary for the production of the substance causing the spot, (b) both taxa have the necessary biogenetic system, which is, however, blocked at different points, (c) both taxa have the necessary biogenetic system, which is blocked at the same point, (d) both taxa have the necessary biogenetic system, but the amounts produced are too small to be traced in the chromatograms. The conditions under (b) must be regarded to be rather common on account of the complex biogenesis of almost any particular substance. Therefore, a negative match is no strong indication of biochemical identity and must be assigned considerably less significance than a positive match. A distinction of "qualified" negative matches and "normal" ones seems to be rather inadequate owing to the different possibilities for the absence of a spot, discussed above.

(6) *Differences.* A difference, i.e., a spot occurring in one of the taxa compared but not in the other, may be caused by an actual qualitative dissimilarity between the taxa or merely by the production of too small an amount of the actual compound in one of the taxa. As there is no method for separating qualitative and concealed quantitative dissimilarities, the importance of differences is difficult to evaluate.

Of course other features are of interest in qualitative comparisons, e.g., the fixed association of two or more spots or the vicarious occurrence of a number of spots in different taxa. Such features, however, cannot be extracted from the restricted information in single chromatograms. A multiple comparison instead of one, based on pairs of taxa, seems preferable, but is hardly possible to perform in an adequate way. The multiple comparison obtained by clustering the taxa (or individuals) as in a dendrogram (cf. SOKAL & SNEATH 1963) can hardly

be recommended since the relationships between the taxa compared may very well be multidimensional.

An unlimited number of coefficients of association including features of biological interest, discussed above, can be created for a comparison between pairs of taxa. SOKAL & SNEATH (1963) discussed 13 such coefficients. JAWORSKA & NYBOM (1967) restricted themselves to the two most commonly used, i.e., the matching coefficient and the coefficient of similarity (Jaccard's coefficient or the paired affinity index). The formulas for these coefficients are as follows:

$$\text{The matching coeff.} \quad \frac{p+n}{p+n+d} \qquad \text{The coeff. of similarity} \quad \frac{p}{p+d}$$

In the coefficients p means positive matches, n negative matches, and d differences. If the number of spots included in the investigation are N, it follows that:

$N=p+n+d$ and therefore $N-n=p+d$.

The formulas for the coefficients can therefore also be written:

$$\text{The matching coeff.} \quad \frac{p+n}{N} \qquad \text{The coeff. of similarity} \quad \frac{p}{N-n}$$

Both coefficients vary between 0 (no resemblance) and 1 (identity).

JAWORSKA & NYBOM (1967) concluded that the matching coefficient is to be preferred as it also takes into account negative matches, which are not included in the coefficient of similarity. This statement, however, is false as both coefficients can be written as formulas in which positive matches (p) and negative matches (n) are variables together with N, which is a constant (cf. above).

In both coefficients therefore positive and negative matches play an important role. In the matching coefficient positive and negative matches are given the same weight. In the coefficient of similarity negative matches have considerably less influence than positive ones. Thus, from a biological point of view the coefficient of similarity seems to have some precedence. This coefficient has also another advantage. If the number of taxa included in the comparisons increases, it is most probable that the number of compounds (N) will also increase, e.g., by spots restricted to every taxon added. In this way the matching coefficient of all comparisons will increase because of the establishment of an increasing number of negative matches, which are only partly balanced by the higher figure for N. In the coefficient of similarity the

Table 2. A model showing the influence of the number of spots on the similarity coefficients. Further explanation in the text.

Taxa compared	Positive matches	Negative matches	Differences	Coeff. of similarity
Species A — the hybrid	20	—	10	0.67
Species B — the hybrid	10	—	20	0.33
Species A — Species B	—	—	30	0.00

increased number of negative matches will be well balanced by the increasing number of spots (N), which makes the denominator (N−n) constant. Therefore this coefficient is independent of the number of taxa compared.

In both formulas given above, such biologically important features as positive and negative matches as well as differences are taken into consideration. Due notice is also taken of spots occurring in a single taxon, as they increase the number of negative matches in comparisons between other taxa. If "qualified" positive matches are regarded to be of considerably greater importance than "normal" ones, p can be exchanged for, e.g., $p_1 + 2\ p_2$ (p_1 "normal" positive matches and p_2 "qualified" ones).

No attention, however, is paid to the number of spots in each taxon. It can be demonstrated in a model that this number has a considerable influence on the coefficient values. Thus, a comparison can be carried out between a species A having the spots no. 1—20 and a species B having the spots no. 21—30. The hybrid between these species is presumed to have all 30 spots (20 received from the parent A and 10 from the parent B). As no negative matches occur in any comparison the values of the coefficient of similarity and the matching coefficient will be the same. From Tab. 2 is seen that the coefficient for the comparisons with regard to A and the hybrid is 0.67, while being only 0.33 when B and the hybrid are involved. The coefficient values are apparently an inadequate expression of the biological relationships in this case. It is evident that similar conditions have influenced the results in previous investigations, e.g., in the comparison between *Saxifraga aizoides* L., *caesia* L., and their putative hybrid (JAWORSKA & NYBOM 1967) as the parents have 23 and 7 spots respectively (spots occurring in all three taxa excluded), and in *Mentha* (OLSSON 1967), where the number of spots in different cytotypes varies between 7 and

Table 3. Tabulating of paired comparisons between *Mentha arvensis* L. (2n=72), *aquatica* L. (2n=96), and their putative hybrid derivatives. The table is based on information given in Tab. 1.

Comparisons of cytotypes	Positive matches		Negative matches	Differences
	normal	qualified		
72— 78	3	—	10	18
72— 84	6	1	12	12
72— 90	2	—	16	13
72— 96	5	—	8	18
72—120	4	—	12	15
72—132	2	—	15	14
78— 84	9	1	11	10
78— 90	6	1	17	7
78— 96	9	—	8	14
78—120	6	1	11	13
78—132	3	—	12	16
84— 90	6	—	14	11
84— 96	11	—	8	12
84—120	8	—	10	13
84—132	5	—	12	14
90— 96	6	—	12	13
90—120	4	—	15	12
90—132	3	—	19	9
96—120	7	1	8	15
96—132	6	—	11	14
120—132	4	2	16	9

18. From a biological point of view this factor causes a systematic error, but theoretically some correction may be possible. It is difficult to realize, however, how such a correction could be carried out practically.

Conclusions. Results like those figured in Tab. 1 must be interpreted with much caution as (a) they are based on single individuals of each taxon and (b) the chemical constitution of the substances represented as spots is unkown. Besides, the absence of a spot in a chromatogram may merely depend on the occurrence of too small an amount of the actual substance. Therefore qualitative differences found may in reality very well be concealed quantitative ones.

On account of the restricted value of the data available it is highly questionable if any numeric analyses can be defended. The most adequate treatment seems to be a tabulation of the comparisons in accordance with Tab. 3.

If statistical calculations are performed, they should at least be restricted to cases, in which the compared taxa have a relatively similar number of spots. As to the choice of statistical formulas the coefficient

of similarity seems to have some precedence. Possibly it ought to be modified in such a way, that p is exchanged for $p_1+2\ p_2$, where p_1 means "normal" positive matches and p_2 "qualified" ones.

STATISTICAL ANALYSIS OF QUANTITATIVE FEATURES

JAWORSKA & NYBOM (1967) have introduced quantitative analyses, i.e., comparisons of the size of the spots in chromatograms, in order to make better use of the data available, than in a presence/absence analysis.

The studies as yet performed have been made on phenolic compounds in leaves of single individuals of each taxon. There are reasons to presume great variation in the amount of such compounds both within and between populations of a taxon. Apparently also climatic and edaphic conditions as well as the age of the individual plant or organ have a considerable influence on the amount of a substance produced. Therefore quantitative comparisons must be interpreted with even more caution than qualitative ones. An analysis based on herbarium material as in JAWORSKA & NYBOM (1967) seems rather inappropriate.

NYBOM & al. have suggested statistical methods for the interpretation of comparisons based on quantitative features. From a chemical point of view some comments on such a treatment may be made.

(1) For a single compound there may be an approximately linear connection between the amount of the substances and the size of the spot. Therefore no serious objections can be raised to quantitative comparisons from this point of view.

(2) The size of a spot is mainly determined by two factors: (a) the amount of the compound in question and (b) the solubility of the compound in the solvent system chosen for processing of the chromatogram. In two different solvent systems the same amount of a substance may cause spots of very different size. Thus, different results may be obtained concerning biochemical similarities in a group of taxa, if different solvent systems are used.

An unlimited number of coefficients can be used for calculations of the quantitative association between pairs of taxa (or individuals). NYBOM & al. have chosen the correlation coefficient. Because of the laborious calculation of this coefficient they have suggested as an alternative the taxonomic distance (cf. SOKAL & SNEATH 1963), which has been renamed as the biochemical distance. The coefficients will be examined below.

The correlation coefficient. The correlation coefficient is an estimate of the degree of covariation between variables in a number of samples. Thus a correlation coefficient may be calculated, e.g., to estimate the covariation of the size of the spots nos. 1 and 2 in a number of chromatograms. A correlation coefficient based on two chromatograms, each representing one taxon, as suggested by JAWORSKA & NYBOM (1967) is an absurdity. A calculation, however, is technically possible, if the size of the different spots in taxon A is treated as one variable, that of taxon B as another variable, while the different substances represent the individuals. A coefficient obtained by such a misapplication has of course no meaning.

Generally, it can be stated that the use of the correlation coefficient as an estimate of similarity is an abuse, as such a coefficient is solely an expression for the degree of covariation of variables.

Biochemical distance. JAWORSKA & NYBOM (1967) suggest the biochemical distance, as a more easily calculated substitute for the correlation coefficient. It is calculated according to the following formula:

$$\text{Biochemical distance } \sum_{i=1}^{n} (A_{ij} - A_{ik})^2$$

In this formula n means the total number of different substances studied, A_j and A_k the areas (in mm^2) of the corresponding spots of the taxonomic units j and k. The formula means that the differences in size of the spots of every single substance are calculated. These differences are squared and summed. The sum obtained is the biochemical distance. A low value indicates good agreement whereas a high value expresses considerable biochemical difference between two taxa compared.

The biochemical distance is a true estimate of similarity, in contrast to the correlation coefficient. According to JAWORSKA & NYBOM (1967) the biochemical distance seems to vary in about the same way as the correlation coefficient. The coefficients are in reality wholly independent of each other. Some critical comments concerning the use of the biochemical distance may be made.

(1) The formula may be generalized and written:

$$B = \sum_{i=1}^{n} |A_{ij} - A_{ik}|^x$$

In this formula B means a generalized biochemical distance, x is a variable exponent, and the vertical lines surrounding $A_{ij} - A_{ik}$ indicate

that all differences are expressed as positive numbers. In the calculation of the biochemical distance JAWORSKA & NYBOM (1967) used the exponent $x=2$.

An investigation of this mathematical expression shows that if $x \to 0$, then $B \to d$, where d is the number of qualitative and quantitative differences in the comparison. If $x \to \infty$ the value of B will be dominated by the largest difference, while others are negligible. These extreme values of x are of course uninteresting from a biological point of view, but give valuable information concerning tendencies. Starting from $x=1$ (i.e., the differences are simply summed), a smaller value of x (e.g., $x=1/2$, i.e. the square roots of the differences are summed) will mean that the importance of the number of differences increases, while the importance of the largest differences decreases. On the contrary, higher values of x (e.g., $x=2$, as in the calculations of NYBOM & al.) will mean that the importance of the absolute number of differences decreases, while large differences will have an increased influence on the value of B. Thus, the choice of the exponent in the mathematic formula has a very large influence on the values of the coefficient, and therefore also on the interpretations of biochemical similarity of taxa studied. From a biological point of view it seems difficult to give preference to any of the exponents such as 1/2, 1 or 2. Therefore, only in cases where a number of different exponents give similar results, adequate conclusions can be drawn.

(2) No attention is paid to the total size of the spots in the taxa compared. The variation in this feature may be considerable. Thus, in the six cytotypes of *Mentha* tabulated in Tab. 4 the total size ranges from 141 mm^2 to 421 mm^2. If two taxa, both having a low total size of the spots, are compared, the biochemical distance will in most cases be small, irrespectively of the resemblance of the chromatograms. The total size of the spots in a taxon is most certainly of secondary importance from a biological point of view. Therefore calculations of biochemical distance should be restricted to comparisons between taxa having approximately the same total size of the spots. A correction for this systematic error is of course conceivable, but may be difficult to perform in a biologically and statistically acceptable way.

(3) The coefficient is wholly based on quantitative differences. This fact is not necessarily of vital importance for its usefulness, as there is no way of separating qualitative differences from concealed quantitative ones (cf. p. 34).

Table 4. The occurrence and size of spots of phenolic compounds investigated in *Mentha arvensis* L. (2n=72), *aquatica* L. (2n=96), and their putative hybrid derivatives (from OLSSON 1967).

Spot no.	Polyploid levels (2n)						
	72	78	84	90	96	120	132
1	60	50	50	40	75	25	20
2	—	40	25	20	25	40	12
3	—	40	40	40	50	50	40
4	—	20	16	16	25	—	—
5	—	8	5	—	—	16	—
6	—	20	12	8	25	—	8
7	8	20	8	16	25	25	—
8	—	—	8	—	—	—	—
9	8	—	8	—	16	—	16
10	—	12	12	—	—	—	—
11	5	—	5	—	—	—	—
12	5	8	5	—	12	—	—
13	8	—	8	—	—	16	—
14	16	16	12	12	16	12	—
15	16	—	20	—	25	16	12
16	—	—	40	—	20	16	—
17	—	12	12	—	16	—	—
18	40	—	—	—	—	—	—
19	50	—	—	—	—	—	—
20	5	—	—	—	—	—	—
21	—	—	—	—	30	16	16
22	—	—	—	—	20	—	—
23	—	8	—	—	12	12	—
24	—	—	—	—	8	—	—
25	—	—	—	—	5	—	—
26	—	—	—	—	8	—	—
27	—	—	—	—	8	—	—
28	—	12	—	30	—	—	—
29	—	—	—	—	—	8	5
30	—	—	—	—	—	25	12
31	—	20	—	—	—	16	—
32	—	8	—	—	—	—	—
Total size of spots ..	221	294	286	182	421	283	141

Conclusions. Tabulation of the size of the spots in different taxa (cf. Tab. 3) gives of course more information than merely a presence/absence statement (cf. Tab. 1) and is hence definitely preferable.

NYBOM & al. have suggested a statistical evaluation of the biochemical similarity based on the differences in size of the spots. As the spot size is controlled not only by the amount of the substance in question but also by the solvent system used for processing the chromatograms, any evaluation of statistical calculations seems inadequate.

A statistical treatment may possibly be defensible in special cases. The coefficients suggested by JAWORSKA & NYBOM (1967), however,

can hardly be used. Thus, the correlation coefficient can only be calculated by a misapplication of the formula. Besides it is no estimate of similarity. The values of the biochemical distance are heavily influenced by the choice of exponent in the formula and by the total size of the spots in the taxa compared.

SIGNIFICANCE TESTS OF COEFFICIENTS

A numerical estimate of the similarity between different chromatograms, each representing a single taxon, may be defensible. Calculation of the significance for a difference between two chromatograms (e.g., representing two taxa) is an absurdity, as all significance tests presuppose information about variability. SOKAL & SNEATH (1963 p. 310) also state that "The heterogeneity of the column vectors makes ordinary tests of significance inappropriate".

The same authors also state that "However, lacking better ones we might employ the conventional tests as rough guide lines. Thus for a simple association coefficient, such as S_{sm} [matching coefficient] and S_j [coefficient of similarity] we may use the standard error of the binomial as an approximation". Such a calculation is mathematically untenable and the result meaningless.

The importance of significance tests have generally been overestimated by biologists. Thus, e.g., the genetic diversity in outbreeding plants makes it possible to find a significant difference in almost any character provided sufficiently large samples are chosen (cf. SOKAL 1965 p. 349). Thus, lack of significance for differences in such a test is usually only a consequence of too small samples. From a taxonomic point of view the main interest should be concentrated to the size of the difference and not to significance tests.

GENERAL REMARKS ON CHROMATOGRAPHIC CHEMOTAXONOMY

The investigations as yet published, dealing with the occurrence and size of spots in chromatograms, have mostly been based on a single individual of each taxon. In such a scanty material comparisons based on statistical calculations seem rather inadequate. A better understanding and use of the data in chromatograms can only be obtained by analyses of qualitative and quantitative variation within and between populations in different taxa. In such a case, appropriate statistical methods can be applied. Only few attempts to study intraspecific variation have as yet been performed, e.g., in *Lathyrus* by BRUNSBERG (1965).

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Contributions towards a Revision of Monsonia (Geraniaceae)

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ABSTRACT

The author gives some critical remarks concerning R. KNUTH's monographic treatment of *Monsonia*. Sect. *Umbellatae* KNUTH and sect. *Rotundatae* KNUTH cannot be upheld and their species are easily placed in sect. *Plumosae* BOISS. The author takes the opinion that the genus *Monsonia* is best divided into the following three sections: *Monsonia*, *Plumosae* BOISS. and *Barbatae* BOISS. A new species is described from S.W. Africa (*Monsonia trilobata*, sect. *Barbatae*).

NOTES ON THE SECTION PLUMOSAE BOISS.

In his monograph, R. KNUTH subdivided the genus *Monsonia* into seven sections. Out of these, the following five were described as new: *Genistiformes*, *Ovatae*, *Rotundatae*, *Biflorae*, and *Umbellatae*. The remaining two sections were *Plumosae* BOISS. and *Odontopetalum* DC. (KNUTH 1912 p. 291).

By creating these five sections mentioned, KNUTH abandoned and remodelled BOISSIER's section *Barbatae*, which was based on *Monsonia senegalensis* GUILL. & PERR. This section was originally opposed to sect. *Plumosae* BOISS., established for *Monsonia nivea* (DECNE) WEBB and *M. heliotropioides* (CAV.) BOISS. (BOISSIER 1867 pp. 897—898).

Sect. *Odontopetalum* DC. comprises some few species confined to the Cape Region. They have large, solitary flowers with dentate-lobate apical petal-margins and leaves which are more or less dissected. The section includes the type species and should be named sect. *Monsonia*.

According to KNUTH, sect. *Plumosae* BOISS. shows a Saharo-Sindian type of distribution. This group is distinguished by the following mericarp characters. The mericarp-beak is ciliated in a featherlike manner ("plumose" type), the upper parts of the beak remain straight on the liberated mericarps and the valves— with the seeds — easily fall off.

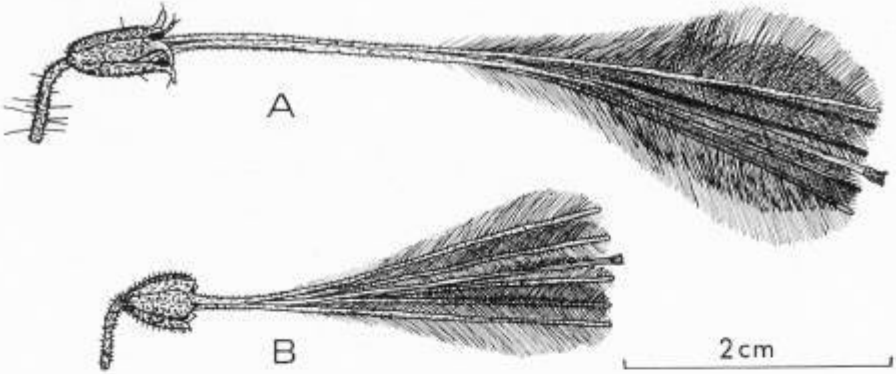

Fig. 1. Ripe capsules in *Monsonia* sect. *Plumosae* Boiss., showing the featherlike ciliation of the beaks. — A. *Monsonia umbellata* Harv. (Kers no. 929 from S.W. Africa, Herb. Stockholm). — B. *Monsonia heliotropioides* (Cav.) Boiss. (Samaritani from "Prope Cairo", Herb. Stockholm).

In the species of the other sections the valves are long persisting on the much recurved beak (cf. Knuth 1912 p. 16, Fig. 8 K and L, showing identical mericarp features in *Erodium*).

While investigating some collections of *Monsonia* made in S.W. Africa I have found that Knuth's treatment of *Monsonia* is unsatisfactory. In the following I will give some criticism and remarks.

I have found that the sections *Rotundatae*, *Biflorae*, and *Umbellatae* were separated from each other by means of rather artificial and variable features, e.g. duration of plants, outline of leaves, number of flowers on the peduncles, and types of calyx. Thus in the material investigated it has been quite impossible to find a real difference between Knuth's important key characters "*Calyx apertus, campanulatus*" and "*Calyx tubulosus*", the last character said to separate clearly sect. *Umbellatae* from all other sections. At least in species belonging to the sections *Rotundatae*, *Biflorae*, *Umbellatae*, and *Plumosae* the calyx is similar: "campanulate" with all sepals free from near the base. An additional character of sect. *Umbellatae* was said to be the many-flowered peduncles. But peduncles with only two flowers do in fact occur, though rarely, in *Monsonia umbellata* Harv. (sect. *Umbellatae*), and as a matter of fact Knuth himself stated *M. parvifolia* Schinz (sect. *Umbellatae*) to have 1—2 flowered peduncles (Knuth 1912 p. 307). On the other hand many-flowered peduncles normally occur in sect. *Rotundatae*, e.g. in *M. deserticola* Dinter ex Knuth and *M. ignorata* Merxmüller & Schreiber 1966. Furthermore, the same

outline of leaves may be found in different sections, e.g. in *Ovatae*, *Rotundatae*, *Umbellatae*, and *Plumosae* (rounded, ovate or cordate).

The most serious mistake made by KNUTH was his failure to recognize the "plumose" type of mericarp shown by many species confined to southern Africa. I have found that the same mericarp type, which distinguishes the two original members of sect. *Plumosae* BOISS. (*M. nivea* and *M. heliotropioides*) is characteristically developed also in species belonging to sect. *Umbellatae* and sect. *Rotundatae*. Thus there is no essential difference as to the mericarp in *M. nivea*, *M. heliotropioides* (sect. *Plumosae* fide KNUTH), *M. umbellata*, *M. luederitziana*, *M. parvifolia* (sect. *Umbellatae* fide KNUTH), and *M. deserticola* (sect. *Rotundatae* fide KNUTH). I have not managed to discover any character by which these species might be kept in different sections. Therefore I would like to propose that sect. *Umbellatae* and sect. *Rotundatae* are rejected and their members placed in sect. *Plumosae* BOISS.

The following species certainly belong to sect. *Plumosae* BOISS.: *Monsonia nivea* (DECNE) WEBB, *M. heliotropioides* (CAV.) BOISS., *M. umbellata* HARV., *M. luederitziana* FOCKE & SCHINZ, *M. rehmii* SUESSENG., *M. parvifolia* SCHINZ, *M. deserticola* DINTER ex KNUTH and *M. ignorata* MERXM. & SCHREIBER (cf. MERXMÜLLER & SCHREIBER 1965, concerning the two last species). *M. drudeana* SCHINZ is likely to have the plumose type of mericarp, but I have seen no material of this species and I have found no records in the literature as regards this important feature.

It may be noted that *M. luederitziana* and *M. rehmii* recently were listed in the synonymy of *M. umbellata* (MERXMÜLLER & SCHREIBER 1966). I consider them to be clearly distinguished from *M. umbellata*, e.g. by means of size of flowers and length of filaments, anthers and stigma. In sect. *Plumosae*, KNUTH also grouped *M. longipes* KNUTH and *M. ignea* KNUTH. I have seen no ripe capsule of *M. ignea*, and in *M. longipes* I cannot trace the plumose type of mericarp. At least the latter species may not belong to sect. *Plumosae*. Further observations are needed in these two species and also in *M. pumila* STANDLEY (non vidi), which was grouped in sect. *Plumosae* by the author because of similarities to *M. longipes*. At least *M. longipes* has some features in common with the Cape Monsonias (sect. *Monsonia*).

KNUTH's classification of *Monsonia* into seven equivalent sections certainly not elucidates the natural affinities whithin the genus but will cause confusion and difficulties only. I think it is better to retain

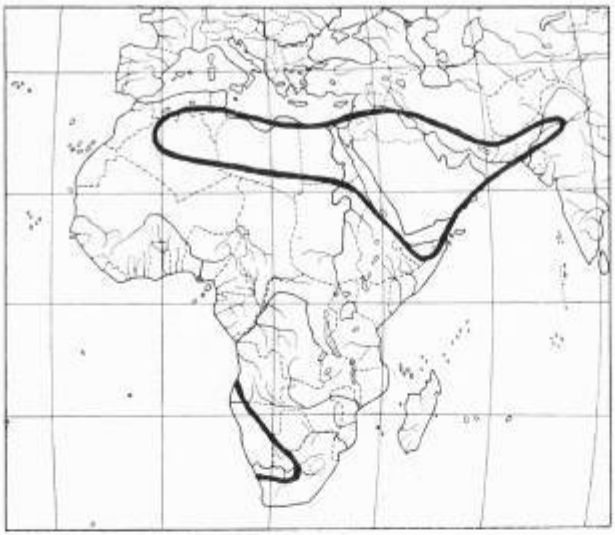

Fig. 2. *Monsonia* : sect. *Plumosae* Boiss. Range of distribution.

the old system of Boissier and De Candolle and recognize the following sections only:

1. *Monsonia* (syn.: *Odontopetalum* DC. Prodr. I. 1824, p. 638.)
2. *Plumosae* Boiss. Fl. orient. I. 1867, p. 896.
3. *Barbatae* Boiss. Fl. orient. I. 1867, p. 898.

All species of sect. *Plumosae* Boiss. show the featherlike ciliation of the mericarp, they have regularly many-flowered peduncles and usually a conspicuous ciliation of the vegetative parts. The five groups of stamens have not been found to be fused in the cup-shaped manner that occurs in sect. *Barbatae*, e.g. in *M. senegalensis* and *M. trilobata* Kers (cf. Fig. 3). Especially *Monsonia nivea* (from Sahara-Arabia), *M. deserticola* and *M. ignorata* (both from the Namib Desert in S.W. Africa) show remarkable similarities with regard to their vegetative parts, which to some degree may be parallel adaptations to similar arid conditions. However, the strong similarities especially in the floral parts in *M. nivea* and *M. deserticola* may reflect a real and close affinity between these two species.

The outline of distribution of sect. *Plumosae* Boiss. can be seen in Fig. 2. The range is split into a large northern portion having few species (2?) and a smaller southern area which is richer in species (at least 6). In southern Africa sect. *Plumosae* is confined to the arid

"Karroo-Namib Region". In this region these Monsonias constitute a group with rich variation offering difficult taxonomic problems.

A NEW SPECIES OF MONSONIA (SECT. BARBATAE BOISS.) FROM S.W. AFRICA

Monsonia trilobata KERS spec. nov.

Herba annua odorata humilis e basi ramosa. *Caules* puberuli, sympodiis prostratis vel decumbentibus c. 30 cm longis, internodiis 2—4 cm longis, foliati. *Folia caulina* opposita, inter se in quoque nodo amplitudine manifeste inaequalia, petiolata, *petiolis* usque 3 cm longis rigidulis apice leviter curvatis stramineis, pilis adpressis puberulis. *Stipulae* triangulares apice caudatae 2—4 mm longae. *Foliorum lamina* ovata—elliptica basi truncata—rotundata margine irregulariter serrato-dentata, usque 2.5 cm longa et 2 cm lata, utrinque pilis adpressis puberula et glandulis sessilibus obsita subtus ad venas pilis brevibus tomentosa, costam secus in sicco plerumque plicata. *Pedunculi* foliis breviores 0.6—1.7 cm longi, pilis adpressis puberuli, 4—8-flori. *Bracteae* subulatae c. 3 mm longae. *Pedicelli* fructiferi recurvati et sub calyce erecti 0.8—1.0 cm longi, pilis brevibus tomentosi. *Sepala* elliptica—obovata 5 mm longa et 2.5 mm lata, pilis hyalinis sericea, ad marginem plusminusve late membranacea, extus apice carinata mucronata, *mucrone* puberulo 1 mm modo longo, a latere compresso a latere viso obtuse triangulato. *Petala* calyce fere duplo longiora, late cuneato-obovata, basin versus minute ciliata, margine apicali trilobata 0.9 cm longa et 0.4 cm lata, rosea. *Stamina* omnia 15 fertilia, filamenta calyce aequilonga vel paulo breviora, basi in tubum per 1/3 longitudinem connata, extus et sursum marginibus ciliata; *antherae* oblongae 1 mm longae. *Stigmata* 1 mm longa. *Fructus maturus* usque 3.2 cm longus; *valvulae* 5 mm longae, pilis adpressis hyalinis obsitae; *rostrum* extus puberulum, intus prope basin pilis longibus hyalinis ciliatum sursum glabrum.

Typus speciei: G. C. THERON no. 1960, 11.IV. 1956, S.W. Africa, 7 miles N. of Narubis (Holotype in Herb. Berlin, isotype in Herb. Kew).

Monsonia trilobata KERS has a superficial resemblance to *Monsonia umbellata* HARV. but differs from this species by its ovate leaves, three-lobed petals, "barbate" type of beak, pink flowers, and type of vestiture, i.e. the absence of long spreading hairs on the stem, peduncles, pedicels and cauline petioles.

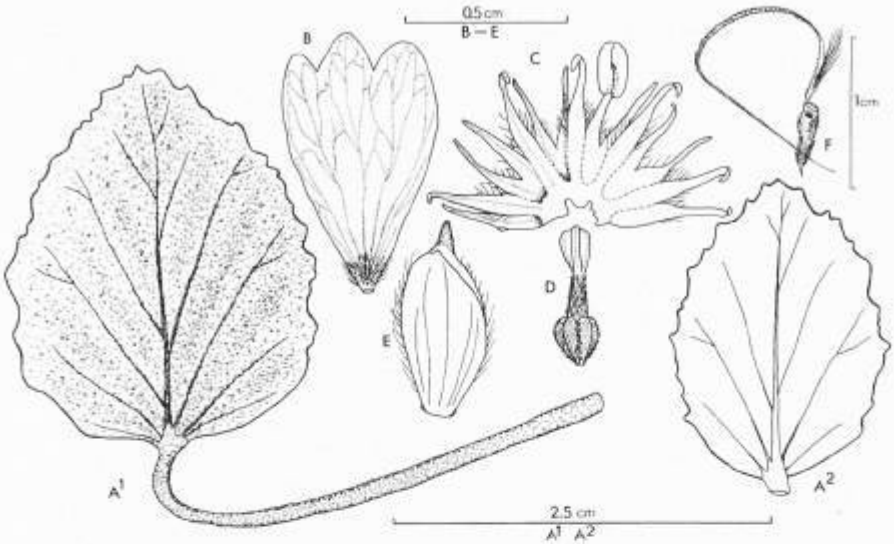

Fig. 3. *Monsonia trilobata* KERS spec. nov. — A^1 & A^2: Cauline leaves, seen from beneath. — *B*: Petal. — *C*: Androecium, split longitudinally before drawn. Only one anther has been illustrated. — *D*: Gynoecium in lateral view. — *E*: Sepal. — *F*: Mericarp. — G. C. THERON no. 1960, Holotype in Herb. Berlin.

I consider that *Monsonia trilobata* KERS is best placed near *Monsonia senegalensis* GUILL. & PERR. Both species belong to the section *Barbatae* BOISS. and show about the same remarkable cup-shaped fusion of the basal parts of their filaments.

The type specimens originate from Keetmanshoop district in southern S.W. Africa where they were collected ESE. of Keetmanshoop along the road to Narubis. Very likely the collections were made on the farms named Warmbakkies 52 and Uchanaris 56, which are situated along the Löwen River just north of the Karas Mtns., and at an altitude of about 800—900 m above sea level.

COLLECTIONS. S.W. Africa, Keetmanshoop distr.: G. C. THERON no. 1960, 11.IV. 1956, 7 miles N. of Narubis. Prostrate. Pink flowers. Strong odour. Frequent (B, K). — DE WINTER no. 3548, 15.V.1955, 25.2 miles ESE. of Keetmanshoop on road to Narubis. Semiprostrate herb with pale pink flowers (K).

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Elymus and Agropyron, a Problem of Generic Delimitation

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ABSTRACT

The tribe *Triticeae* DUM. (*Hordeae* BENTH.) has been divided into a number of entities, which are morphologically distinct and may represent main lines of evolution within the tribe. The subdivision of one of these entities, the *Elymus* group, consisting of *Elymus* L. s.lat. and *Agropyron* GAERTN. s.lat. is discussed on the basis of morphologic, anatomic and cytologic data. The division of the *Elymus* group into 13 genera proposed by NEVSKI is shown to be inappropriate both from a morphologic and an evolutionary point of view. The species within the *Elymus* group have traditionally been referred to *Agropyron* if the spikelets are solitary and to *Elymus* if they are placed in pairs or larger numbers at each node. The division is not very distinct. Thus in some species individuals with solitary as well as such with paired spikelets occur. In other species only the spikelets in the middle part of the spike are paired. Both from morphologic, anatomic, and cytologic points of view it is evident that several species in *Agropyron* have their closest relatives in *Elymus* and vice versa. In reality the genera *Elymus* and *Agropyron* only represent different levels in the reduction of a paniculate inflorescence. The perennial species therefore must be united to a single genus, *Elymus* L. The annual species of *Agropyron* seem to be distinct enough to be kept as a separate genus, *Eremopyrum* JAUB. et SPACH. They are morphologically characterized by basally connected glumes and cytologically by a chromosome structure unique within *Triticeae*. On account of the shape of the palea the annual species of *Elymus* (=*Taeniatherum* NEVSKI) must be removed from the *Elymus* group and transferred to the *Hordeum* group.

INTRODUCTION

Within the tribe *Triticeae* DUM. (*Hordeae* BENTH.) it is very difficult to perform a natural subdivision into genera. At least single species within different genera freely cross with species of other genera. A great number of such intergeneric hybrids occur in the field or have been produced artificially, especially by STEBBINS et al. (1946 a, b, 1949, 1950, 1953, 1954, 1956 b). If a "genetic genus concept" is accepted,

referring all species forming hybrids to the same genus, the consequences would be a genus including, i.a., *Triticum* L., *Aegilops* L., *Secale* L., *Elymus* L. s.lat., *Agropyron* GAERTN. s.lat., and *Hordeum* L. s.lat., as mentioned, e.g., by HYLANDER (1945) and STEBBINS and SNYDER (1956 b). Such a treatment, which from a morphologic point of view seems too drastic, has not been accepted by taxonomists.

The traditional treatment of the tribe is wholly based on characters in the external morphology. In a tribe like *Triticeae*, however, where a number of steps of reduction of the inflorescence occur, there is a great risk, that species in the same stage of reduction will be grouped together, even if they are not closely related. Considerations of this kind have led to the splitting of the large traditional genera *Hordeum*, *Elymus*, and *Agropyron* by NEVSKI (1932, 1933, 1936).

The intention of the present investigation has been a critical examination, also using anatomic and cytologic data, on the following points:

1. The division of *Agropyron* GAERTN. s.lat.
2. The division of *Elymus* L. s.lat.
3. The relationships between *Agropyron* and *Elymus*.

In this treatise HENEEN is responsible for the cytologic observations, while RUNEMARK has made the morphologic and anatomic investigations and the taxonomic treatment of the material.

THE TRIBE TRITICEAE DUM. 1823 (HORDEAE BENTH. 1881)

The most recent detailed investigation of the taxonomy within *Triticeae* was performed by NEVSKI (1933) in connection with the treatment of *Gramineae* in Flora U.R.S.S. NEVSKI subdivided *Triticeae* into 7 subtribes:

1. *Brachypodiinae*	(*Brachypodium, Trachynia*)
2. *Clinelyminae*	(*Clinelymus, Terrella, Asperella*)
3. *Roegneriinae*	(*Roegneria, Anthosachne*)
4. *Hordeinae*	(*Cuviera, Taeniatherum, Psatyrostachys, Crithopsis, Hordeum, Sitanion, Critesion*)
5. *Aegilopinae*	(*Secale, Haynaldia, Eremopyrum, Heteranthelium, Aegilops, Triticum*)
6. *Elyminae*	(*Elymus, Aneurolepidium, Malacurus*)
7. *Agropyrinae*	(*Agropyron, Elytrigia*)

The subtribes were characterized by NEVSKI (1933) as follows:

Brachypodiinae. "Spiculae solitariae, homomorphae, pedicellatae, multiflorae, subcylindraceae; glumae plurinerviae nervis similibus."

Clinelyminae. "Spiculae binae rarius ternae superne interdum solitariae, homomorphae, sessiles vel subsessiles, multiflorae, leviter compressae, flosculis plerumque longiaristatis glumis costato-nervosis scabris. Antherae breves. Caryopsis ventre leviter concava vel fere plana. Plantae sylvestres vel pratenses foliis viridibus tenuibus utrinque scabris planis."

Roegneriinae. "Spiculae solitariae, homomorphae, sessiles vel brevissime pedicellatae, multiflorae, vulgo leviter compressae, flosculis saepissime longiaristatis. Antherae breves. Caryopsis ventre leviter concava vel fere plana. Plantae plerumque sylvestres vel pratenses foliis viridibus utrinque scabris vulgo planis."

Hordeinae. "Spiculae binae vel ternae, heteromorphae, sessiles vel stipitatae, plerumque uniflorae cum rudimento flosculi secundi, raro biflorae, flosculis plus minusve longiaristatis rarius breviaristatis aristis vulgo rectis. Spicae saepissime fragiles."

Aegilopinae. "Spiculae solitariae, plerumque heteromorphae, sessiles, pauciflorae, vulgo flosculis longiaristatis aristis rectis. Spicae saepissime fragiles."

Elyminae. "Spiculae binae—senae (raro solitariae) homomorphae, sessiles vel subsessiles, multiflorae, compressae, flosculis muticis vel breviaristatis glumis saepissime obsolete nervosis. Antherae longae dimidia parte palearum longiores. Caryopsis ventre canaliculata. Plantae in desertis sabulosisque indigenae rhizomate plus minusve stolonifero foliis convolutis glaucis subtus laevibus."

Agropyrinae. "Spiculae solitariae, homomorphae, sessiles, compressae, flosculis muticis vel breviaristatis glumis plurinerviis vel carinatis laevibus. Antherae longae dimidia parte palearum longiores. Caryopsis ventre canaliculata. Plantae rhizomate saepissime stolonifero foliis glaucis vel glauco-viridibus subtus laevibus plus minusve convolutis."

Of these subtribes *Brachypodiinae* must be excluded from *Triticeae*. It is best treated as a separate tribe (*Brachypodieae* HARZ) possibly related to *Bromeae* as suggested by HUBBARD (1948) for morphologic reasons. Cytologic data also make inclusion within *Triticeae* unnatural. Thus the basic chromosome numbers are 5 and 9 (and an apparently secondary number x=14), while the other subtribes have invariably 7. Besides, the chromosomes are much smaller and of a very different shape in *Brachypodiinae* as compared with the rest of *Triticeae*. The epidermal and subepidermal cells of roots within *Brachypodiinae* have numerous bodies which are stained with the normal chromosome staining agents. In this respect *Brachypodiinae* coincides with the tribe *Festuceae* (cf. AVDULOV 1931), but deviates from the representatives within *Triticeae*.

The subtribe *Hordeinae* (excluding *Sitanion*, cf. p. 62) is a morpho-

logically well delimited group of genera, most easily distinguished from the other subtribes by the shape of the palea, which is only slightly curved or bent in the lateral parts. Within other subtribes they are constantly and sharply folded along the nerves, which are developed as sharp, often bearded edges. — A study of the palea types within the grasses (PILGER 1949 a, b) has shown that the different types found are very constant within genera and mostly also within tribes. In addition the subtribe *Hordeinae* is characterized by heteromorphic 1- or rarely 2-flowered spikelets, which are situated 2 or 3 together at each node.

The genus *Henrardia* described by HUBBARD (1946) resembles *Hordeinae* in the shape of the palea. It is, however, very different in other respects. Morphologically it is the most reduced genus within *Triticeae* and is characterized by solitary, homomorphic spikelets (with 1—2 florets) sunken in the spike axis.

The subtribe *Aegilopinae* consists of a number of morphologically distinct genera. However, it seems inappropriate to refer these genera to the same group. *Aegilops* and *Triticum* for a certainty constitute a natural unit, *Secale* and probably *Haynaldia* another natural unit, while *Heteranthelium* has an isolated position. *Eremopyrum* is probably best referred to the *Agropyron-Elymus* complex.

The remaining material, i.e. *Agropyron* s.lat. and *Elymus* s.lat., has been divided into 4 subtribes, *Clinelyminae*, *Roegneriinae*, *Elyminae*, and *Agropyrinae*. However, in reality none of the characters given nor any combination of them can be used for a morphologic separation of the proposed subtribes. Thus characters such as the shape of the caryopses (grooved or not), spikelets either solitary or in groups, anthers either short or long, florets with long bristles or not, plants which are caespitose or rhizomatous, vary widely within the subtribes and also within the genera accepted. For details concerning the variation pattern reference is made to the chapters on *Agropyron* s.lat. and *Elymus* s.lat.

Formerly *Agropyron*, *Triticum*, and *Elymus* were often united to form a single genus (*Triticum* s.lat.), e.g., in ASCHERSON and GRAEBNER (1901). *Triticum* is, however, distinct enough morphologically to be kept separate. The artificially produced "perennial wheats" (cf., e.g. ARMSTRONG and MCLENNAN 1944) based on hybrids between *Agropyron elongatum* (HOST) BEAUV. s.lat. (2n=70) and *Triticum aestivum* L. (2n=42) to a certain extent form an obstacle to such a treatment. The more or less fertile amphidiploid strains obtained must be sought in the unusually high polyploidy of both parents (deca- and hexaploids) and not in a close affinity between the *Agropyron* and *Triticum*

genomes involved. Therefore I regard it also from an evolutionary point of view defensible to treat *Triticum* and *Agropyron* as separate genera.

The genera *Agropyron* and *Elymus* in the traditional sense have been distinguished solely by the number of spikelets at the nodes (in *Agropyron* 1 and in *Elymus* 2—several). The delimitation is not very distinct. Thus in some *Agropyron* species spikelets sometimes occur in pairs (e.g. *A. smithii* RYDB.) and forms with solitary spikelets are common in a few *Elymus* species (e.g. *Elymus salinus* JONES, *E. simplex* SCRIBN.). Besides, several *Elymus* species are characterized by having solitary spikelets on the top and at the base of spikes, while the central part has spikelets in pairs (e.g. *E. ambiguus* VASEY, *E. divaricatus* DROB., *E. fasciculatus* ROSH., and *E. pseudoagropyron* TRIN.).

It has long been evident that the traditional subdivision into *Agropyron* and *Elymus* is artificial. In several cases it can be shown that species within *Agropyron* have close relatives within *Elymus* and vice versa. Examples of such cases are (the generic names from the system of NEVSKI in parenthesis):

Agropyron		**Elymus**
(*Elytrigia*) *junceum* (L.) BEAUV.	—	(*Elymus*) *arenarius* L.
(*Aneurolepidium*) *ramosum* (TRIN.) RICHT.	—	(*Aneurolepidium*) *pseudoagropyron* TRIN.
(*Roegneria*) *schrenkianum* (FISCH. et MEY.) DROB.	—	(*Clinelymus*) *nutans* GRISEB.
(*Roegneria*) *subsecundum* (LINK) HITCHC.	—	(*Clinelymus*) *glaucus* BUCHL.

The problem of the unsatisfactory taxonomy of *Agropyron* and *Elymus* has been tackled in two different ways:

(1) NEVSKI (1933) split the two traditional genera into 13 which were referred to 6 different subtribes. In this way pairs of related genera were created to a certain extent, one from each of the former genera.

(2) GOULD (1947) united *Agropyron* and *Elymus* to form a single genus, *Elymus* s.lat., however, without giving much evidence for such a treatment.

THE SUBDIVISION OF AGROPYRON S. LAT.

NEVSKI (1933) split *Agropyron* into 5 genera, which were fully described by him in 1936:

Agropyron GAERTN. s.str.

"Spicae oblongo-lineares vel ovatae, densae, rectae, rhachide abbreviata.

Spiculae solitariae, 3—10-florae, sessiles, muticae vel breviaristatae, plus minusve patentes spicam disticham vulgo pectiniformem formantes. Glumae carinatae, naviculares, a latere compressae, aequales vel subaequales, inaequilaterales, laeves vel ciliatae marginibus albo-membranaceis. Glumella naviculari, laevis vel pilosa. Antherae longae, dimidia parte palearum longiores. Caryopsis oblongo-linearis, facie inferiore canaliculata. Plantae perennes, caespitosae vel rhizomate repente, foliis saepissime convolutis glaucis vel glaucescenti-viridibus subtus laevibus supra pilosis aut scabris. [Typus gen.: *A. cristatum* (L.) GAERTN.]."

Elytrigia DESV.

"Spicae rectae, laxae vel subdensae, rarius densae, distichae. Spiculae solitariae, 3—11-florae, compressae, sessiles, muticae vel breviter aristatae rarius longiaristatae, glaucescenti-virides vel virides raro plus minusve violaceo coloratae. Glumae lanceolatae vel lineari-oblongae, non carinatae, multinerviae, saepissime laeves, interdum solummodo apice ad nervos scabrae, basi sulco transverso strangulatae, glabrae rarius molliter pilosae vel ciliatae. Flosculi callo nudo abbreviato basi instructi. Glumella laevi, glabra, rarius pilosa. Lodiculae marginibus ciliatis vel superne pilosae. Antherae longae, (3) 4.5—7 mm longae, dimidia parte palearum longiores. Caryopsis oblongo-linearis, ventre canaliculata. Plantae foliis saepissime convolutis, rigidis, glaucis vel glaucescenti-viridibus, subtus laevibus, supra pilosis vel scabris. [Typus gen.: *E. repens* (L.) DESV.]."

Roegneria C. KOCH

"Spicae rectae vel nutantes, plurispiculatae. Spiculae (2)3—9-florae, leviter compressae rachide fragili vel subfragili. Glumae lanceolatae vel lineari-lanceolatae, muticae, rarius breviaristatae, 3-plurinerviae nervis valde prominentibus vulgo scabris vel scaberrimis, basi sulco transverso orbatae pedicello rudimentario cohaerentes. Glumellae scabrae vel pilosae, rarius glabrae. Lodiculae marginibus ciliatis. Antherae 1.5—3.5(4) mm longae (rarissime 5 mm longae), dimidia parte palearum breviores vel subaequantes. Caryopsis oblongolinearis, ventre leviter concava vel subplana. — Plantae foliis vulgo planis, utrinque scabris, glabris vel pilosis, in silvis pratisque subhumidis crescentes. (Typus gen.: *R. caucasica* C. KOCH)."

Anthosachne STEUD.

"Spiculae 6—12-florae, valde compressae, dissitiflorae, rachide fragillima, basi cuneato-angustatae, spicam saepe flexuosam laxam paniculiformem superne ob aristas divergentes dilatatam formantes. Glumae lineari-lanceolatae, attenuato-acuminatae flosculo infimo breviores, laeves vel sublaeves. Flosculi basi callo majusculo glabro vel scabro instructi. Glumellae scabrae vel laeves, longissime aristatae aristis basi dilatatis et subcanaliculatis divergentibus ad 8 cm longis. Lodiculae marginibus ciliatis. Caryopsis ventre subcanaliculata. Plantae foliis plus minusve convolutis subtus vulgo laevibus, in deeliviis saxosis crescentes. (Typus gen.: *A. australasica* STEUD.)."

Eremopyrum JAUB. et SPACH

"Spicae elliptico ovatae vel oblongo-ovatae, densae, rachide fragili abbreviata. Spiculae solitariae, 2—6-florae, sessiles, distiche imbricatae, patentes, compressae, sub-, vel breviaristatae. Glumae carinatae, a latere compressae, demum margine induratae, corneae et basi cohaerentes. Glumella glabra vel pilosa, arista brevi donata. Plantae annuae, humiles, culmis pluribus basi plus minusve geniculatis, foliis planis brevibus scabriusculis et saepe pilosiusculis. [Typus gen.: *E. orientale* (L.) JAUB. et SPACH]."

The 5 genera were placed by NEVSKI in 3 different subtribes: *Agropyrinae* (*Agropyron* s.str. and *Elytrigia*), *Roegneriinae* (*Roegneria* and *Anthosachne*), and *Aegilopinae* (*Eremopyrum*).

Eremopyrum, consisting of the annual species of *Agropyron* s.lat., is apparently a rather well delimited genus, possibly related to *Aegilops*. It is best characterized by the glumes which are basally connected and have cartilaginous margins.

The genera *Agropyron* s.str. and *Elytrigia* have been placed in the same subtribe (*Agropyrinae*). The only difference between the genera is the orientation of the spikelets. In *Agropyron* s.str. the spikes are very dense with spreading spikelets, while *Elytrigia* has ± slender spikes with spikelets adpressed to the main axis. According to NEVSKI (1933) the genera are closely related and in Flora U.R.S.S. (vol. II, 1934) they have been reduced by him to subgenera. It is obvious that *Agropyron* s.str. (sensu NEVSKI) is a group of closely related species with a very characteristic habit. However, as no supplementary differences have been found and as some other groups within *Agropyron* s.lat. are at least as well characterized (e.g. the *Agropyron junceum* group), a subdivision into genera must be regarded as inappropriate in this case.

The genera *Roegneria* and *Anthosachne* have also been placed together in a subtribe (*Roegneriinae*). *Roegneria* consists of many species with a world-wide distribution, while a few species from central and south-eastern Asia are included in *Anthosachne*. This genus is said to differ from *Roegneria* in having spikelets with the florets situated at relatively long intervals and very long awns of the lemma (up to 8 cm). Besides, the Russian species at least have anthers which are longer (4—7 mm) than in *Roegneria* (according to NEVSKI 1.5—3.5 mm in this genus). As far as can be seen, there is little reason for the suggested subdivision into two genera. Thus several *Roegneria* species have long awns (up to 5 cm) of the lemma, and in American *Roegneria* species anthers up to 5—6 mm in length occur.

Agropyron and *Elytrigia* have been placed in a separate subtribe as compared with *Roegneria* and *Anthosachne*, which indicates a relatively

remote relationship between the genera. However, when the distinguishing morphologic characters are analysed, the subdivision of *Agropyron* s.lat. into two different subtribes seems obscure. The characters given for distinguishing the subtribes are as follows:

Roegneriinae	**Agropyrinae**
(*Roegneria, Anthosachne*)	(*Agropyron* s.str., *Elytrigia*)
plants caespitose	plants rhizomatous
leaves soft, green	leaves usually stiff, greyish-green to green
caryopsis grooved	caryopsis subplane to concave on the adaxial side
anthers 1.5—3.5 mm	anthers 4.5—7 mm

The characters listed above cannot be used singly or in combination for a distinct delimitation of the subtribes (or of the genera *Roegneria* and *Elytrigia*). Thus, e.g. *Roegneria macroura* (TURCZ.) NEVSKI has long creeping rhizomes, while *Elytrigia elongata* (HOST) NEVSKI and *Elytrigia caespitosa* (KOCH) NEVSKI are strictly caespitose. Within *Roegneriinae*, e.g., *Anthosachne longiaristata* (BOISS.) NEVSKI has 4—7 mm long anthers and *Agropyron* (*Roegneria*) *spicatum* PURSH. 5—6 mm long anthers, while within *Elytrigia elongata* (HOST) NEVSKI s.lat. different forms have anthers varying from 2 to 6 mm in length. Even the shape of the caryopsis varies and a series of transitions can be presented (the adaxial side: deeply grooved — somewhat grooved — concave — subplane — plane).

The new subtribes and genera have been established on a restricted material. Thus NEVSKI treated only Russian species. NEVSKI's subdivision has been accepted, e.g., by HYLANDER (1953) and TUTIN (1956), who, however, have been mainly interested in the consequences for Scandinavian and British material respectively. Thus TUTIN (1956) in a paper concerning "Generic criteria in flowering plants" separates *Roegneria* from *Elytrigia* in the following way: "the latter differing from the former in having spikelets which fall entire at maturity, instead of glumes remaining attached to the rhachis, larger anthers, deeply grooved caryopsis and long rhizomes". The characters given can certinly be used for a separation of the two British *Roegneria* species from the three British *Elytrigia* species. However, none of the characters mentioned can be used for a separation of the genera.

Many botanists working on *Triticeae* have not accepted the subdivision suggested by NEVSKI (in some cases with the exception that *Eremopyrum* is regarded as a separate genus), e.g., STEBBINS, SIMONET, CAUDERON, CHASE, HUBBARD, and BOR.

THE SUBDIVISION OF ELYMUS S. LAT.

NEVSKI (1932, 1933, and 1936) subdivided *Elymus* s.lat. into 8 genera characterized as follows:

Elymus L. s.str. (correct name *Leymus* HOCHST.)

"Spiculae binae-senae, pallide glaucescenti-viridis vel coloratae, 3—5-florae. Glumae lanceolatae vel anguste lanceolatae, (1) 3—5-nerviae, ad dorsa glumelarum flosculorum infimorum accumbentes glabrae vel pilis mollibus plus minusve vestitae (non scabrae) marginibus membranaceis. Glumella acuminata, mutica vel subaristulata, molliter pilosa. Lodiculae binae, acuminatae, majusculae, superne pilosae. Caryopsis lineari-oblonga, ventre canaliculata. — Plantae maritimae rhizomate longe repente stolonifero, foliis convolutis glaucis rigidis crassinerviis. (Typus gen.: *E. arenarius* L.)."

Aneurolepidium NEVSKI

"Spiculae binae—quaternae, raro solitariae, 2-multiflorae. Glumae anticolaterales, subulato-lineares vel subulatae, subenerviae vel uninerviae rarius obsolete trinerviae superne dorso marginibusque scabrae. Glumellae rachi oppositae, breviaristatae, obsolete nervosae. Lodiculae superne pilosae. — Plantae perennes, in desertis indigenae, rhizomate plus minusve longe repente stolonifero, foliis glaucis rigidis crassinerviis convolutis. [Typus gen.: *A. multicaule* (KAR. et KIR.) NEVSKI]."

Malacurus NEVSKI

"Spicae rectae rachide laevi glabra. Spiculae binae molliter lanatae, 3—4-florae rachilla ad basin flosculi infimi articulata, fragillima, pilosiuscula. Glumae subulato-setaceae, glaberrimae, laeves, flosculo infimo breviores, laterales. Glumella membranaceo-herbacea, multinervis, late-lanceolata, densissime longe villosa, breviaristata, arista 1.5—2 mm longa, sublaevi, subfragili, spiniformi. Lodiculae membranaceae ovato-lanceolatae longe denseque ciliatae.

Genus valde insigne, ab affinibus differt: spicularum rachide fragillima, glumis setaceis glaberrimis laevibus et glumellis membranaceo-herbaceis 7—9 nerviis longissime villosis arista brevi sublaevi, subfragili, donatis." [Typus gen.: *M. lanatus* (KORSH.) NEVSKI.]

Clinelymus (GRISEB.) NEVSKI (correct name *Elymus* L.)

"Genus ab *Elymo* spiculis saepissime binis glumis et glumellis inferioribus costato-nervosis scabris (non laevibus vel molliter pilosis) plus minusve longiaristatis aristis saepe reflexis, antheris brevioribus, lodiculis parvis glabris vel marginibus breviter ciliatis (non pilosis) differt. Generi *Asperellae* HUMB. magis affine sed glumis lineari-lanceolatis vel lanceolatis 3—5 nerviis flosculo infimo subaequantibus distinctum.

Plantae perennes, caespitosae. Culmi erecti vel basi geniculati. Folia plana, saepissime tenuia, utrinque scabra vel leviter pilosa, glaucescenti-virida vel viridia. Spicae lineares, densae, nutantes vel rectae. Spiculae binae (raro inferne ternae) superne interdum solitariae (2) 3—7-florae. Glumae lineares, lineari-lanceolatae vel lanceolatae, breviter aristatae, costato 3—5—(7)-nerviae,

scabrae. Glumellae inferiores longiaristatae (aristae plus minusve divergentes, rarius rectae) scabrae. Antherae dimidio parte palearum breviores vel subaequantes. Lodiculae parvae fere glabrae vel marginibus breviter ciliatis. Caryopsis lineari-oblonga ventre leviter concava." [Typus gen.: *C. sibiricus* (L.) NEVSKI.]

Terrella NEVSKI

"Genus valde insigne, ab omnibus affinibus glumis basi incrassatis, curvatis bene differt. Plantae perennes, caespitosae. Culmi erecti vel basi plus minusve geniculati. Folia plana, utrinque scabra, glauco-viridia vel viridia. Spicae crassae, strictae, valde densae. Spiculae binae (rarius inferne ternae), 2—5-florae. Glumae crassae, basi convexo-curvativae et incrassatae, superne curvatae, saepe leviter contortae, obliquae, costatae, lineari-lanceolatae, longe acuminatae, breviaristatae, ad nervos plus minusve scabrae vel hirsutae, flosculis longiores. Flosculi aristati. Aristae rectae, saepe leviter subcontortae, scabrae. Antherae ochroleucae, dimidio parte palearum subaequantes. Caryopsis lineari-oblonga ventre concava." [Typus gen.: *T. virginica* (L.) NEVSKI.]

Taeniatherum NEVSKI

"Spicae densae, superne ob aristas divergentes dilatatae, rachide tenaci apice spicula terminali. Spiculae binae, sessiles, uniflorae cum rudimento flosculi secundi. Glumae anguste subulatae, rigidae, basi connatae, erectae vel patentissimae, flosculum superantes. Glumella lanceolata, scabra, obsolete nervosa in aristam longissimam digergentem plus minusve validam inferne complanatam producta. Plantae annuae, radice fibrosa, foliis anguste linearibus subplanis.

Genus a *Hordeo* rachide spicae tenaci apice spicula terminali, spiculis binis sessilibus, glumis basi connatis, aristis divergentibus complanatis bene differt. [Typus gen.: *T. crinitum* (SCHREB.) NEVSKI.]"

Asperella HUMB. (*Hystrix* MOENCH)

"Spikes linear; spikelets subarcuately divergent, in pairs, or partly solitary. Spikelets (1)—2—5—(6)-flowered, subsessile; rachilla jointed below the lowest floret. Glumes lacking or weakly developed, subulate, scabrous. Lemmas lanceolate, 5—7-nerved, glabrous or hairy and scabrous, awned. Lodicules pointed, hairy at the top. Anthers long. Caryopsis narrow, linear, hairy on the top, slightly furrowed. Perennials with creeping or short rhizomes and flat, scabrous, and usually hairy leaves." — (Description from NEVSKI's treatment of the genus in Flora of the U.S.S.R. — English translation 1963)."

Sitanion RAF.

"Spikelets 2- to few-flowered, the uppermost floret reduced, usually 2 at each node of a disarticulating rachis, the rachis breaking at the base of each joint, remaining attached as a pointed stipe to the spikelets above; glumes narrow or setaceous, 1- to 3-nerved, the nerves prominent, extending into one to several awns, these (when more than one) irregular in size, sometimes mere lateral appendages of the long central awn, sometimes equal, the glume being bifid; lemmas firm, convex on the back, nearly terete, 5-nerved, the nerves obscure, the apex slightly 2-toothed, the central nerve extending into

a long, slender, finally spreading awn, sometimes one or more of the lateral nerves also extending into short awns; palea firm, nearly as long as the body of the lemma, the two keels serrulate. Low or rather tall tufted perennials with bristly spikes. Type species, *Sitanion elymoides* RAF. (*S. hystrix*)." — As NEVSKI has not published any description of the genus, the description is taken from HITCHCOCK's "Manual of the grasses of the United States" (1950).

NEVSKI placed the genera in three subtribes: *Elyminae* (*Elymus, Aneurolepidium, Malacurus*), *Clinelyminae* (*Clinelymus, Asperella, Terrella*), and *Hordeinae* (*Sitanion, Taeniatherum*).

Of the genera placed by NEVSKI in *Elyminae*, *Elymus* (sensu NEVSKI) is most easily distinguished from *Aneurolepidium* by large spikelets with very broad glumes. The monotypic genus *Malacurus* (from central Asia) is characterized by the fragile and articulate rhachilla and by the subulate glumes. It is apparent that *Elymus* in NEVSKI's sense (*E. arenarius* L. and 2 or 3 closely related species) and *Malacurus* constitute natural entities. Within the large genus *Aneurolepidium*, however, other species or groups of species can be found which are as well characterized as the above mentioned genera, e.g., *Aneurolepidium pseudoagropyron* (TRIN.) NEVSKI and related species. The subdivision within *Elyminae* suggested by NEVSKI has been followed by few botanists. Thus already in Flora U.R.S.S. there is a footnote to the genus *Aneurolepidium* in which it is stated that "the editors consider the separation of the group *Aneurolepidium* NEVSKI from the genus *Elymus* L. as not sufficiently well grounded".

Three genera, *Clinelymus, Hystrix* (*Asperella*) and *Terrella*, are placed together in the subtribe *Clinelyminae*. Of these genera *Terrella* is North American and in reality monotypic, even if NEVSKI regarded several forms as separate species. The genus is characterized by glumes, which are bowed out at the base, leaving a rounded sinus. In other respects, however, *Terrella virginica* (L.) NEVSKI is similar to several *Clinelymus* species, e.g. *Elymus riparius* WIEGAND.

The genus *Hystrix* (*Asperella*), consisting of a small group of related species, was even before NEVSKI's treatment accepted as a separate genus. It is most easily characterized by strongly reduced or aborted glumes. Several species of *Elymus* (*Clinelymus*) also have irregularely reduced glumes, e.g., *Elymus interruptus* BUCHL. Therefore even in this case a morphologically distinct generic delimitation seems difficult to obtain.

The genera *Taeniatherum* and *Sitanion* were referred to *Hordeinae* by NEVSKI. *Taeniatherum* consists of the few annual species within

Elymus s.lat. (the *Elymus caput-medusae* group). These species have been placed alternately in *Hordeum* and *Elymus*. NEVSKI's inclusion of the genus in *Hordeinae* is strongly supported by the shape of the palea (slightly bent in the lateral parts, cf. PILGER 1949 a, b).

Sitanion, a small North American genus on the other hand has paleas folded backwards along the nerves. It has also been regarded by most authors as a section within *Elymus* or as a genus closely related to *Elymus*. When retained as distinct, it is separated on the basis of the readily disarticulating rhachis and the usually narrow, setaceous glumes. According to GOULD (1947) "*Elymus aristatus* as known in California, would appear more *Sitanion*-like than the classically recognized species *Sitanion Hansenii*". According to STEBBINS et al. (1946 a) *S. hansenii* (SCRIBN.) J. G. SMITH (a species with a wide distribution in western North America) consists of a series of hybrids between *Elymus* (*Clinelymus*) *glaucus* BUCHL. and *Sitanion jubatum* J. G. SMITH or *S. hystrix* (NUTT.) J. G. SMITH. A distinct morphologic delimitation between *Clinelymus* and *Sitanion* apparently does not exist. In the system of NEVSKI *Sitanion* ought to be transferred to *Clinelyminae*.

NEVSKI (1932) tabulated the differences between *Elymus* and *Clinelymus* (i.e., the differences between the subtribes *Elyminae* and *Clinelyminae*) as follows:

Elymus	**Clinelymus**
Rhizoma stoloniferum	Rhizoma caespitosum
Culmi saepe crassissimi, elati	Culmi saepe tenues
Folia linearia vel anguste-linearia, rigida, plus minusve convoluta, glauca	Folia linearia, glaucescenti-viridia, vel viridia, plana, saepissime tenuia
Spicae elongatae, strictae, saepe confertae	Spicae nutantes, declinatae vel rectae
Spiculae ternae vel quaternae vel senae, rarius binae, pluriflorae, muticae	Spiculae binae vel superne solitariae, raro inferne ternae, pluriflorae, longiaristatae
Glumae lanceolatae, lineares vel subulatae laeves vel superne leviter scabrae, saepissime obsolete nervosae vel uninerves	Glumae lanceolatae vel lineares, scabrae vel scaberrimae, costato 3—5(7) nerviae, breviter aristatae
Glumellae inferiores lanceolatae, naviculares, acuminatae, muticae, molliter pilosae vel laeves	Glumellae inferiores lanceolatae, acuminatae, longiaristatae (aristae diveregentes, rarius rectae), scabrae, setulis brevissimis adpressis vestitae

Antherae dimidio parte palearum longiores	Antherae dimidio parte palearum breviores vel subaequantes
Lodiculae superne pilosae	Lodiculae parvae, fere glabrae vel marginibus breviter ciliatis

This subdivision has the same weakness as that of *Agropyron* s.lat. No single character or combination of characters can be used for a distinct separation of the genera proposed.

The entire subdivision of *Elymus* s.lat. into 8 genera has been accepted by very few taxonomists. However, many agrostologists (e.g., BOR and CHASE) have regarded single genera as *Taeniatherum*, *Hystrix*, and *Sitanion* as distinct. A few botanists (e.g., PILGER and LÖVE & LÖVE) have accepted a subdivision into *Elymus* s.str. and *Clinelymus*.

ANATOMY

Introduction

Anatomic characters, especially of the leaves, have been used in the taxonomy of grasses ever since DUVAL-JOUVE (1869) made an investigation of the anatomy of the *Agropyron* species of Herault in southern France. Such characters have been extensively used, e.g., in the taxonomy of *Festuca* and *Avena* s.lat. by ST.-YVES and others. PRAT (1931) made an investigation of the epidermal structure of grasses, in which special attention was drawn to the conditions in *Agropyron*. Recently METCALFE (1960) published an extensive monograph on the leaf anatomy of grasses.

Most investigations of grass anatomy have been restricted to the conditions of the leaf, as this organ shows the most specialized structures of the plant. Within the grasses two main types of leaf structures can be distinguished: the panicoid type and the festucoid type. The two types are distinguished, i.a. by the orientation of the mesophyll cells, the construction of the bundle sheaths, and the presence or absence of micro-hairs. This anatomic subdivision of the grasses into two groups coincides well with that made by AVDULOV (1931) on cytologic features (cf. STEBBINS 1956 a).

The anatomic features referred to above have been of value especially for the studies of the interrelationships between the tribes (cf. HUBBARD 1948) and for the correct placing of genera with uncertain affinities (e.g., *Lepturus*, cf. HUBBARD 1946). As the anatomic gross structure of the leaves seems to be very constant within the tribes, it is of little use for the delimitation of genera.

For the delimitation of taxa below tribes other anatomic characters of the leaves have been used, such as the extension of sclerenchyma and the shape of epidermal cells.

Material Studied

Leaf anatomy has been studied mainly on samples taken from herbarium material. In a few cases cultivated material from the greenhouses of the Botanical Garden of Lund has been investigated. Material from ca. 300 specimens of littoral European *Agropyron* species have been studied and ca. 100 specimens of other *Agropyron* and *Elymus* species.

Observations

The general features of the anatomy of the leaves in *Triticeae* can be summarized as follows. The leaves are of the festucoid type, i.e., the outer bundle sheath (parenchymatous sheath) is poorly differentiated, the inner bundle sheath (mestome sheath) has strongly thickened cells, and the chlorophyll tissue is not arranged in any special manner around the bundles, but is disposed between them. The silica-bodies in the epidermal cells are usually elongated and sometimes slightly saddle-shaped. Micro-hairs do not occur.

Qualitative differences in leaf anatomy within *Triticeae* occur mainly in the abaxial epidermis. In this respect the species within *Triticeae* coincide with most other grass species (cf. METCALFE 1960). In a few cases the extension of sclerenchyma also seems to be of taxonomic importance.

THE ABAXIAL EPIDERMIS. The epidermis is composed of long-cells, interrupted by short-cells and stomata (cf. METCALFE 1960).

Long-cells. The long-cells in the material studied are always very elongated (often 10—20 times as long as broad). In many species they have sinuous walls; in others the walls are straight. The character, however, seems to be useful on species-level.

Distinct differences occur in transversal sections of the epidermal cells. This character seems to have been neglected during the investigations of the anatomy of grass leaves (incidentally mentioned, however, by PRAT 1931). The material studied can easily be divided into three groups (Fig. 1 A, B, C): (1) quadratic or almost quadratic sections, (2) elliptic sections, and (3) irregular sections (almost permanently with blunt papills).

Short-cells. The short-cells in the material investigated occur normally in compounds of two cells, one silicified and one (smaller) suberized. They are not evenly distributed over the lamina, but in most cases concentrated in the area below the veins. The short-cells are often converted into prickles and hairs. Two types of such differentiated short-cells occur in the material studied:

(1) Prickles and prickle-hairs (Fig. 1 E, F). They are robust, sharply but usually shortly pointed structures with a swollen base. They often cause aspirity of the lamina [e.g., in *Agropyron caninum* (L.) BEAUV.].

(2) "Crown-cells" (Fig. 1 D). Silicified cells with minute, low conical to rounded protrusions from the outer cell wall, probably wholly consisting of cutin. They are often easily observed directly on the lamina by using a strong lens, depending on their refractive properties. This distinctive structure seems to be mostly neglected by METCALFE (1960), but was observed and figured by PRAT (1931). Crown-cells characterized by thickenings of the outer wall must not be confused with long-cells with papills, which are outgrowths of the cell also including part of the cell lumen.

Stomata. Differences between species in the shape of the subsidiary cells have been reported by METCALFE (1960), but the variation is too great for such differences to be practical for diagnostic purposes. In a few species stomata on the abaxial epidermis of the leaf are entirely or almost entirely lacking.

SCLERENCHYMA. The extension of sclerenchyma in the leaves has been used extensively as a taxonomic character in some groups of grasses (e.g., *Festuca* and *Avena*). However, KJELLQVIST (1962) has shown in experiments that in the *Festuca rubra* aggr. this character is extremely modifiable, and seems to be without taxonomic value.

Most species within *Triticeae* have separate strands of sclerenchyma attached to the vascular bundles and in the edges of the leaves (Fig. 1 H). In a few species the sclerenchyma strands are connected, forming a continuous layer inside the abaxial epidermis (Fig. 1 G).

The modifiability has been tested in *Agropyron junceum* (L.) BEAUV., a species having a continuous sclerenchymatous layer. During cultivation this layer is not normally modified. In greenhouses, however, in very humid conditions in winter, the hexaploid, Mediterranean material sometimes gets a ± subcontinuous sclerenchymatous layer.

DISCUSSION. The anatomic features discussed above occur, not combined at random, but in a few characteristic combinations.

1. Epidermal cells in section quadratic, walls sinuous, prickles, prickle-hairs and crown-cells lacking, stomata lacking or rare on the abaxial surface of the leaf, sclerenchyma well developed, often forming a continuous layer
Agropyron (*Elytrigia*) *junceum* (L.) BEAUV., *rechingeri* RUN., *distichum* (THUNB.) BEAUV., *magellanicum* HACK.
Elymus (s. NEVSKI) *arenarius* L., *mollis* TRIN., *giganteus* VAHL

2. Epidermal cells in section elliptic, walls sinuous, prickles and prickle-hairs rare, crown-cells always occurring above the veins, sclerenchyma never forming a continuous layer.
Agropyron (*Elytrigia*) *intermedium* (HOST) BEAUV., *pungens* PERS., *elongatum* (HOST) BEAUV., *varnense* VEL., *caespitosum* C. KOCH, *campestre* GREN. et GODR., *pertenue* (C. A. MEY.) NEVSKI, *firmiculmis* NEVSKI
Agropyron (*Agropyron* s.str.) *pectinatum* (MB.) BEAUV.
Agropyron (*Eremopyrum*) *triticeum* (GAERTN.) NEVSKI, *orientale* (L.) JAUB. et SPACH
Elymus (*Aneurolepidium*) *paboanus* CLAUS, *dasystachys* TRIN.

3. Epidermal cells in section irregular, walls sinuous or straight, very often with papills, prickles and prickle-hairs always present, crown-cells lacking, sclerenchyma never forming a continuous layer.
Agropyron (*Elytrigia*) *repens* (L.) BEAUV.
Agropyron (*Roegneria*) *caninum* (L.) BEAUV., *latiglume* (SCRIBN. et SM.) RYDB., *panormitanum* BERTOL., *mutabile* DROB.
Elymus (*Clinelymus*) *canadensis* L., *hirsutus* PRESL, *condensatum* PRESL

There is little reason to believe that the complicated structures of the leaf epidermis have evolved independently within different groups of *Elymus* and *Agropyron* as a result of adaptation to special ecologic conditions. Thus all three types found are represented in littoral, maritime species, as *Agropyron* (*Elytrigia*) *junceum*, *elongatum*, and *repens*.

To what extent the leaf anatomy is heterogenous within the genera established by NEVSKI cannot be estimated on the restricted material analysed. In the most intensely studied genus, *Elytrigia*, all three types have, however, been found.

Some remarkable agreements have to be accentuated. In leaf anatomy the *Agropyron junceum* group coincides with the *Elymus arenarius* group, to which attention had already been called by PRAT (1931). The species around *Agropyron* (*Elytrigia*) *intermedium* coincide anatomically with *Elymus* (*Aneurolepidium*) species, and *Agropyron* (*Elytrigia*) *repens* agrees with *Agropyron* (*Roegneria*) species (e.g. *A. caninum*). In all these cases the agreements found support affinities established on purely morphologic basis.

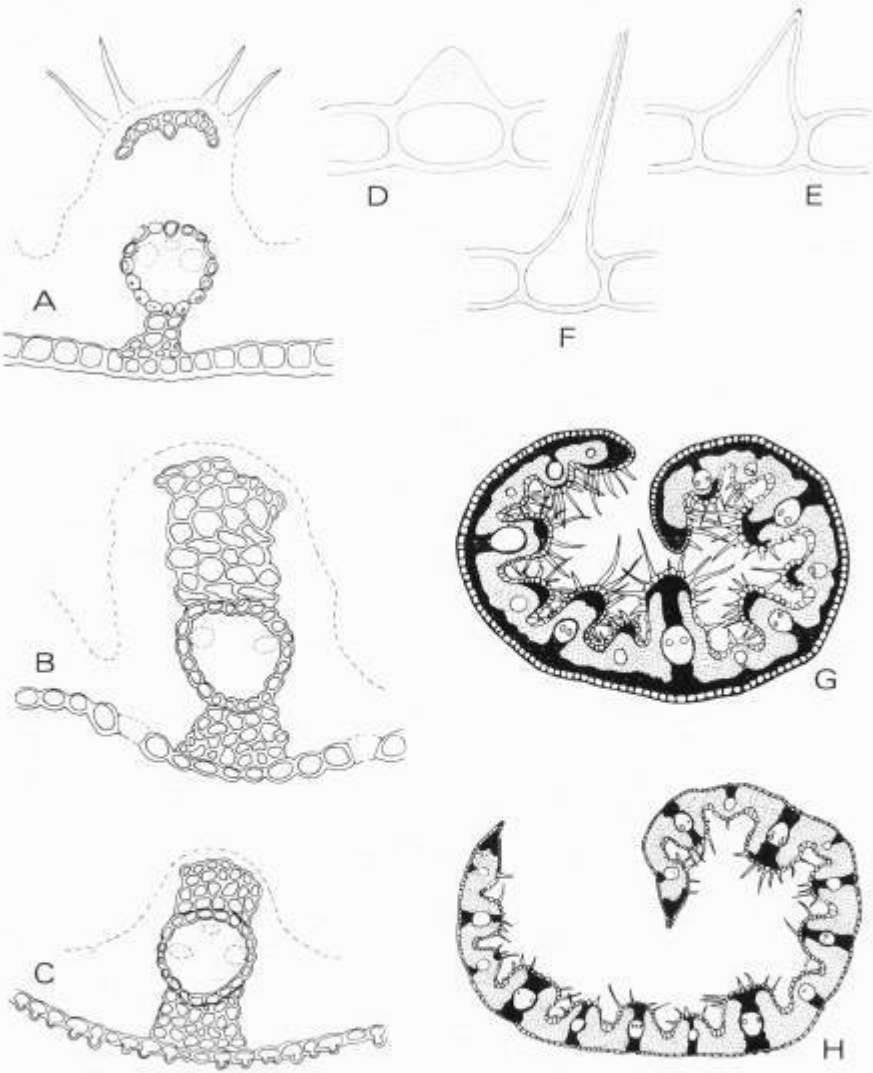

Fig. 1. Transversal sections of leaves illustrating different types of epidermal cells. A: *Agropyron* (*Elytrigia*) *rechingeri*. B: *Agropyron* (*Elytrigia*) *pungens*. C: *Agropyron* (*Elytrigia*) *repens*. — Specialized types of epidermal cells. D: "Crown-cell". E: Prickle. F: Prickle-hair. — Transversal sections of leaves illustrating the extension of sclerenchyma (black). G: *Agropyron* (*Elytrigia*) *junceum*. H: *Agropyron* (*Elytrigia*) *elongatum* ssp. *flaccidifolium*.

CYTOLOGY

Literature Records

A great number of cytologic and experimental studies on the *Agropyron-Elymus* complex have been carried out. Thus, e.g., material from southern and western Europe has been treated by CAUDERON (1958), HENEEN (1962, 1963), HENEEN and RUNEMARK (1962), material from southern Russia and south-western Asia by SARKAR (1956, 1958), material from New Zealand by CONNOR (1954, 1956), material from South America by COVAS (1949) and HUNZIKER (1966), and material from North America by STEBBINS et al. (1946 a, 1946 b, 1949, 1950, 1953, 1954, 1956 b), HARTUNG (1946), SENN et al. (1947), SNYDER et al. (1951), BROWN and PRATT (1960), SCHULZ-SCHAEFFER et al. (1962), BOWDEN (1964), and DEWEY (1967).

Some results of the studies are summarized below:

1. A great number of hybrids within *Agropyron* s.lat. and *Elymus* s.lat. have been produced or found in the field. Many hybrids were totally sterile, but a considerable number were more or less fertile, at least in backcrosses.

2. A great number of *Agropyron-Elymus* hybrids have been produced or found in the field. Most of them were wholly sterile, but exceptionally relatively fertile hybrids were obtained (cf., e.g., DEWEY 1967).

3. Extensive genome analyses in meiosis of hybrids have been performed, especially by STEBBINS et al. Comparisons of the genomes in different species based on chromosome morphology (especially of satellited chromosomes) have been made, e.g., by CAUDERON and SCHULZ-SCHAEFFER. STEBBINS and SNYDER (1956 b) have shown that a genome consisting of chromosomes essentially homologous to those of the diploid *Agropyron spicatum* (PURCH.) SCRIBN. et SM. is represented in the polyploids *Agropyron caninum* (L.) BEAUV., *parishii* SCRIBN. et SM., *trachycaulon* (LINK) MALTE, *Elymus glaucus* BUCHL., *virginicus* L., and almost certainly in *Sitanion jubatum* J. G. SMITH and *hystrix* (NUTT.) J. G. SMITH. The presence of this genome is also regarded as likely in other *Elymus* species such as *E. interruptus* BUCHL. and *villosus* MUHL., and perhaps even in *Hystrix patula* MOENCH. SARKAR (1958) showed that all species of *Eremopyrum* have a genome consisting solely of chromosomes with subterminal centromeres, a feature unique within *Triticeae*. Both diploids and tetraploids occur in the genus, and the tetraploids have in addition to the "*Eremopyrum*" genome, one of "normal" appearance.

4. Apparently introgression has played an important role in the differentiation within polyploids as shown, e.g., by SNYDER (1951) and BROWN and PRATT (1960).

Observations

The sources of the material used in the cytological observations are as follows:

Agropyron (*Elytrigia*) *junceum* (L.) BEAUV. ssp. *boreo-atlanticum* L. et L. — The same material as in HENEEN (1962).

Agropyron (*Elytrigia*) *repens* (L.) BEAUV. — The same material as in HENEEN (1962).

Agropyron (*Elytrigia*) *elongatum* (HOST) BEAUV. — Seeds obtained from JENKINS (produced at Winnipeg 1958, originally from MATSUMARA 1956) and from spontaneous material from Montpellier, France.

Agropyron (*Roegneria*) *caninum* (L.) BEAUV. — Seeds from Botanical Garden, Brno, Czeckoslovakia.

Agropyron (*Roegneria*) *latiglume* (SCHRIBN. et SM.) RYDB. s.lat. — Spontaneous plants from Kopparåsen, Torne Lappmark, North Sweden.

Elymus (*Elymus* s.str.) *arenarius* L. — Plants from the Botanical Garden, Copenhagen and spontaneous material from Lomma and Sandby Bäck, Skåne, South Sweden.

The technique described by ÖSTERGREN and HENEEN (1962) was used for the study of the somatic chromosomes.

The detailed karyotype of *A. junceum* ssp. *boreo-atlanticum* has been described by CAUDERON (1958) and HENEEN (1962). The chromosomes vary in length between about 5 to 8.5 µ, and have median or submedian centromeres (Fig. 2 E). Two pairs of chromosomes have secondary constrictions and are among the relatively large chromosomes in the complement. One pair has large satellites and the constriction divides the short arm into nearly equal parts, while the other pair has small satellites on the short arms. A faint constriction is occasionally seen near the end of the long arm in the pair with large satellites.

The chromosomes of *A. junceum* are larger than those of *A. repens*. The two species also differ as regards the morphology and size of the satellited chromosomes (HENEEN 1962). Differeces in chromosome size and in morphology of the satellited chromosomes also exist between *A. junceum* and *A. elongatum* (2n=14), *A. caninum* (2n=28) and *A. latiglume* (2n=28). The chromosomes of *A. junceum* are somewhat larger than in the other species of *Agropyron* mentioned. In *A. elongatum* and *A. caninum* the chromosomes vary in length between 4.5 and 7.5 µ while in *A. latiglume* the length range is 3.5 to 6 µ which is about the same as in *A. repens*. The mitotic chromosomes of *A. caninum*, *A. latiglume* and *A. elongatum* are shown in Fig. 2 A, B, D.

Diagrammatic drawings of the satellited chromosomes which can be detected in the different species studied are presented in Fig. 3. In *A. elongatum* and *A. caninum* the pair with large satellites has more median centromeres than the equivalent pair in *A. junceum*. The constriction divides the short arm into two unequal parts, the part proximal to the centromere is longer than the satellite, which is not the case in *A. junceum*. CAUDERON (1958), however, described these chromosomes to be similar in *A. junceum* and *A. elongatum*. The second pair with small satellites has somewhat smaller satellites than in the equivalent pair in *A. junceum*.

In *A. latiglume* only one satellited pair can be distinguished in the limited number of metaphase plates studied in this species. The secondary constriction is in about the middle of the short arm. This pair is among the relatively short chromosomes in the complement and looks much alike a similar pair in *A. repens* (HENEEN 1962).

In *Elymus arenarius* (2n=56) the chromosomes are of a relatively large size (4 to 8.5 μ) with median or submedian centromeres (Fig. 2 C). Three pairs of satellited chromosomes can be distinguished and are drawn diagrammatically in Fig. 3 D. They are among the largest chromosomes in the complement. In one pair, small tail-like satellites are attached to the short arms. This chromosome has about the same arm ratio as the chromosome with small satellites in *A. junceum* or *A. elongatum*. However, the satellite size is smaller than in the two *Agropyron* species. The other two satellited pairs are similar in their indices to the pair with large satellites of *A. junceum*. In one of these two pairs, the secondary constriction is in about the middle of the short arm, while in the other pair the constriction is near the end of the long arm.

DISCUSSION. Both *A. junceum* ssp. *boreo-atlanticum* and *E. arenarius* have somewhat larger chromosomes than in the other species of *Agropyron* studied, namely *A. elongatum*, *A. caninum*, *A. latiglume*, and *A. repens*.

There is a certain degree of similarity between *E. arenarius* and *A. junceum* in the morphology of the satellited chromosomes. This is especially with regard to the chromosome with large satellites of *A. junceum* and the possibility of its equivalence to the similar satellited

Fig. 2. Somatic chromosomes at metaphase. A: *Agropyron* (*Elytrigia*) *elongatum* ssp. *elongatum*. B: *Agropyron* (*Roegneria*) *latiglume* s.lat. C: *Elymus* (*Elymus* s.str.) *arenarius*. D: *Agropyron* (*Roegneria*) *caninum*. E: *Agropyron* (*Elytrigia*) *junceum* ssp. *boreo-atlanticum*. — A ×1400; B—E ×1120.

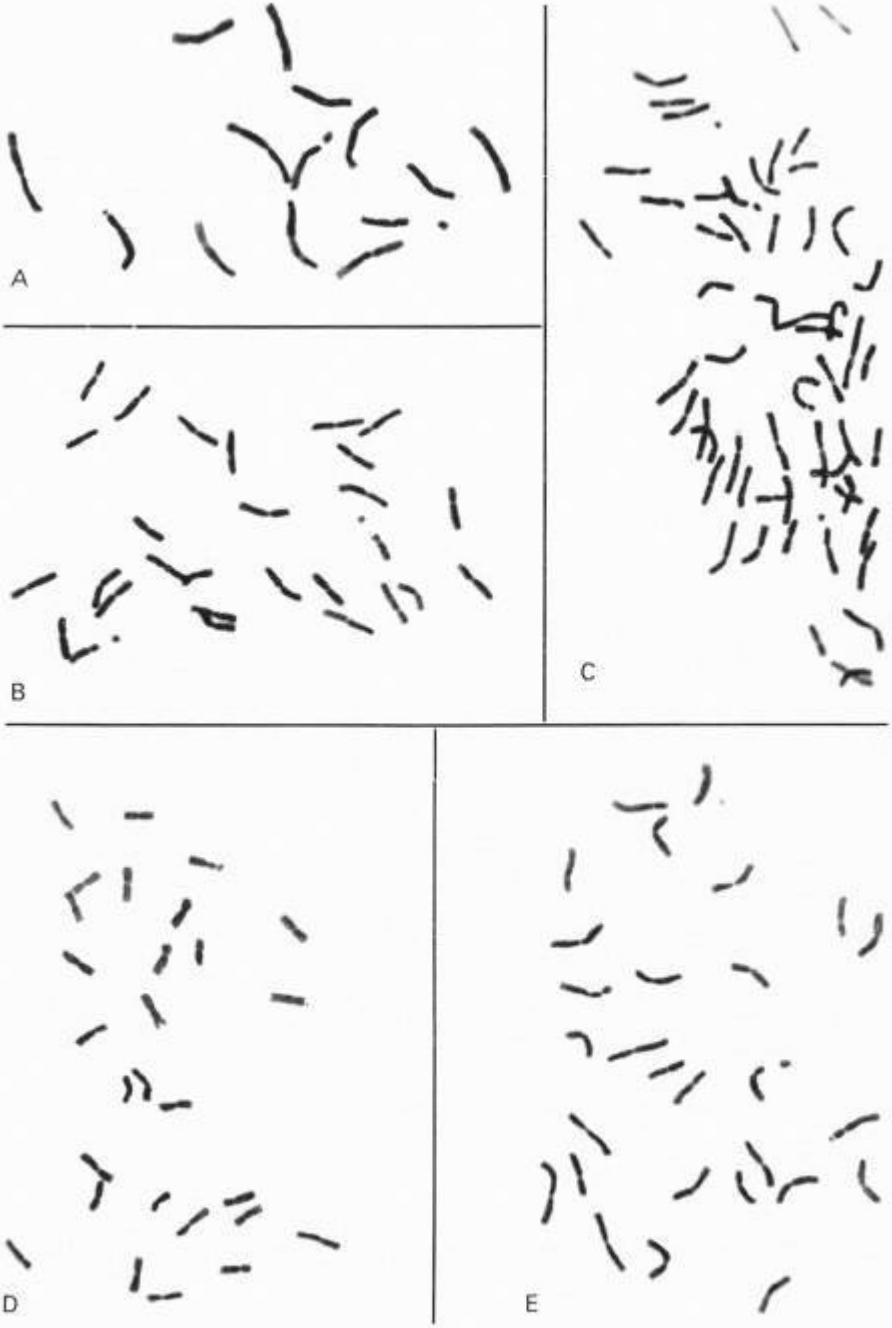

Fig. 2.

chromosome in *E. arenarius*. The same chromosome might even be equivalent to the satellited chromosome with the constriction located in the long arm which is characteristic of *E. arenarius*. The two chromosomes have the same arm index. Probably, the constriction in the short arm became inconspicuous whereas the faint constriction present near the end of the long arm is much accentuated. This chromosome shows such a phenotype in one of the two karyological types found in the natural pentaploid hybrid between *A. junceum* ssp. *boreo-atlanticum* and *A. repens* (HENEEN 1962). The disappearance of the nucleolar constriction present in the short arm was suggested to be due to structural, genotypical or cytoplasmic causes.

In *E. arenarius* the presence of the satellited chromosomes in pairs suggests an allopolyploid nature of this species. *A. junceum* or a related form of it might have been one of the ancestors of *E. arenarius*. The study of the intergeneric hybrid between the two species could be of some interest in this respect. From pairing studies in other hybrids between *Elymus* and *Agropyron* (e.g. STEBBINS and SINGH 1950; HUNZIKER 1955) it was found that they are closely related.

According to the size of the chromosomes and the morphology of the satellited chromosomes, the material investigated may be divided into three groups:

1. *Agropyron* (*Elytrigia*) *junceum*, *Elymus* (*Elymus* s.str.) *arenarius*. Chromosomes larger than in other species investigated. One pair of satellited chromosomes in common (not found in the other groups).

2. *Agropyron* (*Elytrigia*) *elongatum*, *Agropyron* (*Roegneria*) *caninum*. Chromosomes somewhat smaller than in the preceeding group. One pair of similar satellited chromosomes in common (not found in the other groups).

3. *Agropyron* (*Elytrigia*) *repens*, *Agropyron* (*Roegneria*) *latiglume*. Chromosomes smaller than in other species investigated. One pair of satellited chromosomes in common (not found in the other groups).

It is worth mentioning that the differences in chromosome size between *Agropyron junceum* and *repens* is maintained in their hybrid (HENEEN 1962).

From these data and from investigation by other authors it is evident that neither NEVSKI's subdivision nor the separation of the genera *Agropyron* and *Elymus* is in agreement with the cytologic information available.

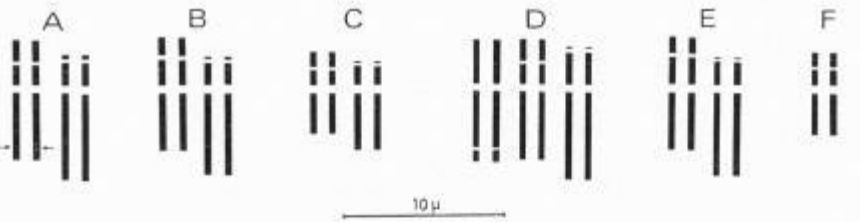

Fig. 3. Diagrammatic drawings of the satellited chromosomes in the *Elymus* and *Agropyron* species studied. The arrows indicate the position of faint secondary constrictions. A: *Agropyron* (*Elytrigia*) *junceum* ssp. *boreo-atlanticum*. B: *Agropyron* (*Elytrigia*) *elongatum* ssp. *elongatum*. C: *Agropyron* (*Elytrigia*) *repens*. D: *Elymus* (*Elymus* s.str.) *arenarius*. E: *Agropyron* (*Roegneria*) *caninum*. F: *Agropyron* (*Roegneria*) *latiglume* s.lat.

CONCLUSIONS

If a "genetic" genus concept is accepted, referring all species forming hybrids to the same genus, the consequences would probably be a single genus within *Triticeae* (cf., e.g., STEBBINS and SNYDER 1956 b). Such an enormous and extremely diverse genus would be very impracticable and has not been accepted by taxonomists. This radical step seems also unnecessary as a number of morphologically distinct groups can be distinguished, which also may reflect main trends in the evolution within *Triticeae*. Such groups, which are not given taxonomic rank, are briefly characterized below.

The Hordeum Group (*Hordeum, Hordelymus, Taeniatherum, Psatyrostachys, Critopsis, Critesion*)

Spikelets 2—3 together at a node, heteromorphic, with two florets (the second floret almost always rudimentary). Glumes placed in front of the florets. Palea curved or slightly bent in lateral parts.

The Henrardia Group (*Henrardia*)

Spikelets sunken in the spike axis, homomorphic, solitary, with 1—2 florets. Glumes enclosing the florets. Palea curved in the lateral parts.

The Elymus Group (*Elymus* s.lat., *Agropyron* s.lat.)

Spikelets solitary or 2—several together at each node, homomorphic, with 2—many florets, rarely with a single floret. Nerves of lemma confluent at the tip. Palea folded along the nerves, which are developed as sharp edges.

The Triticum Group (*Triticum, Aegilops*)

Spikelets solitary, homomorphic or heteromorphic (terminal spikelet differing in appearance), with 2—7 florets, 1—3 of which are sterile. Terminal spikelet at 90° angle to the other spikelets. Nerves of lemma parallel. Palea folded along the nerves, which are developed as sharp edges.

The Secale Group (*Secale, Haynaldia*)

Spikelets solitary, homomorphic, with 2—4 florets. Glumes ± subulate, with 1—2 nerves. Palea folded along the nerves, which are developed as sharp edges.

The Heteranthelium Group (*Heteranthelium*)

Spikelets solitary, heteromorphic (alternating fertile and sterile ones), with many florets (in fertile spikelets, 2 fertile and many clustered sterile ones). Glumes subulate. Palea folded along the nerves, which are developed as sharp edges.

The further subdivision of these groups into genera is at present rather obscure. Thus NEVSKI's splitting of *Hordeum* into 6 genera must be tested by using a combination of morphologic, anatomic, and genetic data. In the *Triticum* group *Aegilops* and *Triticum* most probably have to be united.

Within the *Elymus* group the species have traditionally been referred to *Agropyron* if the spikelets are solitary and to *Elymus* if they are placed in pairs or larger numbers at each node. This subdivision is apparently artificial [cf., however, HUTCHINSON's (1959) subdivision of *Triticeae*], the genera only represent levels in a reduction of a paniculate inflorescence. Thus, several species in *Agropyron* have their closest relatives in *Elymus* and vice versa.

To overcome this unsatisfactory situation NEVSKI (1932, 1933) subdivided the traditional genera into smaller "natural" entities, in this way creating a number of genera, which could be placed in an appropriate position within an evolutionary system. An examination of NEVSKI's system gives the following results:

1. The genera proposed are in most cases not distinct, i.e., they cannot by morphologic characters or combinations of characters be distinguished from other genera (e.g., *Elytrigia-Roegneria, Elytrigia-Aneurolepidium-Clinelymus, Clinelymus-Sitanion*). In some cases small

groups of species or single species constitute new genera (*Elymus* s.str. sensu NEVSKI, *Agropyron* s.str., *Malacurus*, *Terrella*), which are morphologically circumscribable. However, if groups like these are regarded as genera, several other species groups (e.g., the *Agropyron junceum* group) also deserve generic rank.

2. In spite of the strong subdivision made by NEVSKI the large genera (*Elytrigia*, *Aneurolepidium*, *Clinelymus*, and probably *Roegneria*) are composed of discordant elements. The genus *Elytrigia* can be discussed as an example. On morphologic, anatomic, and cytologic grounds the European material of this genus can be subdivided into three groups with wholly different affinities: (1) the *junceum* group, which is morphologically similar to and in anatomy and chromosome morphology coincides with *Elymus* s.str.; (2) the *elongatum* group, which coincides with species of *Aneurolepidium* as regards anatomy and morphology (cytologically the *Aneurolepidium* species in question have not been investigated); (3) the *repens* group, which in anatomy and chromosome morphology and to a certain extent also in morphology coincides with *Roegneria*.

To fulfil NEVSKI's intention of establishing "natural" genera in the *Agropyron-Elymus* complex it would therefore be necessary to split a number of his genera into smaller entities. An attempt in this direction was made by DROBOV (1941) in Flora Uzbekistanica, where *Roegneria* was split into three genera (*Roegneria* s.str., *Semeiostachys* gen. nov., and *Campelostachys* gen. nov.). The result would evidently be chaotic, with genera still more difficult to circumscribe morphologically.

Even from the theoretic point of view such a treatment is precarious. As far as can be seen a number of "primary", well delimited groups of diploids exist in the *Agropyron-Elymus* complex. However, by allopolyploidy between representatives of different primary groups intermediates and intermediate groups of species have been established, obscuring an originally distinct delimitation. Thus a complicated network of relationships exists, as polyploidy has played an unusually great part in the evolution within the complex, probably favoured by the high degree of vegetative propagation (many polyploid species have very low seedsetting, cf. NEVSKI 1933).

For reasons discussed above, NEVSKI's subdivision of the *Agropyron-Elymus* complex or an even more rigorous subdivision serves neither practical nor theoretical aims.

To avoid an artificial taxonomic subdivision of the *Agropyron-Elymus* complex I find it necessary to unite the traditional genera *Agropyron* and *Elymus* (correct name of the united genus *Elymus* L.). This decision is founded mainly on an examination of European material. GOULD (1947) came to the same conclusion in his studies of North American (mainly Californian) material. MELDERIS, who previously accepted NEVSKI's subdivision of *Agropyron*, has also found it impossible to keep *Agropyron* and *Elymus* as separate genera (personal communication 1960) in connection with his studies of Asiatic material. Thus three different investigators, mainly treating material from different parts of the world, have independently come to the same conclusions.

Within the *Agropyron-Elymus* complex a few morphologically characteristic groups composed of a few related species have been kept by many botanists as separate genera, viz., *Eremopyrum*, *Taeniatherum*, *Sitanion*, and *Hystrix*.

Eremopyrum consists of the annual species in *Agropyron* s.lat. On account of the morphologic peculiarities of the spikelets (glumes basally connected and with cartilaginous margins) and the deviating chromosome morphology it seems defensible to keep it as a separate genus as suggested by SARKAR (1958).

Taeniatherum consists of the annual species in *Elymus* s.lat. On account of the morphology of the palea the genus must be excluded from the *Elymus* group and referred to the *Hordeum* group, as has already been suggested by many authors for other reasons.

The genus *Sitanion* (referred by NEVSKI to *Hordeinae*) must without any doubt be included in *Elymus* both for morphologic reasons (cf. GOULD 1947) and because of cytologic and experimental data presented by STEBBINS et al.

The genus *Hystrix* is rather outstanding morphologically. Depending on similarities between North American *Hystrix* and *Elymus* species, GOULD included the genus in *Elymus* s.lat. Cytologic and experimental data confirming the affinities are very much required, however.

The taxonomic consequences of the considerations above will be a subdivision of the *Elymus* group into two genera as follows:

Elymus L.

(Incl. *Agropyron* GAERTN., *Elytrigia* DESV., *Roegneria* KOCH, *Aneurolepidium* NEVSKI, *Clinelymus* NEVSKI, *Terrella* NEVSKI, *Hystrix* MOENCH = *Asperella* HUMB., *Sitanion* RAF.)

Glumes not connected basally. Perennials.

Eremopyrum Jaub. et Spach

Glumes connected basally, becoming cartilaginous. Annuals.

A considerable number of nomenclatural changes on the species level are necessary as a consequence of the new subdivision. No such changes (mostly new combinations) are published in this treatise. They ought instead to be made in connection with revisions and the treatment of the *Elymus* group in regional floras.

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Miscellaneous Notes on Algal Taxonomy and Nomenclature, II

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ABSTRACT

The notes refer to problems of taxonomy and nomenclature in marine *Rhodophyta*.

1. Typification of *Conferva pennata* HUDS. shows that it is referable to the *Phaeophyta*: this is discussed in relation to the red alga *Pterosiphonia pennata* (C. AG.) FALKENB.

2. *Ceramium armoricum* nom. nov. is proposed as a substitute for *C. pennatum* J. AG., non *C. pennatum* (HUDS.) ROTH.

3. *Rytiphloea pumila* C. AG. is shown to be based on a mixture of two species, referable to *Polysiphonia* and *Sphacelaria*.

4. Typification of *Fucus cristatus* L. ex TURN. is discussed in relation to the nomenclature of *Euthora cristata*.

The following notes refer to taxonomical and nomenclatural problems detected during preliminary work for the forthcoming "*Flora of British Marine Algae*."

Pterosiphonia pennata (C. AG.) FALKENB.

The earliest description of the alga known currently as *Pterosiphonia pennata* in usually regarded as that given by ROTH (1800) under the name *Ceramium pennatum*. His name is, however, not based on that description because *Conferva pennata* HUDS. is cited as a synonym and it should be appreciated that the latter is also accepted at the present time as the basionym of a brown alga *Sphacelaria pennata* (HUDS.) LYNGB. The identity of *Conferva pennata* HUDS. is therefore the crucial problem requiring consideration.

The original treatment of *Conferva pennata* by HUDSON (1762 p. 486) is as follows:

"34. CONFERVA filamentis geniculatis ramosis, ramis duplicato pinnatis fuscis.
Conferva marina pennata. *Pet. hort. sicc. R. Syn. 59. Anglis.* Feathered Conferva.
Habitat *in littore marina inter* Margate *et* Dover, *R. Syn. In littore insula* Walney."

This description is based on three elements:

1. Material from Walney Island, Lancashire, which must now be assumed to be lost (DIXON 1959).

2. Material referred to RAY's *Conferva marina pennata* in PETIVER's herbarium. The PETIVER collection forms part of the SLOANE Herbarium (DANDY 1958), preserved at the British Museum (Natural History), but it is not now possible to locate therein any material identified as "*Conferva marina pennata.*"

3. The description of *Conferva marina pennata* given in the third edition of RAY's "*Synopsis methodica stirpium britannicarum*" (RAY 1724) edited posthumously and anonymously by DILLENIUS. The description of *Conferva marina pennata* by RAY is based directly on the alga described by MERRET (1666) under the name *Corallina comis ad instar caudae vulpinae sparsis* and RAY's *Conferva marina pennata* must be typified by MERRET's material. MERRET's herbarium now forms part of the SLOANE Herbarium (DANDY 1958), but the identifications on the specimens are so confused that it is not now possible to identify the MERRET specimens in question, should they have been preserved.

It is therefore impossible at the present time to locate the original material of any of the three elements cited by HUDSON in the initial description of his *Conferva pennata*. It is possible that this binomial was based on material referable to the genus *Sphacelaria* as now understood, but this cannot be proved. Because of the citation of *Conferva pennata* HUDS. in ROTH's treatment of *Ceramium pennatum*, the latter binomial has the same type as *Conferva pennata* HUDS. whatever material have been referred to it by ROTH. ROTH's herbarium was destroyed during the second World War (PILGER 1953), but there is a specimen in the AGARDH Herbarium at the Botanical Museum, Lund, which the annotations suggest was received from ROTH and identified by him as "*Ceramium pennatum.*" This specimen [Herb. Alg. Agardh. 39271], which is of the alga now known as *Pterosiphonia pennata*, could well have formed part of ROTH's original material. The error was appreciated subsequently by ROTH (1806 p. 133), following the receipt of material of a *Sphacelaria*

species from DAWSON TURNER, the latter stating that this was the "true" *Conferva pennata* of HUDSON. ROTH, in attempting to correct his error, renamed the wrong entity and was unfortunately responsible for the present confusion. The epithet *pennata* was retained for the *Pterosiphonia* species and the HUDSON synonym was considered conspecific with *Conferva cirrosa* WULF. ex ROTH (1800 p. 214). From this discussion, it is clear that the name *Ceramium pennatum* based on *Conferva pennata* HUDS., cannot be applied to the species of *Pterosiphonia* under discussion.

Certain synonyms have been applied to the species of *Pterosiphonia* under discussion but none of these antedates *Hutchinsia pennata* C. AGARDH (1824), the first legitimate usage of the epithet *pennata*. *Conferva mollis* of DRAPARNAUD, although published in synonymy by many early authors, e.g. ROTH (1806) and AGARDH (1824), was never validly published, like so many of the binomials attributed to him (cf. SILVA 1952). AGARDH (1824 p. 164) includes in the synonymy of *Sphacelaria cirrhosa* the statement "*Conf. pennata*, Dillw. t. 86. — Huds." so that his citation "*Ceram. pennatum*, Roth" under *Hutchinsia pennata* (AGARDH 1824 p. 146) may be taken to imply what would be written today as "*Ceramium pennatum* ROTH, *pro parte, non Conferva pennata* HUDS." This is clearly a case where Article 72 of the International Code of Botanical Nomenclature may be applied. *Hutchinsia pennata* is therefore a legitimate name, whose holotype was lost with ROTH's herbarium, but of which the specimen now at Lund [Herb. Alg. Agardh. 39271] is an isotype. The correct name for the species is *Pterosiphonia pennata* (C. AG.) FALKENB.

Ceramium pennatum J. G. AG.

Previously (DIXON 1962) a brief discussion was given of the typification of *Ceramium pennatum* J. AG. It was not then appreciated that this binomial is a later homonym of *Ceramium pennatum* (HUDS.) ROTH, discussed in the present paper. The alga described by J. G. AGARDH (1851) under the name *Ceramium pennatum* is still retained in that genus (cf. PARKE & DIXON 1964) and no other name has ever been applied to it. A new epithet is therefore required for this taxon. It would have been appropriate to commemorate either J. G. AGARDH (the describer of the taxon) or the brothers CROUAN (who collected the original material on which the description was based) but combina-

tions using epithets derived from their names exists already in the genus *Ceramium*. The new epithet proposed, *armoricum*, is indicative of the region from which the taxon was originally collected.

Ceramium armoricum nom. nov.

=*Ceramium pennatum* J. G. AGARDH, Sp. Gen. Ord. Alg. 2: 136 (1851).

non *Ceramium pennatum* (HUDS.) ROTH, Catalecta Bot. 2: 171 (1800).

The type of *Ceramium armoricum* is the type of *C. pennatum* J. AG. designated previously (DIXON 1962).

The Identity of Rytiphloea pumila C. AG.

Rytiphloea pumila C. AGARDH (1827) was described from material collected at Trieste. Subsequently, it has been considered by many authors (cf. DE TONI 1903) to be a synonym of *Pterosiphonia pennata*. However, examination of the original material, now preserved in the AGARDH Herbarium at the Botaniska Museet, Lund, shows that the single specimen [Herb. Alg. Agardh. 39263] consists of tangled clumps of material containing several species of algae. The components present in greatest quantity consist of a species of *Polysiphonia* with four pericentral cells and a *Sphacelaria*, but with no trace of any representative of *Pterosiphonia* as now understood. The various thalli in the clumps of material are minute and very entangled. Without total destruction it is not possible to state categorically that the type specimen of *Rytiphloea pumila* C. AG. does not contain any material of *Pterosiphonia*, but if any is present it cannot constitute more than a minute fraction of the whole. It would appear most probable that the original descripion of *Rytiphloea pumila* was a misinterpretation involving the two genera, *Sphacelaria* and *Polysiphonia*, which occur most abundantly in the type material. The overall form of the plant was described from the *Sphacelaria* fragments, while the cellular detail was taken from the *Polysiphonia*. The name *Rytiphloea pumila* accordingly cannot be considered to apply to the species of *Pterosiphonia* with which it has been associated.

A Study of Euthora cristata

Euthora cristata is widely distributed on both sides of the North Atlantic Ocean. A routine typification of the basionym during the pre-

paration of the 'Flora of British Marine Algae' disclosed a very confused situation. The generally accepted usage of the basionym was shown to be a *nomen nudum*, the eventual valid publication of this was found to be an illegitimate name because of an earlier homonym, and there was confusion with totally unrelated members of the *Rhodomelaceae*.

The first description of *Euthora cristata* was published by TURNER (1808) as *Fucus cristatus*, on the basis of material preserved in the Linnaean herbarium, and this description was accompanied by figures of Linnaean specimens. TURNER states quite clearly that the specimens were attached, together with some fragments of other species, to a sheet inscribed "*cristatus*" in LINNAEUS's hand. Thus, the epithet and type material are of Linnaean origin but there is no evidence to indicate that LINNAEUS ever published a description of the material in question, or applied the epithet to this or any other taxon. Because of this, the authority for the binomial has been widely misquoted, TAYLOR (1937, 1957) being one of the few authors to appreciate that *Fucus cristatus* L. is a *nomen nudum* and to cite the authority for *Euthora cristata* correctly as "(L. ex TURN.) J. AG." *Fucus cristatus* L. ex TURN. is, however, an illegitimate later homonym of *F. cristatus* WITHERING (1796). The citation by WITHERING of *Ulva ramosa* HUDSON (1762) and a reference to the later treatment by HUDSON (1778) of *Fucus crispatus* L. in the synonymy of his *Fucus cristatus* suggest that WITHERING applied the latter binomial to the alga now known as *Cryptopleura ramosa*.

Because of the similarity between the two epithets *crispatus* and *cristatus*, it might be questioned whether the *cristatus* of WITHERING was nothing more than a typographic error. This would appear to be most unlikely, in that WITHERING (1796) cites *cristatus* consistently in both text and index, and the epithet is repeated in subsequent editions of the work (WITHERING & WITHERING 1801, 1812, 1830). Thus, although *Fucus cristatus* WITHERING is a superfluous name (because of the citation of synonyms in the original treatment) it cannot be dismissed as a mere typographic error. TURNER (1802 p. 151), in his earliest comments on the material annotated by LINNAEUS as *cristatus*, also considered the possiblity that a typographic error might be involved, stating "it must, therefore, be supposed either that the specimen in question was intended to have been so called in some future publication, or that he purposed writing *crispatus*." Later, with the publication of the description of *Fucus cristatus*, TURNER (1808) accepted the

first supposition. One explanation which does not appear to have been considered is that the name written on the sheet by LINNAEUS may not have been intended to refer to the alga to which it was subsequently applied. As stated previously, there are fragments of two other algae attached to the sheet; these belong to the species currently known as *Phycodrys rubens* and *Membranoptera alata*. It is possible that the name *cristatus* had been intended for either of these two Delesseriaceous algae but, whatever the intentions of LINNAEUS may have been, the Linnaean material described and figured by TURNER under the name *Fucus cristatus* is referable to the alga now known as *Euthora cristata*.

Thus, both *Fucus cristatus* WITHER. and *F. cristatus* L. ex TURN. are validly published but illegitimate names, the latter because it is a later homonym of the former. Although not strictly relevant to a consideration of the correct name for the species, the two infraspecific taxa associated with *F. cristatus* in the original treatment (TURNER 1808) merit some consideration because they indicate the confusion prevailing at the time of the initial description of the taxon and, in turn, they were the cause of many of the later difficulties. Of the two infraspecific taxa, the β *valentiae* was based on material from the Red Sea. The figures given by TURNER (1808 Pl. 23 Figs. f, g) are not sufficient for identification and in view of the absence of the original material, which cannot now be located in the Herbarium of the Royal Botanic Gardens, Kew, it is not possible to comment on the identity of the β *valentiae*. The second intraspecific taxon, γ *articulatus* is based on material from the Mediterranean Sea and near Bayonne, collected by MERTENS. The figure given by TURNER is clearly of a Rhodomelaceous alga, bearing no relation to the species of *Euthora* under discussion. Furthermore, as was also the case with β *valentiae*, the two original localities are well to the south of the southern limit of distribution of *Euthora*. Two specimens, now in the Herbarium of the Royal Botanic Gardens, Kew, are probably the original material on which TURNER based his treatment of *F. cristatus* γ *articulatus*. One of these is annotated "Fucus cristatus Linn. Bayonne IX" in MERTENS' hand, while the other is labelled "Lapudi coll. Klutsciss" in the same hand. Both specimens are referable to the genus *Pterosiphonia*, as now understood, not to *Euthora*. How this material came to be associated with the *Euthora* specimens of the Linnaean herbarium is not known although, as will be seen, the confusion resulting from this association continued for some considerable time.

In order to determine the correct name for the alga known currently as *Euthora cristata*, two alleged synonyms must be examined critically as well as the epithet *cristata* from its first legitimate usage (by article 72 of the International Code of Botanical Nomenclature). In fact, neither of the two alleged synonyms is applicable. The first epithet is derived from *Fucus corymbiferus* GMELIN (1768), which was stated by TURNER (1802) "to be the *F. cristatus* Linn." It is difficult to see why this statement should have been made and it was subsequently rejected by him (TURNER 1808). The original material of *Fucus corymbiferus* GMEL. was collected in Kamtschatka and the Mediterranean Sea, both localities outside the range of the species under discusson. The type material cannot now be located but the illustration is reasonably good and the general concensus of opinion refers *Fucus corymbiferus* to the genus *Odonthalia*. This suggested relationship between *F. cristatus* and a Rhodomelaceous alga cannot be explained. The second epithet, is derived from *Gigartina fabriciana* LYNGBYE (1819), which was described on the basis of material collected in Greenland. The subsequent nomenclatural transfers are a little complex but, briefly, the entity was given infraspecific status under *Sphaerococcus cristatus* by C. AGARDH (1822), then regarded as a species of *Rhodomenia* (=*Rhodymenia*) by J. G. AGARDH (1841), and later transferred to *Euthora* by the latter (J. G. AGARDH 1847). Finally, having appreciated that his own material was not conspecific with LYNGBYE's original specimens, J. G. AGARDH (1852) retained his own material in the genus *Euthora* and compared the LYNGBYE specimens with *Delesseria rostrata*, which is now referred to the Delesseriaceous genus *Pantoneura*. Examination of the original LYNGBYE material of *Gigartina fabriciana* in the Botanical Museum, Copenhagen, and isotype fragments in the AGARDH Herbarium at the Botanical Museum, Lund [Herb. Alg. Agardh. 31766] confirms that this entity is referable to *Pantoneura* and is not synonymous with the species of *Euthora* under discussion. There are thus no epithets derived from synonyms applicable to the species under discussion. There is therefore no alternative to adopting the epithet *cristatus* from its first legitimate usage. Although it might appear that LAMOUROUX (1813) was the first author to transfer the entity from the genus *Fucus*, investigation shows that this conclusion cannot be accepted. LAMOUROUX, in his treatment of *Plocamium cristatum*, cites "*Fucus cristatus* Herb. Linn." as the alleged basionym. This is *not* a reference to the first valid publication of *Fucus cristatus* by TURNER, in that LAMOUROUX distinguished clearly between the citation under *Plocamium cristatum* and the cita-

tions of TURNER's publication under other species. Moreover, from the illustrations given (LAMOUROUX 1813 Pl. 2 Figs. 1, 2, 3), which are of a species of *Pterosiphonia*, it would appear that at some time LAMOUROUX had examined or had information on the original MERTENS material on which *Fucus cristatus* γ *articulatus* was based. It would thus appear very probable that LAMOUROUX intended the binomial *Plocamium cristatum* to refer to a species of *Pterosiphonia*, an opinion supported by the occurrence of specimens of *Pterosiphonia complanata* in the herbarium of BONNEMAISON, a close friend of and co-worker with LAMOUROUX, now preserved in the Bibliothèque Municipale, Quimper, identified by him as "*Plocamium cristatum* Lamour." No description is given by LAMOUROUX of *Plocamium cristatum* and there is no reference to a previously published valid description so that the latter binomial is a *nomen nudum*. Because of this, it must be ignored in any discussion of the nomenclature of the species of *Euthora* under discussion. C. AGARDH (1817) in transferring the taxon to the genus *Sphaerococcus* must be recognized as the first author to treat it other than as a species of *Fucus*.

The correct binomial and authority for this alga is, therefore, *Euthora cristata* (C. AG.) J. G. AG. The type of *Sphaerococcus cristatus* C. AG. is the type of *Fucus cristatus* L. ex TURN., that is, the material mounted on sheet 1274/69 of the Linnaean Herbarium and figured by TURNER.

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Studies in the Ecology of Baltic Sea-Shore Meadows
I. Some Chemical Properties of Baltic Shore-Meadow Clays

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ABSTRACT

The present paper is a study concerning certain chemical properties of some heavy clays from a sea-shore meadow in the parish of S:t Anna, province of Östergötland. The amounts of major metal elements dissolved in the soil water, adsorbed by the soil colloids and contained in the minerals are mapped according to a terminology, adapted to the present study. Particularly emphasized are the adsorption properties of the major metal cations and the acid release of metals from unexchangeable fractions of the soil. Measured gradients in the exchangeable amounts of different cations are also discussed on the basis of an ion exchange experiment. The ecological importance of separating the amounts originating from the soil solution from the amounts truly exchanged, both obtained together in routine extractions with neutral salt solutions, is discussed in respect to sodium.

INTRODUCTION

The present study is intended to illustrate certain chemical properties of some heavy clays from a sheltered sea-shore meadow in the province of Östergötland. Particularly emphasized are the adsorption properties of the more important metal cations and their occurrence in the soil solution, on the interior surfaces and in the minerals.

In the study of the adsorption properties of the metal cations, aqueous solutions of NH_4Ac in various concentrations have been used, being an easily available and commonly used non-metallic neutral salt. Data published in this context may contribute to the interpretation of other data obtained by NH_4Ac-extractions on these and similar clayish soils in more extensive routine work. Comparative extractions with HCl, HAc and ethanol, as well as total digestion and measurements in the press-water fraction, contribute to a more detailed knowledge of the occurrence and distribution of the more important metal ions in these shore-meadow clays. Information of this kind is not only of a theo-

retical importance. A knowledge of the chloride gradients or extractable amounts of various elements on different levels of the sea-shore may often be an insufficient basis for the interpretation of certain soil — plant relationships. A more detailed study in the distribution of the major metal cations, e.g. between the soil solution and the soil colloids, may be essential or even necessary to the understanding of differences in the uptake of these elements between various stands or plant communities.

FIELD METHODS AND VEGETATION

On the 17th of September 1967, samples were taken at four points, situated on and above the sea-shore meadow at Älskär (Fig. 1) on the island-chain Yxnö—N. Finnö, ca. 125 km SSW Stockholm. The locality has been described briefly in a previous paper (TYLER 1967). The vegetation of these four sampling points (in the following called point A, B, C, and D), representing different levels and plant communities in the zonation of the shore, is listed in Table 1.

Point D is situated in a dense *Deschampsia caespitosa*-meadow well above the sea-shore meadow proper, thus nowadays never submerged by the sea. The floristic composition of this epilitoral meadow is quite different from the vegetation of the shore-meadow, and all species with a distribution confined to sea-shores are lacking. Sampling point C is situated in the upper part of the geolitoral, just below the distinct "*Deschampsia* limit" (cf. Fig. 1). It is occasionally reached or even submerged by the sea, though very rarely in the spring and summer months. In the vegetation of point C, *Carex nigra*, *Potentilla anserina* and *Leontodon autumnalis* are most conspicuous, but all more important shore-meadow species are already represented. On points A and B, these shore-meadow species predominate with *Juncus gerardi*, *Plantago maritima*, and *Glaux maritima* as the most important representatives, but point B is further characterized by the presence of *Festuca rubra* and several other species present in C but absent in A (Table 1). During the winter half of the year, points A and B are often submerged, sometimes continuous for weeks, or covered by ice, but in the summer only point A is reached more or less regularly, point B sometimes being above the level of the sea for months.

On each of these points 10 samples were cut out vertically with standard steel cylinders (385 cm^3, length 100 mm), distributed over an area of about 0.5 square metre. Throughout, the samples were taken

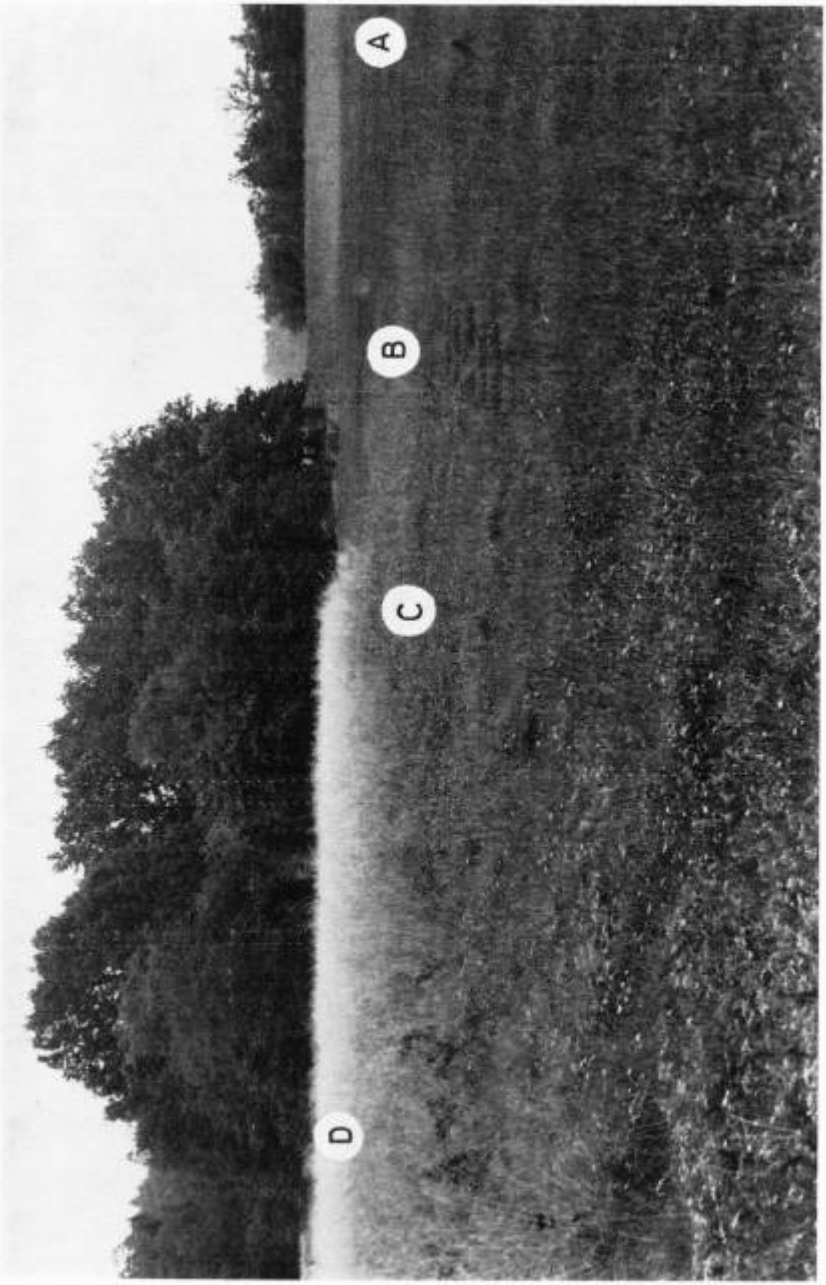

Fig. 1. The sea-shore meadow at Ynnö Älskär with the location of the sampling points. Sept. 17, 1967.

Table 1. Floristic composition of the vegetation on the sample points. Degrees of cover according to HULT-SERNANDER-DU RIETZ. Size of sample area 4 square metres.

	Sea-shore meadow			Terrestrial meadow
Sample point	A	B	C	D
Eleocharis uniglumis	1	.	.	.
Triglochin maritimum	1	1	1	.
Glaux maritima	2	3	1	.
Plantago maritima	2	4	1	.
Juncus gerardi	5	2	1	.
Agrostis stolonifera	3	1	2	.
Trifolium fragiferum	.	1	.	.
Trifolium repens	.	1	.	.
Campylium polygamum	.	5	2	.
Poa pratensis ssp. *irrigata*	.	1	1	.
Leontodon autumnalis	.	1	4	.
Festuca rubra	.	2	2	1
Potentilla anserina	.	1	3	1
Carex nigra	.	.	4	.
Carex panicea	.	.	1	.
Galium palustre	.	.	1	1
Agrostis tenuis	.	.	1	2
Ranunculus acris	.	.	1°	1
Deschampsia caespitosa	.	.	1	5
Elytrigia repens	.	.	.	3
Brachythecium sp.	.	.	.	2
Geum rivale	.	.	.	1
Galium uliginosum	.	.	.	1
Ranunculus repens	.	.	.	1
Galium verum	.	.	.	1
Rumex acetosa	.	.	.	1
Achillea millefolium	.	.	.	1

at the depth of 20—30 cm (the upper edge of the cylinder 20 cm below the level of the ground). At the same level a larger sample was collected close to every second cylinder sample, without determination of volume. The soil on all points were heavy clays without discernible interspersion with organic matter. Only scattered single roots occurred, penetrating from the shallow rhizophere proper.

All samples were transported to the laboratory in double polythene bags for temporary storing in a cold store at ca. +4°C.

LABORATORY METHODS

The weights of the intact samples were determined and the samples cut finely in order to separate scattered gravel and single stones from the fine earth (sand—clay). The heavy clay made sifting impossible. Stones and gravel, removed by hand, were washed and weighed; these weights were subtracted

from the weights of the intact samples for calculation of g fresh fine earth per dm^3 intact soil.

From all samples 25 g of fresh fine earth were extracted with 100 ml of the following solutions on a rotating board for 10 hours: 1.0, 0.5, 0.2, 0.05 and 0.02 M NH_4Ac and 1.0 M HCl; every second sample with 1.0 M HAc and 40 % ethanol as well. Immediately after the extractions the samples were filtered (Munktell Filtering Paper 1 F), the filtrates collected and stored in closed polythene bottles. In addition, every second sample was shaken with 0.5 M NH_4Ac and then leached with another 500 ml of this solution in five portions during two days for determination of total exchangeable amounts of metal cations.

Determination of water contents of the fine earth was carried out gravimetrically by drying at 105°C.

About 500 g of fine earth from each of the large samples were treated for 1—2 days in a pressure-membrane apparatus (cf. RICHARDS 1941) with a pressure of 15 atm. for subsequent determination of the cation amounts dissolved in the soil solution. The draining water was collected, though the first 10—15 ml were not included to avoid the effect of a slight ion exchange by the membrane used.

Digestion was performed with HF—HCl-technique, described by PAWLUK (1967), for determination of total amounts of metals and silica.

Determination of metal cations (Na, K, Mg, Ca, Mn, and Fe) was performed by means of atomic absorption (Perkin-Elmer Atomic Absorption Spectrophotometer Mod. 303, acetylene-air burner) directly in the extracts after appropriate dilutions, Mg and Ca in the HCl- and total digestion extracts with 1 % $LaCl_3$ in samples and standard solutions. Total Al was determined in the total digestion extracts, using a high-temperature acetylene-N_2O burner. In all, the study is based on ca. 2200 cation determinations.

Chloride was analyzed titrimetrically in the press-water fraction with 0.05 or 0.02 M $AgNO_3$ and K_2CrO_4.

Silica was determined gravimetrically after ignition as the HCl-insoluble residue from the total digestion.

Mechanical analysis was performed on the fresh fine earth with the hydrometer method (cf. GANDAHL 1952).

CALCULATION OF TOTAL ERRORS

As previously mentioned, 5 or usually 10 determinations were carried out from each of the sampling points. Total errors (analytical and sampling errors combined), chiefly depending on inhomogeneities of the substrate, are calculated as standard deviation of the means, according to HENRYSSON (1962 p. 23).

TERMINOLOGY

The following terminology is particularly adapted to the present study. In the subsequent text, as well as in figures and tables, the cor-

responding abbreviations are usually given. As the basis of calculation one gram of fresh fine earth has been used throughout.

Extractable (Ext) is a neutral term, referring to all cation fractions obtainable in extractions with various solutions.

Dissolved (D). The cation fraction found in the press-water is considered to belong to the soil solution and designed dissolved (D).

Leachable (L). Cation fractions obtained by leaching with a strong neutral salt solution, in the present case 0.5 M NH_4Ac, are designed leachable (L). Fraction D is included.

Exchangeable (Exc) and total exchangeable (Exc_t). The cation fraction obtained by equilibrium extraction with neutral salt solutions, reduced by the corresponding value of D, is called exchangeable (Exc) with this solution and total exchangeable (Exc_t), obtained by the leaching procedure. Distinction is thus made between exchangeable and extractable. Exc_t is considered a direct measure of the cation fraction adsorbed by the soil acidoids (cf. e.g., BLACK 1957 p. 102).

Total in minerals (M_t) comprises the total contents (T) of the element in the sample, obtained by HF-HCl-technique, after subtraction of Leachable (L; Exc_t+D). It includes metals in primary or secondary minerals, possible occurring fixed potassium, iron precipitated as ferric compounds, etc. With 1 M HCl these unleachable fractions are partly extractable ($Ext_{HCl}-L$), partly unextractable (M).

Briefly, the following simple relationships are valid for the facts mentioned above:

$T=M_t+Exc_t+D$

$Exc_t+D=L$; $M_t=M+Ext_{HCl}-L$

In equilibrium extractions with neutral salt solutions the equilibrium is gradually established between the cations still adsorbed on the soil particles and those dissolved in the extract. If the neutral salt solution is sufficiently concentrated (e.g., 1.0 M NH_4Ac), the metal ions adsorbed are almost quantitatively replaced by NH_4^+. The values of $Exc_{1\ M\ NH_4^+}$ thus usually approach Exc_t, obtained by leaching.

CONVERSION TO VOLUME AND DRY WEIGHT UNITS

As basis of calculation the weight of fresh fine earth has been used throughout. However, field sampling and laboratory methods also allow calculation on dry weight and intact volume, as well as on the clay fraction.

Conversion from µmol/g fresh fine earth to mmol/dm^3 intact soil (excl. stones) is brought about through multiplication with the following average factors (standard deviation in brackets, n=10):

Point A	1.874 (0.036)	Point C	1.842 (0.021)
„ B	1.868 (0.069)	„ D	1.682 (0.065)

The standard deviation, stated in brackets, is a measure of the field sampling error, comprising the natural variation according to inhomogeneity of the substrate as well as the direct errors involved in the sampling technique.

A similar conversion to µmol/g dried fine earth is performed through multiplication with another series of average factors:

Point A	1.319	Point C	1.295
„ B	1.277	„ D	1.238

Finally, calculation of metal cations as µmol per g clay may be performed, if the values of the tables are multiplied with the following factors:

Point A	2.03	Point C	1.96
„ B	2.25	„ D	1.78

MECHANICAL COMPOSITION

In Table 2, illustrating percentage mechanical composition of fine earth, exceedingly high values for clay are revealed. However, as shown by the standard deviation of the means, the substrate is not quite uniform, primarily due to variations in the amounts of the lower sand fraction (0.6—0.2 mm). The largest variations in the clay contents are found in point A, whereas the substrate of point C shows a marked homogeneity. Similar differences in S.D. between the sampling points recur in the cation tables, demonstrating the importance of the clay fraction to the exchange capacity of these soils.

CHEMICAL COMPOSITION OF THE CLAY FRACTION

Fresh samples of 50 g fine earth were dispersed in 400 ml aq.dest. and the suspension transferred to a measuring cylinder (500 ml). After sedimentation at constant temperature for ten hours, 100 ml of the supernatant liquid, containing the clay fraction, were extracted with 100 ml 2 M NH_4Ac, filtered and leached with 1 M NH_4Ac to remove exchangeable metals. Drying at 105°C was followed by digestion of 1 g with HF-HCl-technique (PAWLUK, op.cit.). In that way the M_t of the clay fraction was obtained.

Determination of the mineral composition of the clay fraction was only performed on five samples from point C. The values obtained are compiled as arithmetical means (with standard deviation, n=5) in the following table, together with the corresponding figures for the M_t of the entire fine earth, calculated as mmol/g dried weight for comparison with the figures for clay.

Table 2. Percentage mechanical composition of fine earth. Arithmetical means (with standard deviation) of ten separate samples from each point

Particle diameter, mm	Sand		Fine sand		Silt		Clay
	2—0.6	0.6—0.2	0.2—0.06	0.06—0.02	0.02—0.006	0.006—0.002	< 0.002
Point A	4.1 (1.6)	10.4 (5.5)	8.4 (4.0)	2.7 (0.6)	2.9 (0.8)	6.6 (1.3)	65.0 (10.6)
B	8.1 (2.1)	14.5 (2.9)	8.9 (1.4)	3.2 (0.8)	2.8 (0.6)	6.0 (0.7)	56.6 (4.0)
C	5.6 (1.5)	7.9 (1.5)	8.3 (1.7)	3.3 (0.7)	2.3 (1.1)	6.2 (0.8)	66.5 (2.1)
D	5.3 (1.5)	8.8 (3.4)	6.6 (2.6)	1.8 (0.7)	2.3 (0.5)	6.0 (0.9)	69.3 (6.6)

Table 3. The contents of metal cations and chloride in the press-water and in sea-water with 95—105 mmol Cl^-/l. Arithmetical means (with standard deviation) of five (sea-water ten) samples, as mmol/l.

Point	Na	K	Mg	Ca	Σ Me	Σ Me as m.e./l	Cl
A	143 (7.6)	3.30 (0.13)	21.7 (0.97)	5.25 (0.25)	173 (9.1)	200 (10.2)	175 (9.1)
B	41.3 (1.6)	1.57 (0.02)	5.15 (0.08)	1.86 (0.12)	49.9 (1.8)	56.9 (2.0)	49.8 (1.5)
C	11.5 (1.2)	0.29 (0.05)	0.81 (0.09)	0.23 (0.03)	12.8 (1.3)	13.8 (1.5)	10.7 (1.0)
D	3.1 (0.4)	0.07 (0.01)	0.27 (0.07)	0.24 (0.04)	3.7 (0.4)	4.2 (0.5)	2.2 (0.3)
Sea-water	87.7 (3.4)	1.88 (0.08)	8.71 (0.45)	2.29 (0.07)	101 (4.0)	112 (4.6)	101 (2.7)

	Na	K	Mg	Ca	Mn	Fe	Al	Si
M_t fine earth	0.41 (0.02)	0.63 (0.12)	0.22 (0.03)	0.079 (0.010)	0.011 (0.001)	1.38 (0.05)	1.86* (0.17)	1.93* (0.31)
M_t clay	0.30 (0.03)	0.61 (0.06)	0.22 (0.01)	0.052 (0.003)	0.011 (0.001)	1.07 (0.03)	—	2.80 (0.26)

* T: L not determined.

The mineral composition stated above reveals, together with the exchange properties discussed later in this paper, a predominantly micaceous clay of the "illite" type (cf. GRIM 1953), illite being the most important clay mineral in Swedish soils (cf. WIKLANDER & LOTSE 1966). Interlayer potassium bridges between aluminum and silicon sheets is the generally accepted model of this group of clay minerals. As with the clay under examination, the calcium contents are usually small. Magnesium is present in appreciable amounts, probably as a lattice substitution for aluminum. Iron is a regularly occurring constituent of the illites, but the large amounts found in this clay may to some extent be due to the presence of ferric oxides, precipitated through oxidation of more soluble ferrous compounds (cf. DEB 1950).

None of the six metals of the present study is concentrated in the clay fraction, compared with the amounts present in the entire fine earth. The values of K, Mg, and Mn are the same, those of Na, Fe, and Ca even lower in the clay than in the entire fine earth.

COMPOSITION OF THE PRESS-WATER FRACTION

The pronounced electrolytic gradient always found, when sampling along transects on sea-shore meadows, usually demonstrated with chloride determinations in soil extracts, may also be characterized more in detail by cation and chloride determinations in the press-water fraction.

Data compiled in table 3 reveals, that the soil solution of point A, situated in the lower geolitoral (Fig. 1), was almost 50 times as rich in electrolytes as that of point D in the epilitoral, nowadays never submerged by the sea. In fact, it was more concentrated than sea-water of full salinity, as a result of evaporation with capillary transport from below during the summer months. However, on all sampling points the proportions between the major cations are almost the same as in the sea-water (Fig. 2). Consequently, even the soil water of point D may roughly be characterized as a very diluted sea-water with about 85 % of the metal ion sum as Na, the cation least readily adsorbed by

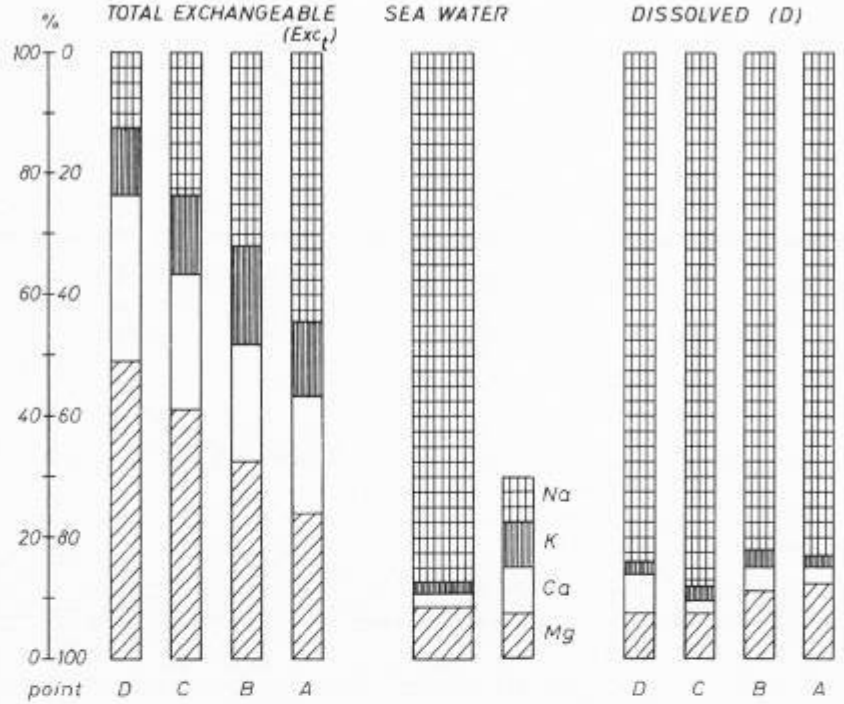

Fig. 2. Percentage composition of total exchangeable amounts of metal cations (Exc_t), compared with the composition of the press-water fraction (D) and sea-water.

the clay colloids. These relations are not too different from the cation composition found by MALMER (1962) in the pressure water of hummock and mudbottom peat from ombrotrophic areas of the Åkhult mire in southwestern Götaland, but the share taken by sodium of the molar metal ion sum is larger. The probable cation composition of the precipitation, calculated from the "Current Data" in TELLUS (e.g., 1958—60) comprises relatively more potassium and much more calcium than the soil water and the sea-water of the area, sodium making only 30—50 % of the molar sum of these four cations. This fact also demonstrates the weak adsorption of the sodium ions by the clay colloids.

As is evident from tables 4—5 and Fig. 3, however, the metal fraction dissolved in the press-water (D) is usually small compared with the amounts obtained by leaching with 0.5 M NH_4Ac ($D+Exc_t$) and almost negligable compared with the total contents (T), obtained with

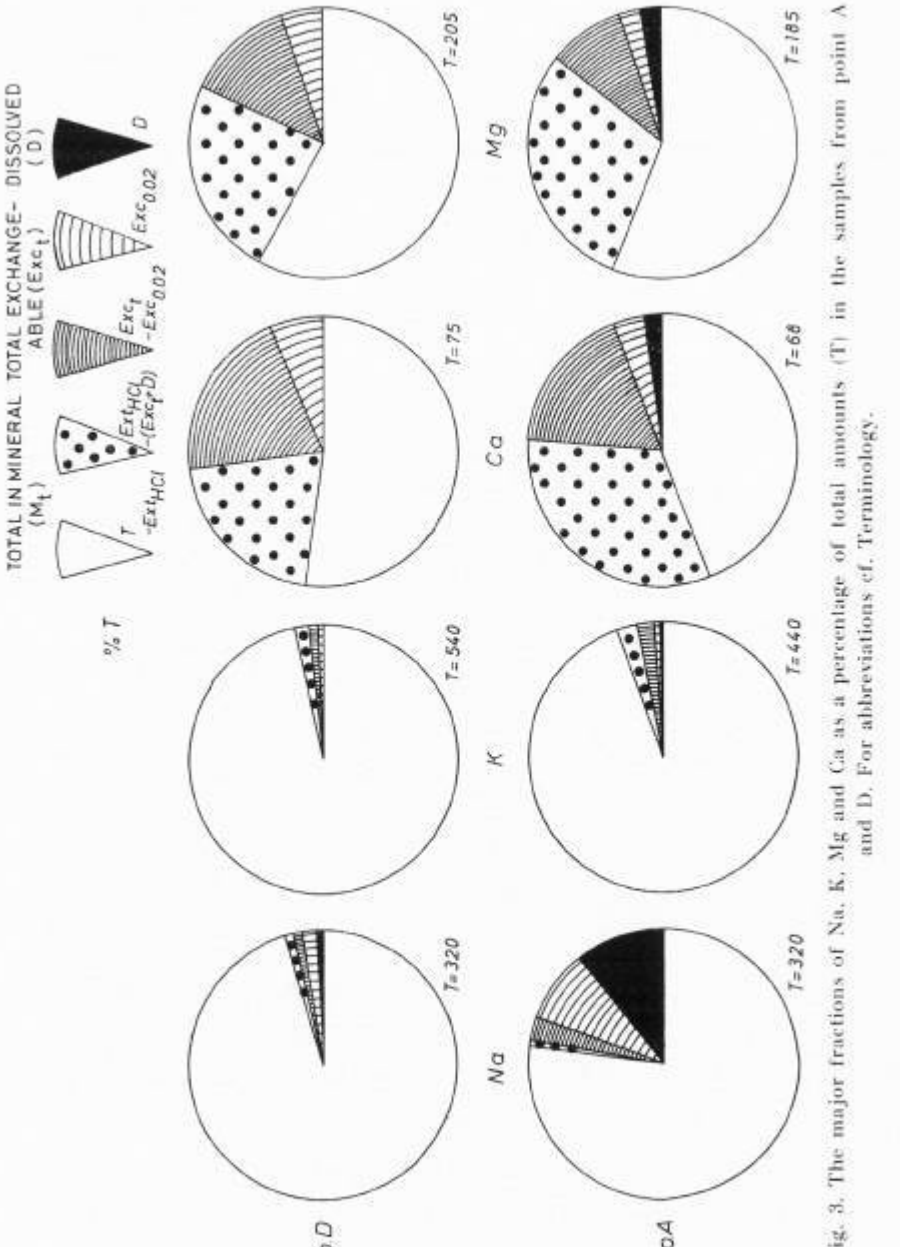

Fig. 3. The major fractions of Na, K, Mg and Ca as a percentage of total amounts (T) in the samples from point A and D. For abbreviations cf. Terminology.

HF-HCl-technique. On the epilitoral sampling point D, the fraction dissolved of K, Mg, and Ca amounts to ca. 0.2 % of the corresponding values obtained by leaching. Dissolved Na, constituting 84 % of the metal ion sum in the press-water, makes up only 6 % of L, the remaining 94 % being adsorbed and exchangeable. On the saline sampling point A, with a soil solution containing 0.17 mol metal ions per litre, 53 % of leachable Na, 80 % of Mg, 92 % of Ca and 94 % of K is still present in a state adsorbed by the acidoids.

Dilution of the soil solution, demonstrable as the gradient in the substrate from point A to point D, favours the adsorption of the divalent cations over the monovalent Na- and K-ions. The two quantitatively most important metal cations, Na and Mg, thus exhibit quite the opposite gradients in Exc_t (Fig. 2), Mg (and Ca) replacing Na (and K) towards point D, though the proportions between the mono- and divalent metal cations of the soil solution are kept constant. These empirically found relationships are further illustrated by an ion exchange experiment, described later in this paper. They are in accordance with the Donnan principle (cf. also SCHACHTSCHABEL, HAAR & KÖSTER 1958; SCHACHTSCHABEL & KÖSTER 1958).

EXTRACTIONS WITH ETHANOL

Extraction or leaching with ethanol is a standard procedure in separating soluble and exchangeable salts, particularly of soils rich in chlorides (PIPER 1950). However, a certain hydrolysis of exchangeable sodium seems to be inevitable (cf. BOWER et al. 1952); on the other hand sulphates are little soluble in aqueous alcohol. Moreover, clear extracts are equally difficult to obtain as with aq.dest. in soils rich in colloids.

A series of extractions using 40 % aqueous ethanol was carried out on all samples. Cation determinations were only performed in the extracts from sampling point A and B, owing to difficulties in getting clear extracts from points C and D.

The data obtained, calculated per g fresh fine earth, are approximately the same as the corresponding values of the press-water, being slightly higher for sodium, slightly lower for potassium, calcium and magnesium. In fresh clayish soils with moderate or large water contents, not too rich in electrolytes, cation determinations in the press-water must be preferred.

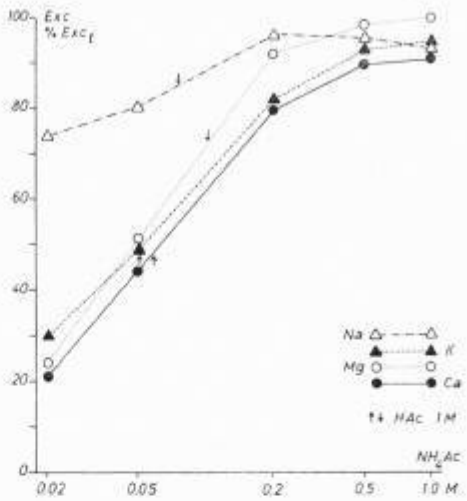

Fig. 4. Exchangeable Na, K, Mg and Ca in equilibrium extractions with 0.02—1.0 M NH_4Ac and with 1.0 M HAc, measured as a percentage of total exchangeable amounts.

EXCHANGEABLE CATIONS

A survey of the results with equilibrium extractions and leaching with NH_4Ac, calculated as µmol/g fresh fine earth, is presented in tables 4—6. In these tables the amounts dissolved (D) are included, but the values of Exc (with leaching Exc_t) are easily calculated for Na, K, Mg and Ca if the corresponding figures of D (right column) are subtracted.

The total exchangeable amounts ($Exc_t = L - D$) of sodium, potassium, magnesium, and calcium on the four sampling points, calculated per g fresh fine earth, are compiled in the following table:

	Na	K	Mg	Ca	Σ	
	µmol				µmol	µ.e./g clay
Point A	38	12	21	15	86	247
„ B	24	12	24	14	74	252
„ C	19	11	34	18	82	262
„ D	9	8	36	21	74	234

Though the sum of exchangeable metal ions are approximately the same on all sampling points, the proportions between the different ions exhibit distinct gradients. On point A a molar relationship Na > Mg > Ca > K is revealed, on point D, however, Mg > Ca > Na, K, and the molar quotient Me^+/Me^{2+} (Exc_t) decreases from 1.4 to 0.3 between these points. The replacement of Na with divalent cations, especially

Mg, upwards in the zonation of the sea-shore is very obvious and has previously been discussed (cf. Fig. 2).

Equilibrium extractions with 0.02—1.0 M NH_4Ac were performed in order to get a more detailed picture of the strength in the adsorption of the different cations. Figure 4 summarizes the amounts exchanged by equilibrium extractions on all samples, measured as a percentage of the corresponding amounts exchanged by leaching (Exc % Exc_t). Using the proportion 25 g : 100 ml between sample and extraction liquid in equilibrium extraction, an 0.5 M solution of NH_4Ac replaces 90—100 % of Exc_t. With decreasing NH_4^+-concentrations, however, the equilibria for K, Mg and Ca are displaced, making the exchange more incomplete. With 0.02 M NH_4Ac only 20—25 % Exc_t of Mg and Ca and 30 % Exc_t of K could be exchanged, compared with almost 75 % for Na (Fig. 4). The insignificant strength in the adsorption of Na compared with the three other cations is thus clearly demonstrable.

In studying the values of % L, at least for Na and K obtained with 0.02 M NH_4Ac, certain differences between the sampling points are revealed. From point A towards point D Na and K become less readily exchangeable (Table 4). As a whole the exchangeable Na and K seems to be more strongly adsorbed towards the terrestrial region, compared with the larger exchangeable fraction of these cations in the saline substrate of the sea-shore meadow proper. Calculated as $Exc_{0.02\ M\ NH^+_4}$ these differences are somewhat reduced.

I r o n exchangeable with NH_4Ac (Table 6) was not found in quantities reaching the detection limit of the method (0.01 µmol/g). Exchangeable m a n g a n e s e (Table 6), exceeding the detection limit (0.005 µmol/g), could be measured only in the samples from point A and traced from point B, but merely with the strongest NH_4Ac-solutions. On point A an average of 0.045 (S.D. 0.009) µmol/g, extractable with 1.0 M NH_4Ac, corresponds to the average 0.017 (0.003) µmol/g with 0.5 M NH_4Ac. It seems most probable, that the amounts of Mn, obtained with neutral NH_4Ac, only or chiefly are derived from manganese, adsorbed as the divalent cation by the clay colloids and thus truly exchangeable (Donald Sherman et al. 1942, Piper 1950). The larger amounts obtained already with a weak acid (1 M HAc) probably originate from solution of higher oxides. This question is further discussed in connection with the HCl-extractions.

Table 4. Sodium and potassium. Total, extractable with various solutions and dissolved in the press-water fraction. Upper row: arithmetical means (with standard deviation), calculated as µmol/g fresh fine earth. Lower row: left figure calculated as % L, right figure as % T.

	Total (T)	Extractable		Leachable (L)	Extractable, NH_4Ac					Dissolved (D) press-water
		1.0 M HCl	1.0 M HAc	0.5 M NH_4Ac	1.0 M	0.5 M	0.2 M	0.05 M	0.02 M	
n=	5	10	5	10	10	10	10	10	10	5
1. Sodium										
Point A	320 (60)	73.6 (5.8)	68.5 (5.7)	73.1 (7.0)	67.2 (4.7)	69.2 (6.7)	72.5 (7.8)	64.6 (6.1)	63.6 (4.3)	34.7 (3.6)
	—/100	101/23	94/21	100/23	92/21	95/22	99/23	88/20	87/20	47/11
B	350 (40)	36.6 (3.1)	31.9 (1.9)	32.5 (2.8)	34.1 (2.8)	34.5 (3.0)	35.1 (3.4)	30.4 (2.3)	28.8 (2.4)	9.0 (0.7)
	—/100	113/10	98/9	100/9	105/10	106/10	108/10	94/9	89/8	28/3
C	330 (15)	22.8 (1.8)	20.0 (1.3)	21.8 (0.7)	19.3 (1.2)	19.8 (1.3)	19.5 (1.2)	17.1 (0.7)	15.8 (1.2)	2.6 (0.2)
	—/100	105/7	92/6	100/7	89/6	91/6	89/6	78/5	73/5	12/1
D	320 (50)	12.8 (1.0)	8.7 (0.6)	9.7 (1.0)	8.9 (1.2)	8.9 (1.0)	8.5 (0.7)	7.4 (0.8)	6.6 (0.7)	0.61 (0.10)
	—/100	132/4	90/3	100/3	92/3	92/3	88/3	76/2	68/2	6/< 1
2. Potassium										
Point A	440 (75)	23.9 (1.9)	7.6 (0.5)	13.2 (2.1)	12.2 (1.0)	12.2 (1.3)	11.1 (1.0)	7.1 (0.5)	5.0 (0.2)	0.80 (0.08)
	—/100	181/5.4	58/1.7	100/3.0	92/2.8	92/2.8	84/2.5	54/1.6	38/1.1	6/0.2
B	400 (55)	21.8 (1.4)	7.4 (0.3)	12.5 (1.8)	12.7 (1.0)	12.6 (0.6)	11.1 (0.8)	6.8 (0.5)	4.0 (0.2)	0.34 (0.02)
	—/100	174/5.5	59/1.9	100/3.1	102/3.2	101/3.2	89/2.8	54/1.7	32/1.0	3/0.1
C	500 (100)	19.3 (1.0)	4.9 (0.3)	10.8 (0.6)	9.9 (0.7)	9.5 (0.6)	8.3 (0.5)	4.9 (0.2)	3.2 (0.2)	0.076 (0.020)
	—/100	179/3.9	45/1.0	100/2.2	92/2.0	88/1.9	77/1.7	45/1.0	30/0.6	1/< 0.1
D	540 (40)	17.5 (0.7)	3.2 (0.2)	8.3 (1.0)	7.7 (0.7)	7.3 (0.6)	6.4 (0.4)	3.7 (0.2)	2.2 (0.1)	0.014 (0.002)
	—/100	211/3.2	39/0.6	100/1.5	93/1.4	88/1.4	77/1.2	45/0.7	27/0.4	0.2/< 0.1

Table 5. Magnesium and calcium. Total, extractable with various solutions and dissolved in the press-water fraction. Upper row: arithmetical means (with standard deviation), calculated as µmol/g fresh fine earth. Lower row: left figure calculated as % L, right figure as % T.

	Total (T)	Extractable		Leachable (L)	Extractable, NH_4Ac					Dissolved (D) press-water
		1.0 M HCl	1.0 M HAc	0.5 M NH_4Ac	1.0 M	0.5 M	0.2 M	0.05 M	0.02 M	
n=	5	10	5	10	10	10	10	10	10	5
1. Magnesium										
Point A	185 (15)	81.5 (8.5)	19.8 (1.4)	26.4 (2.3)	26.1 (1.9)	25.1 (2.5)	24.8 (1.8)	15.3 (1.4)	9.0 (0.5)	5.3 (0.6)
	—/100	309/44	75/11	100/14	99/14	95/14	94/13	58/8	34/5	20/2.9
B	190 (30)	72.4 (5.6)	19.2 (0.9)	25.3 (2.0)	27.1 (1.8)	26.1 (1.2)	24.1 (0.6)	14.4 (1.0)	7.1 (0.3)	1.12 (0.08)
	—/100	286/38	76/10	100/13	107/14	103/14	95/13	57/8	28/4	4/0.6
C	200 (30)	82.2 (5.2)	22.2 (0.7)	33.9 (1.4)	32.5 (1.3)	32.9 (1.9)	31.0 (1.1)	17.2 (1.0)	8.8 (0.2)	0.18 (0.02)
	—/100	242/41	66/11	100/17	96/16	97/16	91/16	51/9	26/4	0.5/0.1
D	205 (10)	85.6 (6.1)	24.0 (1.4)	36.3 (3.1)	35.2 (3.8)	35.6 (3.4)	31.6 (2.3)	18.9 (1.4)	10.3 (0.5)	0.06 (0.01)
	—/100	236/42	68/12	100/18	97/17	98/17	87/15	52/9	28/5	0.2/< 0.1
2. Calcium										
Point A	68 (19)	37.8 (1.8)	7.9 (0.2)	16.1 (1.8)	12.5 (0.6)	12.1 (0.9)	11.0 (0.8)	6.8 (0.5)	3.9 (0.2)	1.27 (0.12)
	—/100	235/56	49/12	100/24	78/18	75/18	68/16	42/10	24/6	8/1.9
B	82 (14)	30.4 (1.5)	7.9 (0.2)	14.6 (1.3)	14.6 (1.1)	14.1 (0.5)	12.7 (0.8)	7.2 (0.7)	3.4 (0.2)	0.41 (0.04)
	—/100	208/37	54/10	100/18	100/18	97/17	87/15	49/9	23/4	2.8/0.5
C	80 (8)	31.0 (0.9)	8.1 (0.2)	18.3 (1.0)	15.5 (0.6)	16.1 (0.9)	14.4 (0.6)	8.1 (0.5)	3.9 (0.1)	0.051 (0.007)
	—/100	169/39	44/10	100/23	85/19	88/20	79/18	44/10	21/5	0.3/0.1
D	75 (6)	36.3 (0.9)	10.1 (0.5)	20.5 (1.3)	20.7 (2.2)	20.1 (1.8)	17.6 (1.4)	9.5 (0.6)	4.9 (0.2)	0.045 (0.005)
	—/100	177/48	49/13	100/27	101/28	98/27	86/23	46/13	24/7	0.2/0.1

Table 6. Manganese and iron. Total and extractable with various solutions. Upper row: arithmetical means (with standard deviation), calculated as µmol/g fresh fine earth. Lower row: calculated as % T.

	Total (T)	Extractable		Leachable (L)	Extractable, NH_4Ac		
		1.0 M HCl	1.0 M HAc	0.5 M NH_4Ac	1.0 M	0.5 M	0.2–0.02 M
n=	5	10	5	10	10	10	3×10
1. Manganese							
Point A	10.0 (1.0)	1.7 (0.4)	0.22 (0.03)	0.012 (0.004)	0.045 (0.009)	0.017 (0.003)	< 0.005
	100	17	2.2	0.1	0.5	0.2	< 0.1
B	8.0 (0.7)	0.75 (0.12)	0.036 (0.014)	< 0.005	0.012 (0.005)	0.006 (—)	< 0.005
	100	9	0.5	< 0.1	0.2	0.1	< 0.1
C	8.1 (0.3)	0.80 (0.05)	0.019 (0.005)				
	100	10	0.2		< 0.005		
D	8.4 (0.6)	0.90 (0.10)	0.050 (0.017)		< 0.1		
	100	11	0.6				
2. Iron							
Point A	870 (60)	117 (11)	0.66 (0.10)				
	100	13	0.1				
B	890 (75)	107 (9)	0.87 (0.23)				
	100	12	0.1		< 0.01		
C	1060 (40)	156 (10)	1.62 (0.15)				
	100	15	0.2				
D	1040 (45)	130 (7)	0.77 (0.14)				
	100	13	0.1				

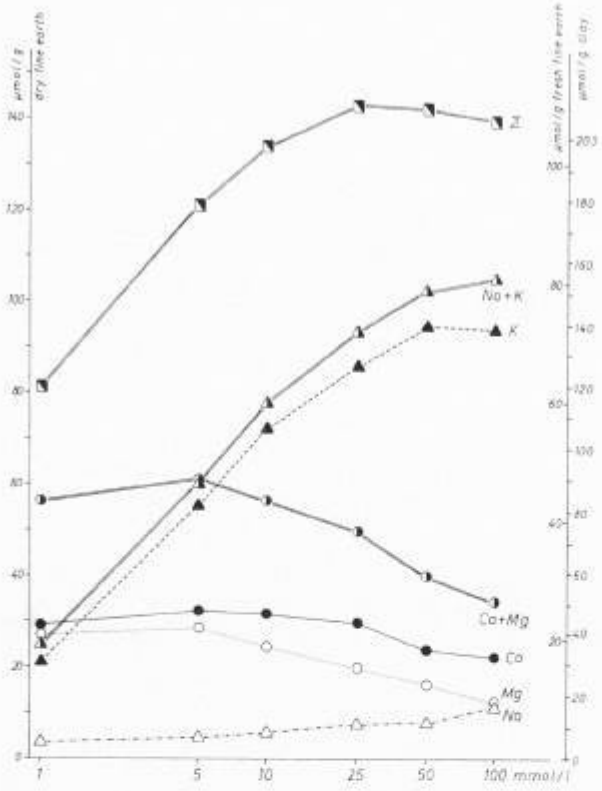

Fig. 5. Adsorption of Na, K, Mg and Ca in samples from point C, obtained with solutions of varying concentrations, containing equal molar amounts of these cations.

AN EXPERIMENT ON ION EXCHANGE

In order to further illustrate the adsorption properties of the major metal cations in the heavy clays under examination, an experiment was performed, concerning substitution of ammonium ions by metal cations in samples saturated with NH_4Ac, by washing with varying concentrations of metal chloride solutions, containing equal amounts of these metal ions.

Samples of 25 g fresh fine earth from point C were extracted with 100 ml 1.0 M NH_4Ac for 10 hours. After filtering, the samples were washed with solutions, containing either 1, 5, 10, 25, 50 or 100 mmol/litre of Na, K, Ca and Mg, the total molar concentrations thus being four, the equivalent concentrations six times these values. Washing was performed during five days with 10×100 ml. With each solution five duplicates were run.

After washing, the samples were collected in crucibles and thoroughly mixed. Subsamples of 10 g were extracted with 100 ml 1.0 M NH_4Ac for five hours. On the remaining part the water contents were determined. After

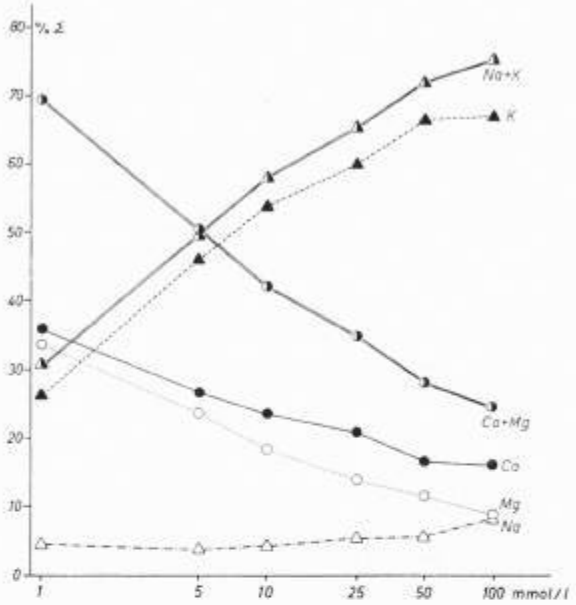

Fig. 6. Relative adsorption of Na, K, Mg and Ca in samples from point C, obtained with solutions of varying concentrations, containing equal molar amounts of these cations.

filtering, determination of Na, K, Mg and Ca was carried out according to the method previously described. The values obtained were reduced with a fraction corresponding to the amount of never adsorbed metal ions in the remaining washing solution.

The results of this experiment are illustrated in Figs. 5 and 6. Data obtained confirm the relationships previously discussed. Dilution of the washing solution favours the adsorption of the divalent cations Ca and Mg, whereas concentration of the solution increases the degree of adsorption of the monovalent cations, chiefly K, at the expense of Ca and Mg. In the sea-water and soil water of the shore-meadow, where the K-concentration amounts to less than 1/40 of the Na-concentration, and the contents of Mg are about four times those of Ca, the main competition must take place between Na and Mg (cf. Fig. 2).

Calculated as microequivalents per g, saturation of the exchange capacity and replacement of NH_4^+ with metal cations is already obtained through washing with a solution, containing 5 mmol/litre of each cation (20 mM MeCl+$MeCl_2$). The exchange capacity according to this method, calculated per g of the clay fraction, amounts to 285 µ.e., corresponding to 262 µ.e. metal ion saturation of the clay fraction of the intact samples, the small difference probably occupied by hydrogen

and aluminum ions. The average cation exchange capacity of the clay fraction (chiefly illite) in about 20 clayish soils, most of them sedimentary, amounted to 220 μ.e./g with NH_4^+ and 373 μ.e./g with Ba^{2+} in the study of WIKLANDER & LOTSE (1966).

EXTRACTIONS WITH ACETIC ACID

Though 1.0 M HAc on many, perhaps on most soils has proved equally effective as 1.0 M NH_4Ac to release exchangeable cations in equilibrium extractions (cf., e.g., SJÖRS 1961), its low cation activity was quite insufficient to displace all exchangeable metal ions in the heavy clays under consideration. As an average for K and Ca only 45—50 % of the amounts exchangeable by leaching with 0.5 M NH_4Ac (Exc_t) were obtained in equilibrium extractions with 1.0 M HAc (Fig. 4). The corresponding value for Mg was 72 % and for Na 85 %. However, H^+ must be considered essentially more powerful than NH_4^+ in replacing exchangeable metals, if the cation activities of the solutions used in equilibrium extractions are taken into account. Values obtained with 1.0 HAc (cation activity ca. 0.005 as H^+) are the same as those obtained with NH_4Ac with cation activities of ca. 0.05—0.10 as NH_4^+.

The almost non-exchangeable metals, iron and manganese, exhibit a quite different picture. Iron, not even traceable with neutral NH_4Ac, was extracted in appreciable amounts with HAc (Table 6), though still very little compared with the large total amounts of this metal. No doubt, the occurrence of iron in the HAc-extracts is the result of a weak attack on ferric oxides or ferriferous aluminosilicates, insoluble and unexchangeable with neutral salts (cf., e.g., MACKENZIE 1954).

A similar result was obtained with manganese. In samples from points A and B about four times more was extracted with HAc than with 1.0 M NH_4Ac, apparently due to a beginning reduction of rather unstable higher oxides, e.g. MnO_2, to active cations (cf. SCHOLLENBERGER 1928; PIPER 1950). As for iron, the data obtained for manganese with acids should not be regarded as equilibrium values.

EXTRACTIONS WITH HYDROCHLORIC ACID AND DETERMINATION OF TOTAL MINERAL AMOUNTS

In order to get a measure of the unexchangeable but "least unavailable" fractions, i.e. the mineral amounts most susceptible to a future possible release by weathering, extractions with a strong diluted acid,

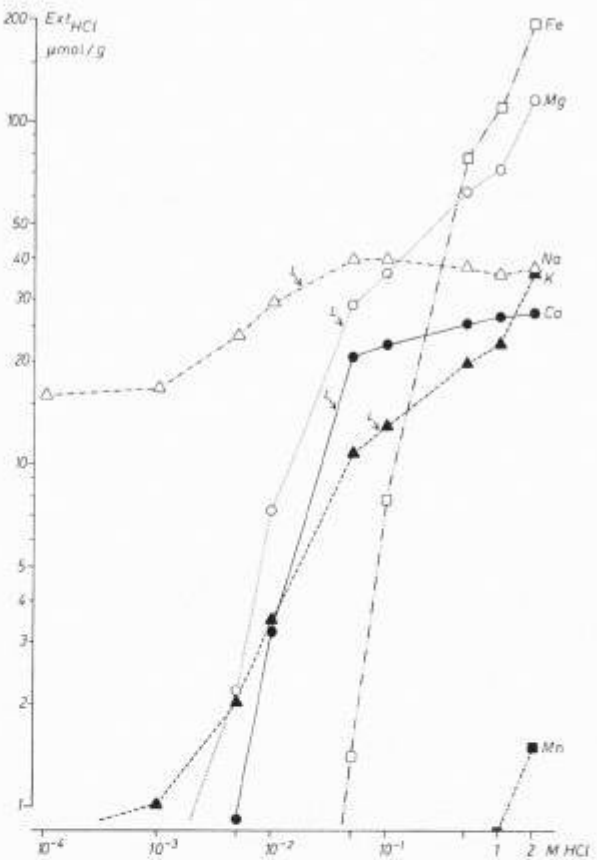

Fig. 7. The amounts of Na, K, Mg, Ca, Mn and Fe, extractable with HCl of varying concentrations from one sample of point B.

1.0 M HCl, were performed. Considerable differences between the cations were obtained. They are illustrated in the following table, comprising average figures for all samples, calculated from the values of fresh fine earth in Tables 4—6.

	Na	K	Mg	Ca	Mn	Fe
$Ext_{HCl} - (Exc_t + D)$, µmol/g	2.4	9.5	50	17	1.1	128
M_t, µmol/g	300	460	165	59	8.6	970
$[Ext_{HCl} - (Exc_t + D)]$ % M_t	0.8	2.1	30	29	13	13

In the amount of metal cations, connected to the lattice of the minerals or present in some other unexchangeable form, in the present study designed M_t, the fraction extractable with 1.0 M HCl, $Ext_{HCl} - (Exc_t + D)$, is small as far as the monovalent cations are concerned, though obviously large quantities are held in the lattice of the minerals (cf. Fig. 3).

The release of sodium is surprisingly small, demonstrating a pronounced distinction between exchangeable and unexchangeable Na. Natural release of sodium, held in the lattice of these clay minerals, will therefore proceed very slowly.

The release of unexchangeable potassium with 1.0 M HCl was also rather small, though almost equal to Exc_t. Much of the potassium actually released may originate from amounts previously remineralized through fixation, considering the generally accepted principle of an existing equilibrium between adsorbed and fixed potassium (BRAY and DETURK 1938; DETURK et al. 1943; cf. KARLSSON 1952, BLACK 1957).

A quite different picture is revealed with the divalent cation Mg. 50 µmol/g or almost one third of the M_t of this element is released and extracted with HCl (cf. Fig. 3). The low values of Ext_{HAc} must indicate that no or very little Mg and Ca will be present as acid soluble carbonates. However, a more precise determination of the origin of this fraction is outside the scope of this study.

In order to get a more detailed knowledge of metal release at different concentrations of H^+, extractions with 9 different HCl-solutions, ranging from $1 \cdot 10^{-4}$ to 2.0 M were carried out on samples from point B, quite according to the method previously described. Data obtained are plotted logarithmically in Fig 7 as µmol extractable per g fresh fine earth. The corresponding values of leachable are indicated by "L" and an arrow.

The most conspicuous feature of the diagram is the level trend of the sodium curve. Not even 2 M HCl takes out appreciably more sodium from the samples than the corresponding amounts obtained by leaching, whereas disintegration of the lattice constituents containing magnesium and potassium takes place rapidly with increasing acidity. From these elements no cation fraction, corresponding to the Exc_t, obtained with NH_4Ac, seems possible to delimit with H^+ as the displacing agent. The attack on unexchangeable lattice fractions probably starts before the exchange of Mg and K is approximately complete.

A somewhat remarkable result is obtained with Ca. In absolute figures the M_t of this element is small, only about 60 µmol/g, and as an average almost 30 % of this fraction is released with 1 M HCl. However, the Ca-curve of Fig. 7 shows a pronounced bend at the concentration 0.05 M HCl, being rather level through the larger concentrations. The behaviour of calcium to strong acids is thus not far different from sodium, but it is to be observed that the curves of Fig. 7 are based on single samples, not on averages as in the previous contexts.

Though present in very different absolute amounts, iron and man-

ganese occupy some kind of intermediate position between the mono- and the divalent cations already examined, an average of 13 % M_t being released with 1.0 M HCl. The huge absolute amount of Fe, obtained with strong HCl, will not only be derived from solution of simple ferric oxides but also from attacks on less stable ferriferous complexes and lattice constituents containing iron (but apparently no sodium). That appreciable amounts of ferric iron really are reducible under natural conditions is revealed by the biologically catalyzed intense oxidation of ferrous iron, easily recognizable on the surface of many sea-shore meadows in early spring after several months of high water-table.

A certain kind of dynamic equilibrium is considered to exist between the small traces of Mn^{2+}, dissolved in the soil solution, the small but often measurable amounts of Mn^{2+}, exchangeable from the soil acidoids, and the more or less reducible higher oxides of varying chemical composition (LEEPER 1947). The potential availability of certain of these higher oxides, primarily MnO_2, through reductions favoured by a low pH, is considered necessary for the vegetation on most soils as a source of manganese. The surplus manganese obtained with HAc in comparison with NH_4Ac might be attributed to acid reduction of the most reactive manganic fractions of the soil. The much larger surplus amounts, obtained with strong HCl, are thus derived from less active manganic forms.

CONCLUDING REMARKS

Division of the composite gradient, obtained in routine extractions with neutral salts on samples from transects across sea-shore meadows, into the components exchangeable (Exc) and dissolved (D) is often necessary to explain certain ecological relationships or, as it may seem, lack of relationship. This is particularly true for sodium. With this element, the amount contained in the soil water fraction decreases much more rapidly than the truly exchangeable amounts in the direction upwards in the zonation. The sodium gradient in $Ext_{NH_4^+}$ is thus composed of an exceedingly strong gradient D and a much smaller gradient Exc. This explains the much more rapid decrease in the sodium contents of the vegetation than in the contents of extractable sodium of the soil from the central part of the shore-meadow towards the epilitoral meadows, clearly demonstrable in a regional study on cation uptake by vegetation (TYLER, unpubl.). Exchangeable sodium

seems ecologically almost inactive, as it does not influence the osmotic potential of the soil directly and selective uptake of exchangeable sodium probably does not occur.

In routine extractions with neutral salt solutions on shore-meadow soils, the very distinct opposite gradients in Exc_t for the mono- and divalent cations (particularly sodium and magnesium) are concealed. A separation of the truly exchangeable fraction from the fraction dissolved in the soil water may even in this respect be more than theoretically important.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Laborator NILS MALMER, Head of the Department of Plant Ecology, for offering valuable criticism concerning the manuscript. I also want to thank Miss MAJ-LIS OLSSON, who carried out the hydrometer analyses.

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Wurmbea hamiltonii, a New Afroalpine Species of Liliaceae

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ABSTRACT

The new species *Wurmbea hamiltonii* WENDELBO from Mt. Elgon in Kenya is described. It is distinguished from *W. tenuis* by the purple-spotted perigone with more connate, clawless segments and by the longer basal leaf, and from *W. goetzei* by the smaller flowers and total size, the less developed spike, and the clawless perigone segments.

Wurmbea hamiltonii WENDELBO, sp. nov.

Cormus subsphaericus, c. 7 mm diametro; tunicae exteriores brunneae, papyraceae, in collum longum protractae. *Caulis* 2.5—8 cm longus, tenuis. *Vagina* basalis solitaria, 2.5—3 cm longa, apice rotundata, hyalina. *Folia* 3, filiformia; folium basale 10—18 cm longum, 1—1.3 mm latum, erectum; folium medium caulinum usque ad 7.5 cm longum, 0.5—1 mm latum, basi vaginiformi amplexicauli usque ad 3.5 mm lata; folium superius basi folio medio simili, lamina autem e rostro usque ad 1 cm longo consistens. *Spica* (1—)2—4-flora, rachis usque ad 14 mm longa, angulato-flexuosa. *Perigonium* 6 mm longum, album purpureo-maculatum; segmenta basi per vix 1.5 mm in annulum incrassatum connata; segmenta libera elliptica, obtusa, quinquenervia, basi per c. 1.5 mm manifeste incrassata, parte incrassata post filamenta secus medium sulco instructa apice utrinque fovea purpurea (nectario?) provisa. *Filamenta* c. 2 mm longa, lineari-subulata, carnosa, alba, prope basin partis liberae segmentis inserta; antherae latiuscule ovoideae, c. 1 mm longae. *Ovarium* tricoccum, trilobum, stylis liberis. *Fructus* ignotus.

Kenya. Trans-Nzoia: East side of Mount Elgon, track from Endebess, 3600 m, open, rather wet ground, 29th August 1967, HAMILTON and WENDELBO; W. 6616, holotype GB; isotype MHU.

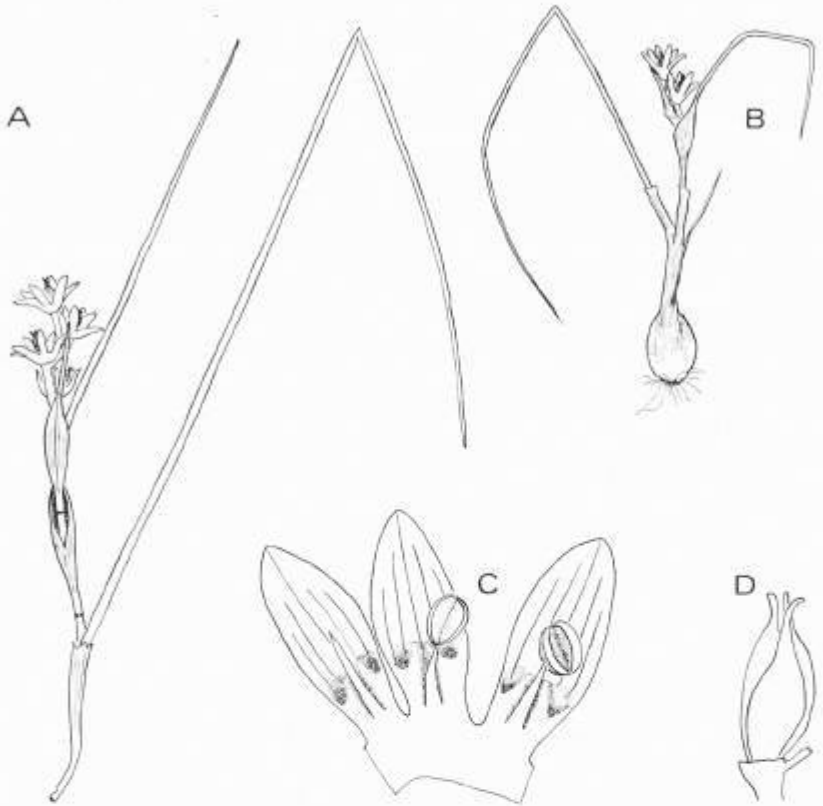

Fig. 1. *Wurmbea hamiltonii* WENDELBO sp. nov. (W. 6616). — A—B: Habit of large and small plant, 5/6. — C: Part of perigone, ×6. — D: Ovary, ×6. — ELLEN SCHJÖLBERG del.

W. hamiltonii was found in open rather wet ground at about 3600 m altitude. It was growing by the main path leading to the crater, but due to its small size it is easily overlooked. Possibly it also has a rather short flowering period. But even so this find, as well as others we did during the rather casual collecting trip to Mount Elgon, shows that the flora of the Central African mountains may not be as well known as one would expect.

The new species is named in honour of my fellow traveller and collector, the ardent young botanist ALAN HAMILTON of the Botany Department, Makerere University College, Kampala, Uganda.

W. hamiltonii is distinguished from *Wurmbea tenuis* (HOOK. F.) BAKER by the two purple markings of the perigone segments which

also have no distinct claw and which are connate for a longer distance at the base, by the much longer basal leaf, and by the sheath of the cauline leaves which is more marked. From *W. goetzei* ENGL. the new species is distinguished by the less well developed spike, the indistinct claw of the segments as well as the smaller flowers and the smaller size of the whole plant. The two mentioned species are pictured by KRAUSE (1930 Fig. 95).

The most recent contribution to the knowledge of the genus *Wurmbea* is that of NORDENSTAM (1964). He described no less than 5 new species of this small genus, all of them from South Africa.

The genus consists of between 10 and 15 species which occur in Australia and Africa. Most species are found in South Africa. Phytogeographically *Wurmbea hamiltonii* is of interest as the only marked alpine species and thus it belongs to the group of Afroalpine species (cf. HEDBERG 1957).

I am indebted to Professor K. H. RECHINGER of Vienna for kindly translating my description into Latin. I am also much indebted to the staff of the Botany Department of the Makerere University College for all kind assistance that made the expedition to Mt. Elgon possible.

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The Discovery of Medemia Palm in the Nubian Desert of Egypt

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ABSTRACT

The fruits of the palm *Medemia argun* (MART.) WÜRTTEMB. ex H. WENDL. were often found in the tombs of Ancient Egypt among offering gifts. However, this palm was first discovered in a living condition in 1837 in the Sudanese Nubia; its presence in Egypt was doubtful. In November 1963 it was discovered in Dungul Oasis in Egyptian Nubia and in December 1964 in Nakhila, c. 200 km west of Aswan; only one palm was seen in every locality.

Medemia argun palm is an unbranched fan palm with small brown-violet edible fruits. Fruits from the two localities in Egyptian Nubia show a considerable difference in size. *Medemia argun* and *M. abiadensis* H. Wendl. are known from Sudan. The author considers the latter as a synonym of the former as the differences between both species mainly refer to the size of the fruits.

Medemia argun (MART.) WÜRTTEMB. ex. H. WENDL. is a palm of ancient tradition in Egypt; its fruits were found in the tombs among offering gifts. They were named *Areca passalacquae* by KUNTH (1826) after PASSALAQUA, the man who first found them. In 1837, the palm was discovered growing in a valley of the Nubian desert in Sudan by Prince PAUL V. WÜRTTEMBERG, who made the combination *Medemia argun*, and the famous explorer THEODOR KOTSCHY. UNGER (1859) made the final redetermination of the tomb material and stated that *Areca passalacquae* of KUNTH is identical to *Medemia argun*.

The palm played an important role in Ancient Egypt; it is frequently pictured in the tombs and had a special hieroglyphic name "Mama en-xanini" (or Mama-n-khanen) to separate it from "Mama", the dom palm in the ancient texts. Its fruits are found in the tombs almost as frequently as the fruits of date and dom palms. The oldest known specimens date from the 5th dynasty. The most recent fruits date from the 6—7th Century A.D., and were found in the Monastery of Epiphanius at Thebes.

Fig. 1. *Medemia argun* palm, to the left some seedlings, Dungul Oasis, November, 1963. LOUTFY BOULOS photo.

The fruits were initially thought to be non-edible, thus it was difficult to explain their presence as offering gifts. E. DE PRUYSSENDERE found out that the natives in Nubia ate the fruits after they had been buried in the ground for a certain period. This treatment gave the endosperm a sweet taste similar to that of the coconut. If this technique was known and practiced in ancient Egypt it would explain their use as offerings. For further details, see the account in TÄCKHOLM and DRAR (1950) on *Medemia* of Ancient and Modern Egypt.

Although the palm was well known to the pharaonic people, it has not been known to exist in Modern Egypt. TÄCKHOLM and DRAR (1950) make reference to one uncertain record that an unbranched fan palm with small fruits called "Doleib" was growing at Nakhila Oasis. Doleib is also the name of *Borassus aethiopum* MART. known from Sudan, which has much larger fruits. On this basis TÄCKHOLM and DRAR (1950) write about *Medemia* as a plant "to be looked out for", and TÄCKHOLM et al. (1956) put an interrogation mark for its occurrence in Egypt.

Medemia argun closely resembles the dom palm, *Hyphaene thebaica*

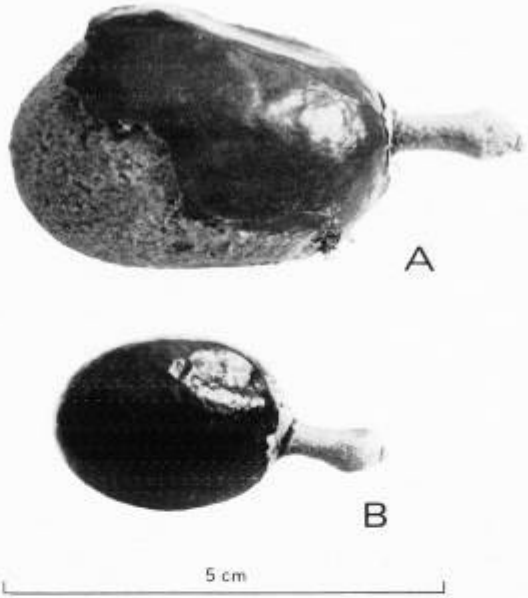

Fig. 2. *Medemia argun*, fruits; the larger from Dungul and the smaller from Nakhila, photo MARJA HELLENDOORN.

(L.) MART. It too, is a fan palm, but its stem is unbranched, not forked as in *Hyphaene*, and its fruits are small and brown-violet, not large and brown like the dom nuts. It is well illustrated by BECCARI (1924).

In November 1963, Professor VIVI TÄCKHOLM of the Cairo University, Dr. M. ZAHRAN of the Desert Institute, and the writer, visited Dungul, an uninhabited oasis in the Nubian desert some 220 km SW. of Aswan, to study its vegetation. The principal trees were, as expected, dom and date palms; the existence of any other palm species was quite unexpected. For this reason, it was a great sensation during one of our excursions to see in front of us a tall fan palm with unbranched stem. An immense amount of small brown-violet fruits was found scattered over the ground and others were hanging down from the crown in large clusters. There was no doubt that a real *Medemia argun* was before us. We were not able to find more than that single specimen and a few small seedlings in the immediate vicinity (Fig. 1), but its presence in Modern Egypt was thereby demonstrated.

In December 1964, Mr. BAHAY ISSAWY of the Egyptian Geological Survey penetrated to the west and reached Nakhila Oasis about 200 km W. of Aswan, the place from which the mystical record of the fan palm with unbranched stem was quoted by SICKENBERGER. Mr. ISSAWY was

aware of the old story and thus was looking for *Medemia*. He succeeded in finding one specimen growing together with a single dom palm and about 30 date palms. Other associated plants were: *Juncus arabicus* (ASCH. et BUCH.) ADAMS., *Desmostachya bipinnata* (L.) STAPF and *Cressa cretica* L. Mr. ISSAWY adds that about five *Medemia* palms must have grown there earlier but were cut down, most probably by passing nomads.

It seems that both in Dungul and Nakhila, *Medemia* palms were visited by bedouins who collected their fruits and leaves, the latter reputed to yield strong and excellent ropes.

ANDREWS (1956) records two *Medemia* species from Sudan: *M. argun* and *M. abiadensis* H. WENDL. and gives as the main difference between the two species that the fruits are slightly smaller in *M. abiadensis*. The writer observed that the fruits from Dungul are smaller than those of Nakhila (Fig. 2), but does not consider this of any great taxonomic importance. He agrees with TÄCKHOLM and DRAR (1950) who consider *M. abiadensis* a synonym of *M. argun*. It seems therefore, that only one species occurs in Egypt and probably also in Sudan, viz. *M. argun*.

The writer also states that the fruits of *Medemia argun* (Fig. 2) are edible, without their having been buried in the ground. They have a slightly sweet taste and may have been eaten without ageing by the ancient Egyptians, although they are not very attractive to modern taste. Nonetheless, for desert inhabitants any edible fruit is appreciated.

Medemia argun is accordingly no longer an extinct species. It is a member of the modern Egyptian Flora, living as a relic in the Libyan desert of Egyptian Nubia. Its history from ancient days is still uninterrupted.

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A Sphagnum Collection from Norrbotten, Northern Sweden

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ABSTRACT

The *Sphagnum* flora has been investigated in a part of Norrbotten Province. Between the Lule and Kalix Rivers, northwards to the Arctic Circle, 44 peatland localities were visited. Twenty-eight species were collected and two more are reported from other parts of the province. Woodland species, however, are under-represented with respect to number of localities. *S. pulchrum*, new to Norrbotten, is here at its northernmost known station in Sweden.

INTRODUCTION

The *Sphagnum* flora of Sweden is quite well known but especially in the northern part large areas remain which have not yet been visited by sphagnologists. Norrbotten Province (see Fig. 1) is one of these areas in which the *Sphagnum* flora was until recently almost unknown, except near the Torne River where unpublished collections have been made by Mr. O. LÖNNQVIST, Övertorneå.

In August 1967, we made extensive collections of *Sphagnum* in the part of Norrbotten situated between the Kalix and Lule Rivers (see Fig. 2). A total of 44 peaty areas (see Table 1) have been visited but time did not permit us to investigate moist forest to which certain species are restricted; for example *Sphagnum wulfianum* GIRG.

All the determinations of *Sphagnum* samples have been made by the author while the doubtful ones have been revised by Prof. H. SJÖRS, Uppsala University. Nomenclature of *Sphagnum* follows that of ISOVIITA (1966). Duplicates of a part of the collection have been deposited as voucher specimens in the *Sphagnum* herbarium of Växtbiologiska Institutionen, Uppsala.

THE INVESTIGTED AREA

The investigated area is situated in the Province of Norrbotten, Northern Sweden, between latitudes 65°35′N and 66°34′N. The Lule

Fig. 1. Map of Northern Sweden showing provinces and investigated area. (From The Plant Cover of Sweden. Acta Phytogeogr. Suec. 50.)

and Kalix Rivers border the area to the west and to the east respectively. This territory belongs to the low coastal region; altitude varies from sea level to 300 m in the northern part. In the south, it consists of an undulating plain with gently sloping low hills. Towards the north, the hills increase in number and elevation.

The bedrock mainly consists of Pre-Cambrian silicious rocks mostly covered by glacial drift. As the ice border retreated, the region was nearly all under water; silt and clay sediments accumulated at the bottom of the sea. When the land emerged from the sea by uplift, these sediments were washed away from the hills and re-deposited in the lower parts where later peat formation took place.

The peat areas are generally minerotrophic, i.e. with fen vegetation (Du Rietz 1949). "Poor fen" prevails over "rich fen". In the interior many of the mires have well-developed ridges ("string-bogs"). Wet parts in these mires are termed "flarks". See, e.g., Sjörs, Björkbäck & Nordqvist 1965.

According to Sjörs (1963, 1965), the area belongs to the Main Boreal sub-zone of the Boreal forest region of Northern Europe. It is largely covered by *Pinus silvestris* and *Picea abies* forest intermingled with wooded or open peatlands.

THE SPHAGNUM FLORA

Sphagnum magellanicum Brid.

This species is distributed all over the area but never forms extensive mats. It occurs mostly on ridges of the string bog formation and in *Pinus silvestris*

bog forest where *Betula nana* covers an important part of the surface. It is also present on hummocks together with *Sphagnum fuscum* but very seldom grows in very wet places.

Sphagnum centrale C. JENS.

We have collected *Sphagnum centrale* only in seven of our localities (nos. 8, 11, 22, 28, 30, 41, 44, see Table 1). The species grows in small cushions, in relatively rich sites, and is mostly associated with *Salix lapponum* and *Betula nana* bushes. It has also been found in *Pinus silvestris* forest near the mire border.

Sphagnum papillosum LINDB.

Associated with *Scheuchzeria palustris, Carex limosa, C. rostrata, C. livida, C. lasiocarpa* and *Eriophorum vaginatum*, this species of *Sphagnum* is nearly restricted to the flarks of the string bog formations where it often forms large and dense carpets. We noted too that it can grow in small cushions in pine forest bordering the mire.

The species is much more frequent than evident from the map by SONESSON (1967).

Sphagnum compactum DC.

Restricted to pools where it grows in quite small cushions, this species tends to spread out after drainage of the bog. Its frequency is relatively low: it has been found in fifteen localities only (13, 15, 20, 25, 26, 29, 30, 33, 34, 35, 36, 37, 40, 41, 42).

Sphagnum squarrosum CROME

This *Sphagnum* species colonizes rich sites such as moist *Betula pubescens* forest, *Alnus incana* and *Salix lapponum* scrub and lake borders together with *Sphagnum riparium*. It was not very frequent in our collections, because, as previously mentioned, we did not have time to visit moist forests where one can expect its presence (localities: 1, 2, 4, 5, 9, 12, 18, 21, 30, 39, 41).

Sphagnum teres (SCHIMP.) ÅNGSTR.

Sphagnum teres is also a species restricted to rich sites such as lake edges and rich fens. It can also occur under *Betula nana* and *Salix lapponum* bushes and in moist *Betula pubescens* forest. It has not been found frequently within the area but it would not be impossible to find this species in moist forest that we did not visit (localities: 1, 2, 12, 13, 21, 22, 25, 28, 29, 39, 44).

Sphagnum aongstroemii C. HARTM.

Very scattered in the area, *Sphagnum aongstroemii* has been found in only six of our localities (18, 20, 27, 36, 39, 44) where it was growing in small and flat cushions. We collected it in a rich fen and in moist *Betula pubescens* forest, also in relatively poor sites such as *Carex chordorrhiza* and *Carex rostrata - C. limosa* communities. We also collected it northeast of our area, in Korpilombolo parish (see below).

Table 1. Location of the mires visited and numbers of *Sphagnum* species found in the mire (in parenthesis).

1. — Nederluleå parish, N. Sunderbyn, On Lule River bank. (2)
2. — Do., 3 km S of Rutvik. (6)
3. — Do., 2 km NE of Sundom. (8)
4. — Råneå parish, Lake Laviken. Along road E4, 8 km E of Råneå. (3)
5. — Do., Högsön. On the shore of Högsöfjärden. (1)
6. — Do., Jämtön. On the shore of Mettträsket. (1)
7. — Töre parish, Långrätmyren, 4.5 km SW of Töre. (10)
8. — Do., mire along E4 road, 2 km E of Ökvattnet. (11)
9. — Råneå parish, Vitån, Degermyren. (4)
10. — Do., Oppmyren, 2 km NW of Vitåfors. (5)
11. — Do., mire 4 km SW of Prästholm. (6)
12. — Nederluleå parish, Höträsket, 4.5 km SW of Vibbyn. (5)
13. — Edefors parish, Nybyn, Stormyren. (14)
14. — Do., Sandträsk, Svanamyren. (7)
15. — Do., mire 4 km SE of Gullträsk stn. (8)
16. — Do., Randatjärn, 4.5 km W of Gullträsk stn. (9)
17. — Do., little mire along the road, 5 km W of Lakaträsk. (7)
18. — Do., mire 5 km N of Lakaträsk stn. (12)
19. — Do., little lake along the road, 4 km E of Lakaträsk stn. (5)
20. — Råneå parish, Mårdsel. (15)
21. — Do., mire 3 km S of Välvträsk, along Råne river. (5)
22. — Do., Myrträsk, Myrträskmyren. (6)
23. — Do., Sörbyn, Skorvmyren. (4)
24. — Do., Grundträsk, mire S of Mörtträsket. (11)
25. — Do., Grundträsk, mire S of Storträsket. (12)
26. — Do., mire 4 km SW of Flakaberg. (5)
27. — Do., Rismyrtjärn, 4 km S of Lake Stuor Saivets. (5)
28. — Överkalix parish, S of Dockarträsket, 5 km SE of Lake Stuor Saivets. (11)
29. — Råneå parish, Tallberget, mire along Vitån, 2 km S of Grönforssel. (13)
30. — Do., Långsund, mire between the road and Vitån. (15)
31. — Do., Lillberg, near Lillbergsselet. (11)
32. — Do., 1 km S of Avafors. (14)
33. — Do., E of Avafors, 1.5 km N of Hatarträsket. (11)
34. — Do., Långsel, Holmbergsmyren. (14)
35. — Överkalix parish, mire 3 km SE of Mugglom, E of Tallån. (10)
36. — Do., 3.5 km NE of Talljärv, Pörtmyren. (8)
37. — Do., Bredträsk, Körvägmyren. (11)
38. — Do., Kölmjärv, Kölmmyren. (8)
39. — Do., mire 9 km NE of Marsjärv, E of Bönälven. (11)
40. — Do., between Långträsket and Kopparsjärv. (10)
41. — Råneå parish, Sörbyn, S of Katisträsket (2)
42. — Do., mire 4 km S of Flakaberg. (11)
43. — Do., Livasudden, Livasmyren. (8)
44. — Överkalix parish, 10 km NW of Gyljen, Anttjärnmyren. (12)

Sphagnum platyphyllum (Braithw.) Warnst.

We have not seen this species within our investigated area but we collected it during a visit with Prof. Sjörs to a mire situated farther north-east: No. 429, Korpilombolo parish, south of Lake Vankajärvi, in a rich fen. In the Herbarium of Naturhistoriska Riksmuseet in Stockholm is kept a specimen of *S. platyphyllum* collected by Conr. Indebetou in 1868 at Hedenfors, Över-

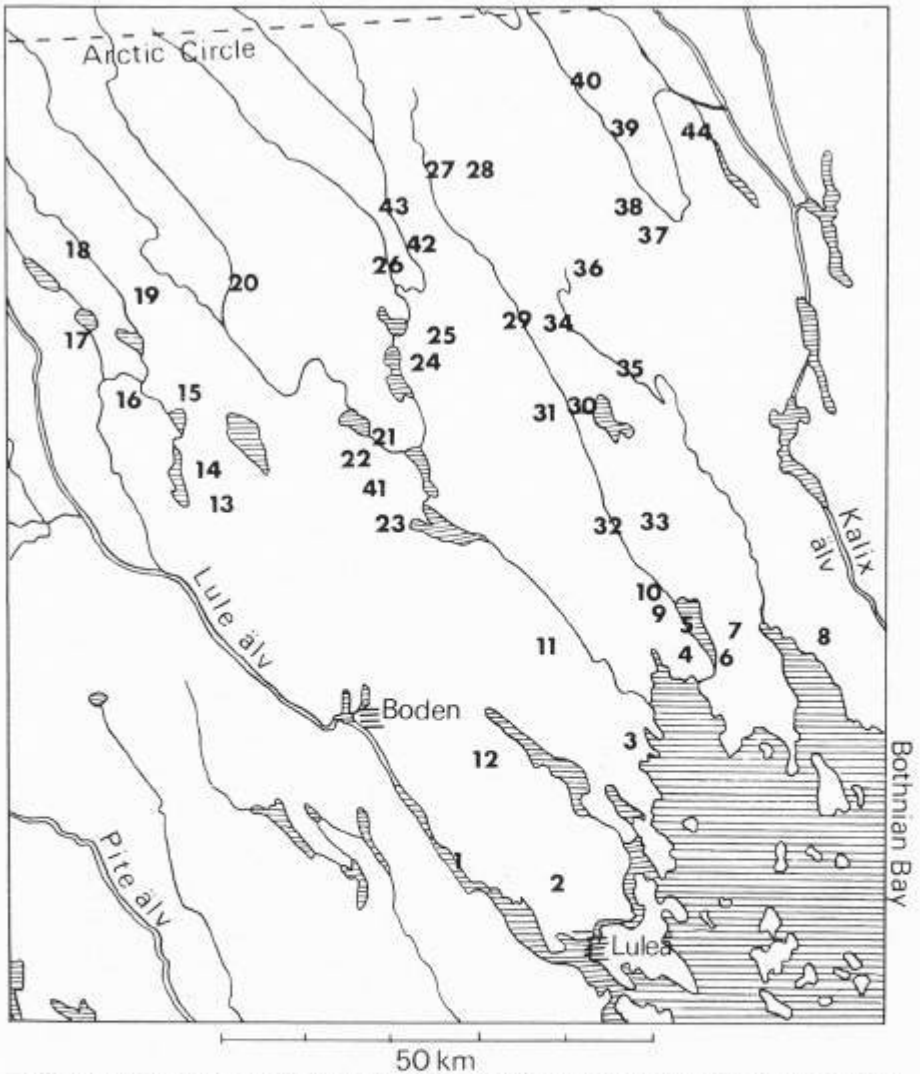

Fig. 2. Map of the investigated area. Each locality visited is indicated by a number which refers to Table 1.

luleå parish. Judging from the appearance of the specimen, it has probably been collected within the inundation zone of Lule River.

Sphagnum subsecundum NEES

This species is mostly restricted to "flarks" of rich fens where it grows in small tufts often submerged in water. It is a common species throughout the area. We collected this *Sphagnum* in nearly all the rich fens we visited.

Sphagnum tenellum (BRID.) BRID.

This species seems to be uncommon in Norrbotten (SONESSON 1967). Our three collections are the following: No. 766, Råneå parish, 1.5 km south of Avafors (32), in a pool of a steeply sloping string bog; No. 789, Råneå parish, Holmbergsmyren, 3 km north-east of Långsel (34), in an *Eriophorum vaginatum - Sphagnum balticum - S. lindbergii* community; No. 798, Överkalix parish, 3 km south-east of Mugglom (35), in an *Eriophorum vaginatum - Sphagnum papillosum - S. compactum* community. A fourth collection was made by E. MARKLUND also in 1967: Överkalix parish, Bredträsk, Bredträskmyren.

Sphagnum majus (RUSSOW) C. JENS. [*S. dusenii* C. JENS. ex RUSSOW & WARNST.]

Widespread throughout the area, this species is restricted to very wet habitats. It grows in pools of string bog formations associated with *Carex* spp., *Scheuchzeria palustris* and *Eriophorum vaginatum* (poor fen). It is uncommon in rich fen and in *Pinus* forest bordering the mires, where a few individuals can be found in deep wet hollows.

Sphagnum jensenii H. LINDB.

Like the preceding species, *Sphagnum jensenii* grows under very wet conditions, within the same plant communities. However, it is much less common than *Sphagnum majus* and has never been found in *Pinus* bog forest (localities: 8, 13, 18, 19, 20, 29, 30, 32, 34, 38, 42).

Sphagnum balticum (RUSSOW) C. JENS.

This *Sphagnum* seems here to have about the same habitat requirements as the two preceding species and it belongs to the same plant communities. It is not a common species in our area, and we have found it in only 10 of our localities (10, 25, 28, 29, 31, 32, 33, 34, 38, 40).

Sphagnum pulchrum (BRAITHW.) WARNST.

Sphagnum pulchrum is new to the *Sphagnum* flora of Norrbotten Province. The only specimen collected (No. 796) has been found in Holmbergsmyren (34), 3 km north-east of Långsel in Råneå parish. It was growing in quite dense mats, on the low ridges of a string fen formation where *Molinia coerulea* was the dominant species. *Carex echinata, Menyanthes trifoliata, Oxycoccus palustris* were the other important species of the community. In the bottom layer, we noted the presence of very small tufts of *Sphagnum magellanicum* and *S. robustum*. *Sphagnum papillosum* was of a little more importance than these two species.

Sphagnum fallax (KLINGGR.) KLINGGR. [*S. apiculatum* H. LINDB.]

Found in only six of our localities (9, 18, 23, 27, 31, 36), this species seems not to be common within the area. We collected it in moist forests of *Betula*

pubescens, and of *Pinus silvestris* and *Picea abies*. It was also present in open poor fen with *Carex rostrata*, *C. limosa*, and *C. lasiocarpa*. Once we collected it in a ditch.

Sphagnum angustifolium (RUSSOW) C. JENS. [*S. parvifolium* (WARNST.) WARNST.]

This common species is mostly restricted to borders of mire, growing in *Pinus silvestris* bog forest with *Betula nana* and *Ledum palustre*. It can also be found in moist *Betula pubescens* forest and under *Betula nana* and *Salix* bushes where it forms extensive mats. Less often, it grows in open *Carex* fens.

Sphagnum flexuosum DOZY & MOLK. [*S. amblyphyllum* (RUSSOW) ZICK.]

It seems that this *Sphagnum* species prefers moderately wet habitats. We have collected it in only seven localities (16, 20, 24, 31, 32, 33, 40) in different plant communities: *Carex chordorrhiza* comm.; *C. lasiocarpa* comm.; *Salix lapponum - Betula nana - Sphagnum riparium* comm.; wet hollows of moist *Betula pubescens* forest and *Pinus silvestris* forest bordering the mire; on low hummock with *Sphagnum fuscum*, *Betula nana* and *Empetrum hermaphroditum*; on a ridge of a "string-bog" formation with *Pinus silvestris*, *Calluna vulgaris*, *Empetrum hermaphroditum* and *Sphagnum fuscum*.

Sphagnum obtusum WARNST.

Sphagnum obtusum is another uncommon plant in this part of Norrbotten where we collected it in only six localities (10, 12, 16, 17, 43, 44). It was growing in small cushions in a rich fen, in a pool of a string bog and in flarks within *Carex limosa* communities. It can also occur under *Betula nana - Salix lapponum* bushes or in open fens with *Carex rostrata*, *C. limosa* and *C. canescens*. It was first recorded from Norrbotten by O. LÖNNQVIST (unpublished) and also H. SJÖRS has collected it more to the east (Karl Gustav parish: Kaartivuoma, Koivuvuoma, Veitsivuoma).

Sphagnum riparium ÅNGSTR.

Moderately common in the investigated area (localities: 4, 5, 8, 9, 12, 16, 18, 19, 20, 21, 28, 29, 30, 44), *Sphagnum riparium* was forming extensive mats on every lake's edge we visited. Large colonies have also been seen under *Salix lapponum* and *Betula nana* bushes. We also collected this species in wet hollows of *Pinus silvestris* forest where it grows in small tufts. We noted the presence of a few individuals in a flark of a rich fen and in moist *Betula pubescens* forest.

Sphagnum lindbergii SCHIMP.

Mostly restricted to open bog or poor fen together with *Carex limosa*, *C. rostrata*, *C. lasiocarpa* and *Eriophorum vaginatum*, this species can also be found in wet hollows in the *Pinus silvestris* forest bordering the mires. We also collected it under dense bushes of *Salix lapponum*, where it formed a dense carpet. It is a species well distributed throughout the area.

Sphagnum wulfianum GIRG.

We have not collected this *Sphagnum* in Norrbotten, because, as previously stated, moist forests have not been visited. One specimen seen is from the herbarium of Naturhistoriska Riksmuseet, Stockholm. It has been collected by HJ. MÖLLER in 1912, at Kengis in Pajala parish. We have also seen one specimen from Övertorneå parish and two specimens from Hietaniemi parish, in O. LÖNNQVIST's private herbarium.

Sphagnum subnitens RUSSOW & WARNST. [*S. plumulosum* RÖLL s.str.]

Very rare in the area, this species has been found in only three localities: No. 795, Råneå parish, Långselet, Holmbergsmyren (34), in a *Carex lasiocarpa - Sphagnum papillosum* community; No. 644, Råneå parish, Mårdsel (20), on low ridges colonised by *Trichophorum alpinum*; No. 572, Edefors parish, Nybyn, Stormyren (13), near the base of a ridge. The first mentioned collection is a very typical specimen for this species but the two others are doubtful and may belong to *S. subfulvum*. Another typical collection was made in Övertorneå parish by O. LÖNNQVIST in 1964, and is kept in his private herbarium.

Sphagnum subfulvum SJÖRS

Quite common in the investigated area, *Sphagnum subfulvum* is nearly restricted to flarks where it grows in small cushions but sometimes can form dense carpets. Very seldom, a few individuals can be found in wet hollows in *Pinus* forest bordering the mires. It was earlier collected in many places by O. LÖNNQVIST.

Sphagnum nemoreum SCOP.

Common all over the area, this species is growing in rather dry places such as the ridges of "string bogs", *Pinus* bog forest and under *Betula nana* bushes.

Sphagnum warnstorfii RUSSOW [*S. warnstorffianum* DU RIETZ]

Occurring mostly in or near flarks of fens, this species is probably common throughout the area even though we collected it from only four localities (7, 13, 21, 30) and noted its presence in some other localities.

Sphagnum rubellum WILS.

Only one specimen of this species has been collected: No. 804, Överkalix parish, in the mire 3 km south-east of Mugglom, east of Tallån (35). In fact, we are doubtful as to the identity of this specimen, to be a *S. rubellum* or not. It might be a type of the very variable *S. nemoreum* to which belong most of the collections from northernmost Sweden believed to be *S. rubellum*, as stated by MÅRTENSSON (1955—56). We have also seen a specimen from O. LÖNNQVIST's herbarium which is likely to be a green form of *S. rubellum*. It was collected in Karl-Gustav parish.

Sphagnum fuscum (SCHIMP.) KLINGGR.

Very common all over the area. *Sphagnum fuscum* mostly occurs in *Pinus* bog forest and on ridges of "string bogs" where it often forms dense carpets. It also forms small hummocks in the flarks of fens.

Sphagnum russowii WARNST. [*S. robustum* (WARNST.) CARD.]

This is also a very common *Sphagnum* in Norrbotten, occurring in all *Pinus* bog forests where it forms numerous small tufts. It is also present, but to a lesser extent, on ridges of "string bogs" and on hummocks in the flarks of fens.

Sphagnum girgensohnii RUSSOW

Restricted to moist forests, this species was observed to grow in large carpets. It is probably a common species in the area (cf. MÅRTENSSON 1955—56) even though we collected it only from four localities (2, 3, 14, 18).

Sphagnum fimbriatum WILS.

Quite common, this *Sphagnum* species occurs under *Salix* and *Betula nana* bushes and in moist *Betula pubescens* forest. It is less common in rich fen where small cushions can be found. Very seldom, we collected it in flarks of fen where it forms small cushions above the water level. It is equally common in more eastern parts of Norrbotten (O. LÖNNQVIST's and H. SJÖRS' collections).

ACKNOWLEDGEMENTS

The work has been carried out at Växtbiologiska Institutionen of Uppsala University, Uppsala.

Material from the following herbaria has been examined: Naturhistoriska Riksmuseet, Stockholm; Växtbiologiska Institutionen, Uppsala; Botaniska Museet, Uppsala; Botaniska Museet, Lund; part of O. LÖNNQVIST's private herbarium.

My wife aided very efficiently in both field and laboratory work.

I wish to express my sincere gratitude to Professor HUGO SJÖRS who provided me with so much help and criticism during all the time I spent at the Institute, working on *Sphagnum* mosses.

Thanks, too, to the Swedish Institute and to the National Research Council of Canada for financial support.

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Från Lunds Botaniska Förenings förhandlingar 1967

24 FEBRUARI. Professor HENNING WEIMARCK redovisade det aktuella läget för inventeringen av den skånska floran samt demonstrerade ett antal kartor över utbredningen av växtgeografiskt intressanta arter i Skåne.

Amanuens ALF ÖREDSSON höll föredrag om skånska *Rubus*-arter. Han beskrev väsentliga drag hos de olika arterna och visade deras frekvens och utbredning i Skåne.

31 MARS. Fil. lic. GUNNAR WEIMARCK höll föredrag om »Sexuell och apomiktisk fortplantning hos *Hierochloë*» (jfr G. WEIMARCK 1967).

7 MAJ. Exkursion med buss företogs till södra Skåne under ledning av trädgårdsmästare JOHN KRAFT. Route: Lund—Malmö—Anderslöv (som var samlingsplats)—Markiehage—Asbjer—Gillesgruvan—S. Lindved—N. Lindved—Svedala—Bökeberg—Roslätt—Svedala—Anderslöv—Malmö—Lund.

Från Markiehage till Asbjer vandrade man genom bokskogen vid södra delen av Börringesjön. Från den stundom rika fältskiktsfloran i bokskogen kan nämnas *Allium ursinum, Anemone nemorosa, A. ranunculoides, Corydalis cava, Galium odoratum, Lamium galeobdolon, Mercurialis perennis, Oxalis acetosella, Stellaria holostea, Viola Reichenbachiana, Milium effusum* och *Poa nemoralis*.

Vid Gillesgruvan berättade exkursionsledaren, JOHN KRAFT, om de »*tortuosa*-bokar», som finns på S. Lindholmens ägor.

Nästa anhalt var vid S. Lindved. I kärrmark c. 200 m sydost om denna gård fanns bl.a. *Andromeda polifolia, Oxycoccus palustris, Calluna vulgaris, Viola palustris, Eriophorum angustifolium, Carex nigra* och *Nardus stricta*. Vitmossor dominerade i bottenskiktet.

I skogsbrynet (av al) mot stranden av Börringesjön (c. 700 m ostsydost om S. Lindved) observerades *Stellaria neglecta, Adoxa moschatellina, Geranium robertianum* och *Glechoma hederacea*.

På den gräsklädda kulle, som utgör Lindholmens slottsruin sägs bl.a. *Astragalus glycyphyllus, Barbarea vulgaris, Capsella bursa-pastoris, Carduus crispus, Cirsium arvense, Glechoma hederacea, Lamium purpureum, Stellaria apetala, Urtica dioeca, Viola arvensis* och *Dactylis glomerata*.

Nästa anhalt blev N. Lindved, där banvallens flora studerades (c. 300 m nordost om gården). Härifrån kan nämnas *Arabis arenosa, A. thaliana, Cerastium semidecandrum, Erophila verna, Glechoma hederacea, Myosotis hispida, Senecio vernalis, Valerianella locusta, Veronica arvensis, Viola tricolor* och *Carex arenaria*.

Exkursionens sista studieobjekt var den berömda »Tutaremossen» vid Roslätt. I ARESCHOUGS flora från 1881 upptas *Saxifraga hirculus* från denna lokal

(jfr H. WEIMARCK 1963 sid. 362). Ett stort område upptas här av den fysionomiskt mycket intressanta vegetationstyp, som har *Carex caespitosa* som dominerande art. Tillsammans med *Carex caespitosa* antecknades bl.a. *Caltha palustris, Cirsium palustre, Epilobium hirsutum, Filipendula ulmaria, Geum rivale, Equisetum fluviatile* och *Juncus effusus*. Vidare bör särskilt nämnas *Viola epipsila*, som stundom fanns växande uppe i *Carex caespitosa*-tuvorna.

Vissa kärrpartier av »Tutaremossen» hyste ganska mycket av *Carex appropinquata*.

På den torrare betesmarken inom området fanns utmed kreatursstigarna bl.a. *Cardamine hirsuta, Erophila verna, Stellaria apetala* och *S. media*.

16 SEPTEMBER. Exkursion med buss företogs till sydvästra Skåne med fil. mag. LENNART JEPPSSON som färdledare. Route: Lund—Malmö—V. Klagstorp — Klagshamn — Gessie — Vellinge — Bernstorp — Håslöv — Skanörs ljung — Skanör — Vellinge — Malmö — Lund.

Första uppehåll gjordes vid backarna 1 km västnordväst om Solnäs i V. Klagstorps socken. På dessa backar, som användes till betesmark, kunde noteras *Artemisia campestris, Carduus acanthoides, Centaurea jacea, C. scabiosa, Daucus carota, Echium vulgare, Galium verum, Medicago falcata, M. falcata* × *sativa, Ononis repens, Pastinaca sativa, Pimpinella nigra, Torilis japonica, Dactylis glomerata, Festuca rubra* och *Phleum phleoides*.

På slänten mot det gamla kalkbrottet vid Klagshamn växte *Lactuca serriola* tillsammans med bl.a. *Cichorium intybus, Daucus carota* och *Pastinaca sativa*.

På gammal utfyllnadsmark vid Klagshamn studerades diminutiva exemplar av *Centaurium pulchellum, Erigeron acre, Euphorbia exigua, Linum catharticum* och *Sagina nodosa*.

En hel del tid anslogs till studiet av Gessie strandängar (c. 3 km västsydväst om Gessie kyrka). Här fanns stora bestånd av *Inula britannica*. Av rariteter kan också framhållas *Limonium vulgare*, som förekom inom *Juncus gerardi*-vegetation med bl.a. *Armeria maritima, Aster tripolium, Glaux maritima, Leontodon autumnalis, Lotus corniculatus, Plantago maritima* och *Agrostis gigantea*.

Nästa exkursionsmål var backen c. 300 m ostsydost om Bernstorp i Vellinge socken. På denna backe brukar man finna *Orobanche major*, vilken i år var ovanligt rikligt företrädd, minst 40 exemplar. På backen antecknades i övrigt bl.a. *Campanula rotundifolia, Centaurea scabiosa, Cuscuta epithymum, Filipendula vulgaris, Geranium sanguineum, Linum catharticum, Ononis repens, Plantago media, Primula veris* och *Scabiosa columbaria*.

Nästa anhalt (i Håslövs socken) hade ett speciellt intresse såsom växplats för en såsom skånsk förut okänd växt, nämligen *Orobanche minor* (jfr L. JEPPSSON 1967 sid. 488). Denna växte dels på en åkerren tillsammans med bl.a. *Achillea millefolium, Agrimonia eupatoria, Convolvulus arvensis, Echium vulgare, Geranium pyrenaicum, Plantago lanceolata, Torilis japonica, Trifolium repens, Festuca rubra* och *Lolium perenne*, dels på ett intilliggande klöverfält. Exkursionen berörde också östra delen av Skanörs ljung, där *Juncus maritimus, Eryngium maritimum* och *Iris spuria* tilldrog sig största intresset.

20 SEPTEMBER. Professor G. KLOTZ, Jena, höll föredrag över »Die Höhenstufengliederung von Flora und Vegetation im Sikkim-Himalaya».

27 OKTOBER. Revisionsberättelse över 1966 års räkenskaper föredrogs. Föreningen beviljade föreslagen ansvarsfrihet.

Professor GUNNAR HARLING, Göteborg, höll föredrag om »Några drag av de equadorianska Andernas vegetation och flora».

21 NOVEMBER. Val av styrelse för 1968 företogs. Valda blev: Professor H. WEIMARCK, ordförande; docent S. SNOGERUP, vice ordförande; fil. mag. J. ERICSON, sekreterare; fil. kand. G. MATTIASSON, vice sekreterare; samt fil. lic. F. ANDERSSON, laborator B. LÖVKVIST, docent S. PETTERSSON, docent H. RUNEMARK och docent S. O. STRANDHEDE.

Till revisorer utsågs docent L. O. BJÖRN och fil. mag. L. PÅHLSSON med fil. mag. Ö. NILSSON och fil. lic. B. NORDENSTAM som suppleanter.

Docent HANS TRALAU höll föredrag om »Skånes mellanjurassiska flora och vegetation».

15 DECEMBER. Fil. mag. TORGNY VON WACHENFELDT höll föredrag om algerna som indikatororganismer. Föredragshållaren behandlade förhållandena i Öresund och de förändringar i algfloran, som kunnat iakttas under de senaste hundra åren.

Jan Ericson

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(Botanical Literature)

HELMUT GAMS: Kleine Kryptogamenflora. Band III. Flechten (Lichenes). — Stuttgart (Gustav Fischer Verlag) 1967. 244 pp. Price DM 28:—.

The "Kleine Kryptogamenflora" issued by Professor H. GAMS, Innsbruck, since 1940, is a successor of the "Kryptogamenflora für Anfänger" (ed. G. LINDAU) wellknown to many European botanists of the first decades of this century as a useful introduction into cryptogam systematics. Two groups have been treated previously in GAMS' Kryptogamenflora, viz. Fungi (vol. II by M. MOSER; reviewed in Bot. Notiser 1953 p. 464 and 1956 p. 114) and Bryophytes and Pteridophytes (vol. IV by H. GAMS; cf. Bot. Notiser 1951 p. 435). Vol. I (Algae by H. GAMS) is still under preparation.

The scope of this flora has gradually developed towards covering the whole Europe. Its limited space has made it impossible to mention all species known. In several large genera, the taxonomy of which is founded mainly on microscopic characters, only a selected number of species are presented. This is especially true in the present Vol. III: Lichens which mentions ca. 2100 species. The specific descriptions are extremely condensed, mostly to 1—3 (rarely up to 6—7) lines in dichotomous keys under families or genera. A large number of line drawings (mainly original by the author) appear in the text. Some of these are very distinct, others will probably prove to be less instructive.

Some introductory chapters give keys to the major groups of the lichens and also to lichen fungi (mycobionts) and lichen algae (phycobionts; formerly known as "gonidia"). Many lichenologists will appreciate this survey of the lichen algae, the taxonomy of which is fairly contradictory. Reference should have been made, however, to AHMADJIAN's instructive papers (e.g. in Bot. Notiser 1958 p. 632). The arrangement of the lichen families and genera presented by GAMS is quite different from the traditional ZAHLBRUCKNER system. He has followed up the important works by NANNFELDT (1932), LUTTRELL (1951) et al. on the morphology of the ascocarps, which give rise to a new lichen system founded on a revised taxonomy of their mycobionts. GAMS has retained the old classes *Ascolichenes* and *Basidiolichenes* and also the subdivision of the former into *Discolichenes* (now beginning with *Lecanora* and related genera and ending in *Graphidiidae*) and *Pyrenolichenes* (*Verrucariaceae*, etc.). The last two pages dealing with *Basidiolichenes* consider the interesting discoveries of the last decade (not least by GAMS himself) that a certain number of European *Basidiomycetes* have green algae as sym-

bionts. The wellknown lichen *Coriscium viride* is the result of a symbiosis between *Omphalina* spp. and *Coccomyxa* algae and should, according to the Rules of nomenclature, be named after its mycobiont.

Some critical remarks. The chapter "Auswahl von Lichenologen" has listed a major number of Central European lichenologists, whereas some authors of wellknown lichen floras of Western Europe (e.g. HARMAND and A. L. SMITH) have been omitted. The journal "The Lichenologist" issued from London since 1961, which is indispensable to any serious lichenologist, should have been mentioned in this connection. Some definitions in the terminological chapter are misleading, e.g. (p. 3) paraplectenchym ("weniger dichte Hyphengewebe als im Plektenchym") and plectenchym ("besonders dicht verflochtene Hyphengewebe"). Some genera (as *Parmelia, Cetraria* and *Physcia*) have been treated in a modern and comprehensive manner, whereas others have been compiled from out-of-date monographs. This is especially true about *Pertusaria* (founded mainly on ERICHSEN's treatment in RABENHORST's Kryptogamenflora), where a large number of untenable "species" (e.g. *P. leioterella* and *P. pulvinata*) have been retained. *Pertusaria subviridis* (p. 35) is also treated as *Ochrolechia s.* (p. 31). Some wellknown species have got wrong authors' names, e.g. *Ramalina calicaris* [(should be (L.) FR.], *Xanthoria parietina* and *X. candelaria* [both should be (L.) TH. FR.]

It is evident that this lichen flora, used with some criticism, can be a valuable introduction also to the lichens of Scandinavia, where the need for a modern handbook has been emphasized ever since the days of TH. M. FRIES.

Finally the reviewer would express his admiration for the treasure of taxonomic knowledge found in the volumes of this Kryptogamenflora. Dr. GAMS, the grand old man of European ecology and plant geography, has demonstrated a survey of the taxonomy of large cryptogam groups which is unsurpassed in the present generation of botanists. We might wish that his floras get a special message to many students of ecology who look upon taxonomy as adiaphora or at most as a necessary evil.

OVE ALMBORN

JOHN W. THOMSON: The Lichen Genus Cladonia in North America. Toronto (University of Toronto Press) 1967. 172 pp. 26 plates, 60 figures. Price $ 12.75.

Professor J. W. THOMSON (Madison, Wis., U.S.A.) is known as the author of monographic treatises of North American lichen genera, e.g. *Peltigera, Xanthoria* and *Physcia* (the latter reviewed in Bot. Notiser 1964 p. 103). The *Cladonias* of N. America have been fairly well studied not least in several works by A. W. EVANS during the last three decades. Nevertheless, the present volume is a well-done and welcome addition to the handbooks of lichen taxonomy.

In the introduction we meet with brief chapters on "The structure and growth of a *Cladonia*" and "Chemical and physical aids in the identification of *Cladonia*". The latter is followed by 60 figures on "The microchemistry of the *Cladoniae*". In fact, all these figures are microphotographs showing crystal

forms of the lichen substances known to occur in *Cladonia*. ASAHINA's crystal method which was developed further by EVANS has often been a useful aid in distinguishing lichen taxa. No doubt, it will soon be superseded by refined methods of thinlayer-chromatography, which enable a rapid analysis of even very small amounts of the lichen thallus. The outlines of this modern technique are also indicated.

The major part of the work is devoted to keys to the sections and species of the N. American *Cladonias* and to descriptions of the 116 species treated. Each species is treated briefly (in one page or less). Nomenclature is kept at a minimum. Most additional data can easily be supplied from VAINIO's classical monograph (1887—1897) or from SANDSTEDE's treatise in RABENHORST's Kryptogamenflora (1931; additions 1938). Chemical reactions ("K+ yellow", etc.) and contents of chemical substances, if known, are mentioned. The range of each species in N. America and in general is recorded in few words. There is no parallel to the detailed lists of localities and dot-maps which are met with in the author's revision of the N. American *Physcias*.

Dr. THOMSON is known as a somewhat conservative lichen taxonomist, which, in the reviewer's opinion, is often a merit. Hence we do not find many taxonomic or nomenclatural novelties. Some changes of wellknown species names should, however, be noted. *Cl. phyllophora* HOFFM. seems to predate *Cl. degenerans* (FLK.) SPRENG., *Cl. subcariosa* NYL. takes precedence over *Cl. polycarpia* MERR., *Cl. subfurcata* (NYL.) ARN. over *Cl. delessertii* (DEL.) VAIN. and *Cl. macrophylla* (SCHAER.) STENHAM. over *Cl. alpicola* (FLOT.) VAIN. The last-mentioned three changes have already been introduced by AHTI. On the other hand, THOMSON has not followed AHTI in his rejecting the wellknown *Cl. sylvatica* (L.) HOFFM. in favour of *Cl. arbuscula* (WALLR.) RABENH.

The subspecific variation is summarized very briefly as "forms" under each species. Several of them are represented in some 200 photographs in 26 plates). Some of the illustrations are of high quality.

As most European species of *Cladonia* occur also in N. America, the present volume will certainly serve as a useful guide also to European students of this polymorphous genus.

OVE ALMBORN

MASON E. HALE, Jr: The Biology of Lichens. — Contemporary Biology. London (Edward Arnold Ltd) 1967. 176 pp. 16 plates, numerous figures in the text. Price 42 s. (boards), 21 s. (paper).

In 1961 Dr. M. E. HALE (Smithsonian Institution, Washington, D.C., U.S.A.) issued a "Lichen Handbook. A guide to the lichens of Eastern North America" (reviewed in Bot. Notiser 1963 p. 110). This volyme contained surveys of morphology and anatomy, reproduction, physiology and growth, lichen symbiosis, chemistry of lichens (with useful discussions on lichen acids and "chemical strains"), economic uses, phytogeography and classification. There was also a key to genera and species of fruticose and foliose lichens and to genera of crustose lichens of N. America. Dr. HALE's Handbook attracted the

interest of students and lichenologists in general to such an extent that the stock soon became out of print.

The present issue has got a somewhat different scope. We find no keys to N. American lichen genera, but the volume has developed to a presentation of problems and results of general lichenology. Some main chapters deal with "Morphology of the thallus", "Morphology of reproductive structures", "Reproduction and dispersal", "Physiology and nutrition", "Symbiosis and synthesis", "Growth and longevity", "Ecology and succession", "Chemistry of lichens", "Biochemical systematics", "Classification and taxonomy", and "Economic uses and Applications".

The limited space has forced the author to make a very selective choise in the vast material available. It is evident that a critical reader will easily find pages where he would have wished a more detailed treatment. The ecological chapter deals mainly with conditions in N. America (and England), whereas the rich literature treating lichen ecology on the European continent is mentioned very briefly.

As in the former issue, the chapters on "Chemistry of lichens" and "Biochemical systematics" are especially interesting. They summarize not only the results contained in ASAHINA's and SHIBATA's classical treatise (1954) but also a good deal of information gained from the literature of the last decade. ASAHINA's method of recrystallizing lichen substances is referred to in some detail, where thin-layer cromatographic methods recently presented by, e.g., WACHTMEISTER and J. SANTESSON are mentioned in few words. In the actual problem what to do with the "chemical species" introduced from various premises by NYLANDER, RÄSÄNEN, GYELNIK, ASAHINA et al. HALE represents an intermediate school. The concept of "chemical strain" proposed by LAMB, which has no status under the Code of Nomenclature, is discussed, and several examples of the importance of "chemical strains" to lichen taxonomy and lichen distribution are given.

Most illustrations are of first-class quality, especially some black-and-white close-ups of lichen thalli showing various morphological concepts.

The reviewer finds very few things to criticize. The formula of polyporic acid (p. 107) has got a superfluous OH in each of the two phenyl groups [cf. HEGNAUER, Chemotaxonomie der Pflanzen I (1962) p. 128]. The list of literature refers to the journals only and does not give the title of the work quoted. The reviewer is afraid that this system, though frequently used in chemical or medical papers, will give rise to objections from many botanical readers.

These minor remarks will not obscure the obvious fact that Dr. HALE has written a most stimulating introduction to modern general lichenogy. Seldom has a student who wants to tackle the various fields of lichen science got so brilliant a survey of principles and problems as in this condensed little volyme.

OVE ALMBORN

VERNON AHMADJIAN: The Lichen Symbiosis. — Blaisdell Publishing Company, Waltham, Mass. 1967. 152 pp. 53 figures, Price $ 5.75.

One hundred years have elapsed since SCHWENDENER (1867) asserted that lichens were not independent organisms but associations of fungi and algae.

SCHWENDENER described the lichen fungus as a parasite living on algae "like a spider on its prey, with a fibrous net of narrow meshes. — The fungus, however, incites the algae found in its net to more rapid activity, even to more vigorous increase". SCHWENDENER's theory was bitterly defeated by most of the leading lichen taxonomists of the past century, e.g. CROMBIE, NYLANDER and MÜLLER ARGOVIENSIS. After the turn of the century, however, it was generally accepted though, even in the 20's and 30's, some odd botanists (F. ELFVING, H. KYLIN) believed in the lichens as non-composite plants producing gonidia as sort of reproductive bodies.

SCHWENDENER's ideas initiated a series of investigations aiming at separating the fungal and the algal components of the lichens in cultures and at resynthesizing a lichen thallus. Up till in the last decade synthesis experiments had no obvious success: only some initial stages of contact between fungal hyphae and algal cells were developed.

Professor V. AHMADJIAN (Clark University, Worcester, Mass., U.S.A.) has recently published important new results concerning the nature of lichen symbiosis. Using new techniques in isolating fungus and alga and new media for cultures he has reached further than any other botanist toward resynthesizing a lichen. Some of his results were presented to a broad public in a well-illustrated article in the "Scientific American" (1963). He has also published valuable treatises on the taxonomy of the algae known as symbionts in the lichens.

The present volume is welcomed as a condensed survey of the standing of present research on the lichen symbiosis. The headings of the main chapters reflect the contents: "Isolation and nature of lichen symbionts", "Physiology of lichen symbionts", "Nature of lichen association", "Physiology of the composite plants" and "Lichen chemistry". The last-mentioned topic where the last few years have seen a flow of important new results is treated very superficially in five pages.

The book is designed as a text-book for the somewhat advanced student and as a reference source in experimental lichenology. The list of literature given in the final chapter is a very selected compilation from an extremely rich literature. Several important references have been quoted with brief annotations.

No doubt Dr. AHMADJIAN's wellwritten little volume will serve as a useful guide to a most fascinating field in modern biological research.

OVE ALMBORN

HOPKINS, DAVID M. (editor): The Bering Land Bridge. Stanford University Press, 1967. 495 sid., rikt illustrerad. Pris 18: 50 doll.

Arbetet är en symposiebok, med 28 författare, till vilken initiativet togs vid VII. internationella kongressen för kvartärgeologi i Boulder, Colorado, 1965. Det är en unik prestation därigenom, att vi här för första gången upplever ett aktivt samarbete mellan amerikanska och ryska forskare till lösandet av ett stort gemensamt problem: de forntida landförbindelserna mellan Gamla och Nya Världen.

Berings Sund är inte bara smalt, ca. 90 km, utan också mycket grunt. En sänkning av strandlinjen på endast 46 m skulle spärra sundet, och de nivåförändringar havsytan varit utsatt för, särskilt under kvartär tid, har ofta betydligt överstigit detta mått. Varje nedisning innebar, att stora mängder vatten undandrogs havet och lagrades som glaciärer på kontinenterna; en världsvid s.k. eustatisk sänkning av havsytan blev följden. Genom samordning av strandlinjestudier i Alaska och på Tschuktsch-halvön, som begränsar Berings Sund i väster, har man nu tämligen exakt kunnat ange dess nivå under olika faser av kvartärtiden. För den senaste nedisningen (Würm = Wisconsin) anses sänkningen ha uppgått till minst 115 m, under den föregående (Riss = Illinoian) till minst 135 m. I båda fallen uppstod en mycket bred landförbindelse, som i söder sträckte sig ända till Pribilof-öarna.

Möjligheter för växter och djur att utnyttja denna landbrygga mellan kontinenterna, bestämdes emellertid i hög grad av klimatiska och andra ekologiska faktorer. Landförbindelsen ägde bestånd under *kalla* perioder. Genom analys av pollen och andra fossil har man visat, att dess vegetation var av stäpp-tundra-karaktär och att skog saknades. Effekten därav ser vi bl.a. i det förhållandet, att inga trädarter är gemensamma för Nordamerika och Sibirien.

Glaciärernas utbredning inom Bering-området (»Beringia») hade naturligtvis avgörande biologisk betydelse, eftersom förbindelsen under kvartär fungerade endast under nedisningsperioder. Det har emellertid sedan länge varit bekant, att stora delar av Alaska, i norr och väster, aldrig varit täckta av is. I denna bok visas (bl.a. av O. M. PETROV), att även NO-Sibirien var mycket ofullständigt nedisat.

Isarnas ringa utbredning inom Beringia innebar inte bara, att förbindelsen fungerade även under nedisningarnas maximum, utan dessutom att floror och faunor tämligen ostört kunde stanna kvar och utveckla sig genom hela kvartär på ömse sidor av sundet. Det stora antalet endemer inom området är en följd av detta.

Om man jämför förhållandena under de båda senaste nedisningarna, Riss (Illinoian) resp. Würm (Wisconsin), åskådliggjorda med två kartor av HOPKINS (p. 462), skall man finna, att isen hade en något större utbredning under Riss, särskilt på den sibiriska sidan, där dessutom en havsarm (»Anadyr Gulf») söderifrån nådde ända fram till Tschuktsch-halvön. Möjligheterna för migration av växter och djur bör alltså ha varit större under Würm.

Förbindelsen var — enligt G. G. SIMPSON's benämning — en typisk »filter bridge», som tillät passage endast av arktiska, och delvis subarktiska, element. Den vidsträckta, ofta obrutet cirkumpolära, utbredningen av sådana arter, både växter och djur, kunde endast för extremt lättspridda arter ha uppnåtts *utan* Bering-förbindelsen.

Nu förekommer det likväl en betydande släktskap mellan Nordamerikas och Asiens floror och faunor även bland former med större värmekrav, främst mellan element i Ostasien och Cordillererna. Redan det förhållandet, att släktskapen här ligger på en högre taxonomisk nivå (släkte eller grupp), antyder emellertid, att vi här har att göra med äldre, pre-kvartära förbindelser. Lyckligtvis har man nu tillgång till växtfossil från flera tertiära horisonter, både i Alaska och NO-Sibirien. Det visar sig, att floran ända fram mot slutet av

miocen dominerades av artrika lövskogar (med *Carya, Juglans, Liquidambar, Platanus*, etc.), vilka anses peka på en juli-temperatur över 20°C., och att dessa först mot övergången till pliocen ersattes med barrskogar av nordligare typ. Det betydelsefullaste i detta sammanhang är, att »Bering-bron», som tydligen hade existerat under tidig tertiär, ägde bestånd ända fram i mellersta miocen, då den alltså var bevuxen med värmekrävande lövskogar.

Människans förhållande till Bering-förbindelsen diskuteras i två uppsatser. Att förfäderna till indianer, eskimåer och aleuter kommit över från Asien denna väg, har länge stått klart, men fattigdomen på arkeologiska fynd gör exakta dateringar omöjliga. De äldsta spåren av människa i Alaska, på den lilla ön Anangula vid Umnak i Aleuterna, är bara drygt 8.000 år gamla. Men betydligt äldre fynd, upp till 25.000 år, nyligen publicerade från Canada och Mexiko, visar, att människan anlände tidigare än i postglacial tid, enligt HOPKINS (p. 478) sannolikt under Würm-interstadialen.

W. S. LAUGHLIN, som skriver om den nämnda Anangula-kulturen, anser att spridningen dit betingats av att de inre Aleuterna hade landförbindelse med Alaska-halvön. Att detta inte varit fallet under sen- eller postglacial tid, framgår emellertid av faunans sammansättning på dessa öar, med en skarp gräns mellan Unimak (närmast fastlandet) och Unalaska-Umnak.

»The Bering Land Bridge» är ett utomordentligt vackert exempel på, vilka goda resultat som kan nås genom ett välorganiserat team-work av geologer och biologer.

CARL H. LINDROTH

BAKER, A. H. and OLIVER, E. G. H.: Ericas in Southern Africa. Purnell, Cape Town and Johannesburg. 1967. LXIV+180 pp. and 167 plates in full colour. Price R 12.50 (ca. 90 Sw. kr.).

Erica is the largest genus of higher plants in South Africa. It is represented by ca. 605 species south of the Limpopo River. Of these the great majority is concentrated in the area of the "fynbos" or sclerophyll, a low scrub vegetation typical especially of the southwestern divisions of the Cape Province with a preponderant winter rainfall. On the Cape Peninsula, not larger than a fraction of the Province of Scania in south Sweden, there are as many as 103 species of *Erica*.

It is difficult for a person not acquainted with the South African flora to imagine the vast range of variation in a genus like *Erica*. The flowers vary from ca. 3 cm long and ampullaceous, as in *E. aristata*, or large and urceolate, as in *E. blenna*, to minute and smaller than in *Calluna*, as in species like *E. hispidula* or *copiosa*. The flowers may have almost any shade of colour (except blue). They may be solitary on long peduncles or assembled in sparse or close spike, head, or umbel-like aggregates on the branch ends. The leaves are usually "ericoid" (i.e. linear and subterete) but they are sometimes flat and rounded, as in *E. oxycoccifolia*. An even greater and systematically more valuable diversity is found in the corolla, stamens, and pistil. Especially the anthers, which frequently have peculiar processes, contribute with a surprising variety of morphological characters.

Such a genus needs highly qualified systematists for a proper handling, and the present work is the result of an extremely lucky cooperation between the several artists and the two authors, the older a devoted *Erica* collector since many years, the younger a botanical scientist with profound experience in the group. This team has produced a book equalled by few in its field. All of the 167 species treated are illustrated in full colour with a branch in natural size and with leaves, flower, pistil, and stamens enlarged. The painting work has a high and even standard in spite of the different artists. The species are selected with great care, and each of all the 41 sections enumerated in the introduction is represented by one or several species.

In the introduction we also find a useful glossary adapted for the genus, an account of the distribution, and observations on habitat, on flowering time, on systematically useful characters, and even on cultivation. In a map of southernmost Africa the total distribution of *Erica* is outlined. The distribution follows closely the area of the "fynbos" vegetation. The descriptions and remarks under each of the species reveal a profound knowledge of the species, their variation in the field, their distribution, etc.

'Ericas in Southern Africa' is a book which should be of great interest not only to the professional botanists and to the South African public interested in botany, but also to horticulturists and amateur gardeners, as many species are cultivated and even many more deserve being introduced into cultivation in greenhouse and, where possible, in rock gardens. I believe that this book will be a stimulus in that respect.

As a botanical work the book has a great interest to anyone who wishes an example of great differentiation within a single genus in a flora where most species occur as regionally limited populations, many ecologically rather specialized.

South Africa is rich in other groups with similar differentiation, and many genera are endemic there. The success of the present book will probably be an encouragement in the publication of similar treatises, e.g. on various genera of *Proteaceae* and other groups which are at present subject of monographic work in the country.

ROLF DAHLGREN

KÖRBER-GROHNE, UDELGARD: Geobotanische Untersuchungen auf der Feddersen-Wierde. I, Textband, 359 S., 13 Beil., II, Tafelband, 84 Tafeln. Franz Steiner Verlag, Wiesbaden 1967.

Die Arbeit von UDELGARD KÖRBER-GROHNE ist das Ergebnis einer sehr eingehenden Untersuchung der vorgeschichtlichen Vegetation in dem nordwestdeutschen Bezirk Feddersen-Wierde, die in Zusammenhang mit mehrjährigen archäologischen Ausgrabungen gemacht wurde. Sowohl die natürliche als die kulturbedingte Vegetation wurde studiert und die Bearbeitung fand durch verschiedene Methoden statt: Untersuchung der Makrofunde, Pollenanalyse, Diatomeenbestimmungen, chemische Analysen usw.; zum Ver-

gleich wurden auch Untersuchungen des heutigen Pollenniederschlages und sogar Anbauversuche in unbedeichter Marsch vorgenommen. Das Ergebnis ist eine sehr allseitige Darstellung, die vor allem eine detaillierte Kenntnis der lokalen botanischen Verhältnisse in den ersten Jahrhunderten unserer Zeitrechnung. (1. bis 3. Jahrh.) ermittelt aber auch ergänzende Angaben von früherer oder späterer Zeit gibt und viele Beiträge von allgemeinem Interesse liefert.

Die Arbeit besteht aus einem allgemeinen Teil und zwei speziellen Teilen, von denen der erstere die verschiedenen Kulturpflanzen behandelt, während in dem zweiten die zahlreichen Wildpflanzen aufgeführt werden, die durch Makrofunde festgestellt wurden, mit Angaben über ihre charakteristischen Merkmale, ihr Vorkommen usw. Der Tafelband enthält zahlreiche gute photographische Abbildungen.

Die wildwachsenden Kräuter der vorgeschichtlichen Zeit waren Ufer-, Wiesen- und Wasserpflanzen, die letzteren sowohl Süsswasser- als Brackwasserarten. Die meisten davon kommen noch immer im Gebiet vor, aber die Verhältnisse haben sich etwas verschoben; offenbar kamen mehr Halophyten in vorgeschichtlicher Zeit vor; durch Bedeichung und vielleicht auch durch Verschiebung der Uferlinie hat sich der Einfluss des Meeres vermindert. Durch Pollenanalyse wurde gezeigt, dass der Wald, der in den höheren Gebieten vorkam, wahrscheinlich ungefähr die doppelte Fläche gegenüber den jetzigen Verhältnissen einnahm. Bei Betrachtung einer längeren Periode zeigte sich, dass die erste schwache Ansteigung der *Fagus*-Kurve bei ca. 960 v.Chr. eintrat, und dass das Maximum etwas nach ca. 650 n.Chr. lag; für die *Carpinus*-Kurve sind die entsprechenden Zahlen ca. 175 v.Chr. und ca. 220 n.Chr. bis früheres Mittelalter.

Unter den Kulturpflanzen, die in den alten Schichten nachgewiesen wurden, waren Gerste und Hafer dominerend. Die Gerste kam hauptsächlich als vierreihige Spelzgerste vor, aber Nacktgerste trat auch in geringerer Menge auf. Der Hafer bestand aus Kulturhafer, Flughafer und — in ansehlicher Menge — auch aus einem „Mischtyp" zwischen den beiden, vielleicht einer ursprünglichen Kulturhaferform. Hirse kam in kleiner Menge vor; die Verhältnisse deuten indessen darauf, dass sie nicht kultiviert, sondern eingeführt war. Von Lein und Leindotter (*Camelina sativa*) wurden viele Funde gemacht; offenbar waren diese Pflanzen wichtige Ölpflanzen; der Lein wurde auch einigermassen als Fiberpflanze benutzt. Saubohne (Vicia faba) und Färber-Waid (*Isatis tinctoria*) waren andere Nutzpflanzen, und Haselnüsse und Holunderbeeren wurden eingesammelt; sonst waren die eingesammelten Wildpflanzen offenbar von geringer Bedeutung, z.B. im Vergleich mit nordischen Verhältnissen.

Die pollenanalytischen Beobachtungen ergänzen zum Teil die Makrofunde; z.B. wurde festgestellt, dass der Roggen, der nicht in den anderen Funden vorhanden war, in den Pollenanalysen um 200—300 v.Chr. auftrat, während der Hafer dort etwas später, ca. 175 v.Chr., sich zeigte.

Die Funde im Feddersen-Wierde-Gebiet werden von der Verfasserin in Zusammenhang mit den Beobachtungen in anderen Gebieten gebracht und Ähnlichkeiten und Differenzen hervorgehoben. Natürlich kann es dabei eintreffen, dass einige Tatsachen übersehen werden; z.B. ist der Waid in vor-

geschichtlicher Zeit nicht nur aus Grossbritannien, Dänemark und Norwegen, sondern auch aus Schweden (Halland) bekannt, und der Dotter ist auch an anderen Orten in Schweden als die angeführten angetroffen. Im allgemeinen hat die Verfasserin jedoch die allgemeinen Zusammenhänge gut beleuchtet, und ihre Arbeit ist ohne Zweifel durch ihre Gründlichkeit und Allseitigkeit ein sehr wertvoller Beitrag zu dem Bild, das wir uns von der natürlichen und anthropogenen Vegetation in dem vorgeschichtlichen Europa allmählich machen können.

HAKON HJELMQVIST

Meddelande

Avdelningen för ekologisk botanik vid Umeå universitet (adress Umeå 6) är i stort behov av litteratur och samlingar och ber om stöd av institutioner och enskilda, som med eller utan ersättning kan avstå sådant material. Varje slag av bidrag kommer att gagna den botaniska undervisningen och forskningen vid universitetet.

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