Drawings of Scandinavian Plants 15–16

Eleocharis R. Br.

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Eleocharis parvula (R. & S.) LINK ex BLUFF, NEES & SCHAUER in BLUFF & FINGERH.

[*Scirpus parvulus* R. & S., *Limnochloa parvula* (R. & S.) REICHB.]

This minute water plant belongs to ser. *Pauciflorae* SVENS.

Creeping shoots rhizomatose or stoloniform, filiform, with a spongy periphery and a wiry center of vascular bundles, with one to a few 5—15 mm long internodes, then producing *a tuft of assimilating shoots or terminating in a 3—5 mm long, beaked, bulbous resting bud. Sheaths of the creeping stems and basal sheaths of the culms inconspicuous, membranaceous,* sometimes with a dark venation of minute vascular bundles near their bases; orifice of the inner culm sheaths inconspicuous, straight or somewhat oblique, most often lacerated.

Culms thin (0.3—0.5 mm in diameter), (1.5—) 2—5 (—7) cm high, ascending to recurved; collenchyma strands weak and few, (3—) 5—12 (—16) epidermal cell rows between them; commonly only one weakly developed palisade layer, but no parenchymatous layer in the interspaces between the few (2—4) and weak vascular bundles, resulting in ± *spongy, translucent, whitish-green or straw-coloured culms.* Cell walls thin and markedly undulated; stomatal guard cells with convex short ends and of about the same length as the subsidiary cells; stomatal length 35—50 (—55) μ, stomata broader than in other species studied (their length < twice their width).

Spikes usually shorter than 3 mm, fusiform, when ripe broadly ovoid, in deeper water often reduced and most of the culms remaining vegetative. *Basal glumes amplexicaul,* reaching to about half the length of

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[1] STRANDHEDE is responsible for the text, DAHLGREN for the drawings.

the spike or more [length (1.0—) 1.3—2.0 (—2.2) mm, width 0.8—1.4 mm], *light-coloured with a broad, greenish midrib, ± membranaceous, commonly empty. Fertile glumes* (1.5—) 1.7—2.5 mm, ovate, obtuse to subacute, commonly *whitish-green* or brown to straw-coloured, sometimes with two brown stripes, ± membranaceous. The total number of flowers up to 10; receptacle density 40—50 (—60) fruits per cm of the rachis. (The exactness of this value is low as the lengths of the racheae commonly are ≦ 3 mm.)

Thecae pale or whitish-yellow, length (0.7—) 0.9—1.2 (—1.4) mm. *Filaments markedly broad and connectives with large, often brownish cells, protruding ≧ 0.1 mm*[2]. Shape of pollen grains rounded; length 32—40 (—44) μ, width 24—32 (—40) μ.

Achene shape pronouncedly trigonous and depressed-pyriform to obovate in outline, without a prominent apex; length 0.9—1.2 mm, width 0.6—0.7 mm; lustrously straw-coloured; surface smooth. Style trifid. *Style bases* triangular, 0.1—0.2 mm long and broad and *confluent to the achenes.* Bristles commonly 6, rarely 3 or 3—6, equalling or somewhat exceeding the achenes, rarely rudimentary; barbs minute and sparse, retrorse.

Chromosome number 2n=10 (according to reports published).

As all other species of *Eleocharis* in Scandinavia, it is perennial. It flowers later than other taxa (July to August), but it remains often completely barren. *E. parvula occurs in the eulittoral zone along the sea coasts, where it forms mats in soft and muddy bottoms of shallow and sheltered bays.* It is sparsely distributed along *the Scandinavian west coast southwards from Nord-Tröndelag in Norway, through Öresund and along the coasts of the Baltic Sea northwards to the southern parts of the Gulf of Bothnia.* It is rare throughout Denmark.

Outside Scandinavia *E. parvula* has been reported from several localities in western Europe and along the Mediterranean Sea. It occurs in saline areas of S.E. Europe and Asia. From North America, it is known from the East and West coasts and from saline areas of the interior. A few reports are known from South America (Venezuela, Brazil), Japan, and South Africa (?).

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[2] Similar tips of the connectives occur in a few other species of *Eleocharis*: > 0.1 mm long in *E. multicaulis*; ≦ 0.05 mm long in *E. quinquefolia* and *E. acicularis*.

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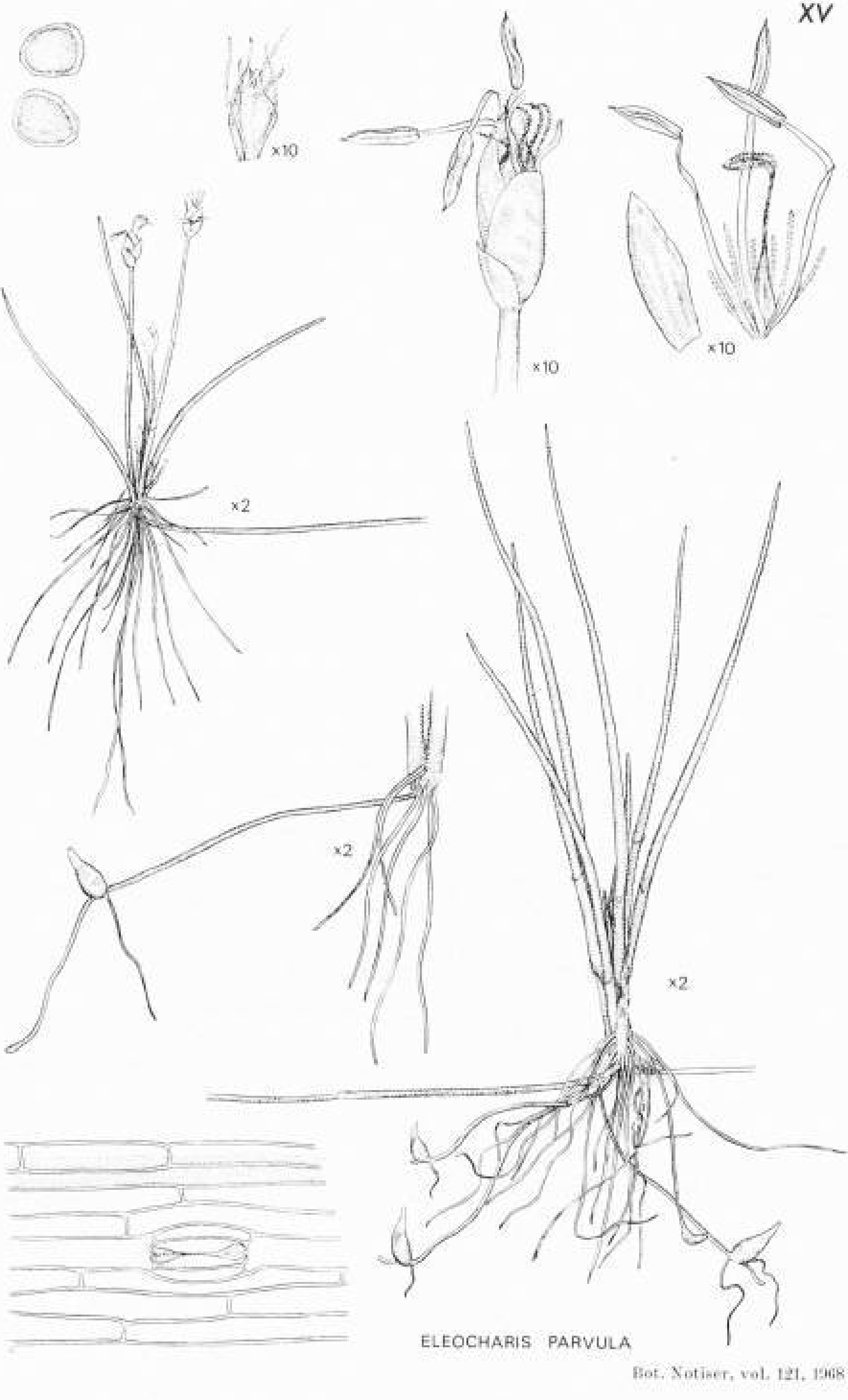


ELEOCHARIS PARVULA

Eleocharis acicularis (L.) R. & S.

[*Scirpus acicularis* L., *Isolepis acicularis* (L.) SCHLECHT., *Limnochloa acicularis* (L.) REICHB.]

This species belongs to ser. *Aciculares* (C. B. CLARKE) SVENS. The species deviates from other species of *Eleocharis* especially in its fruit morphology.

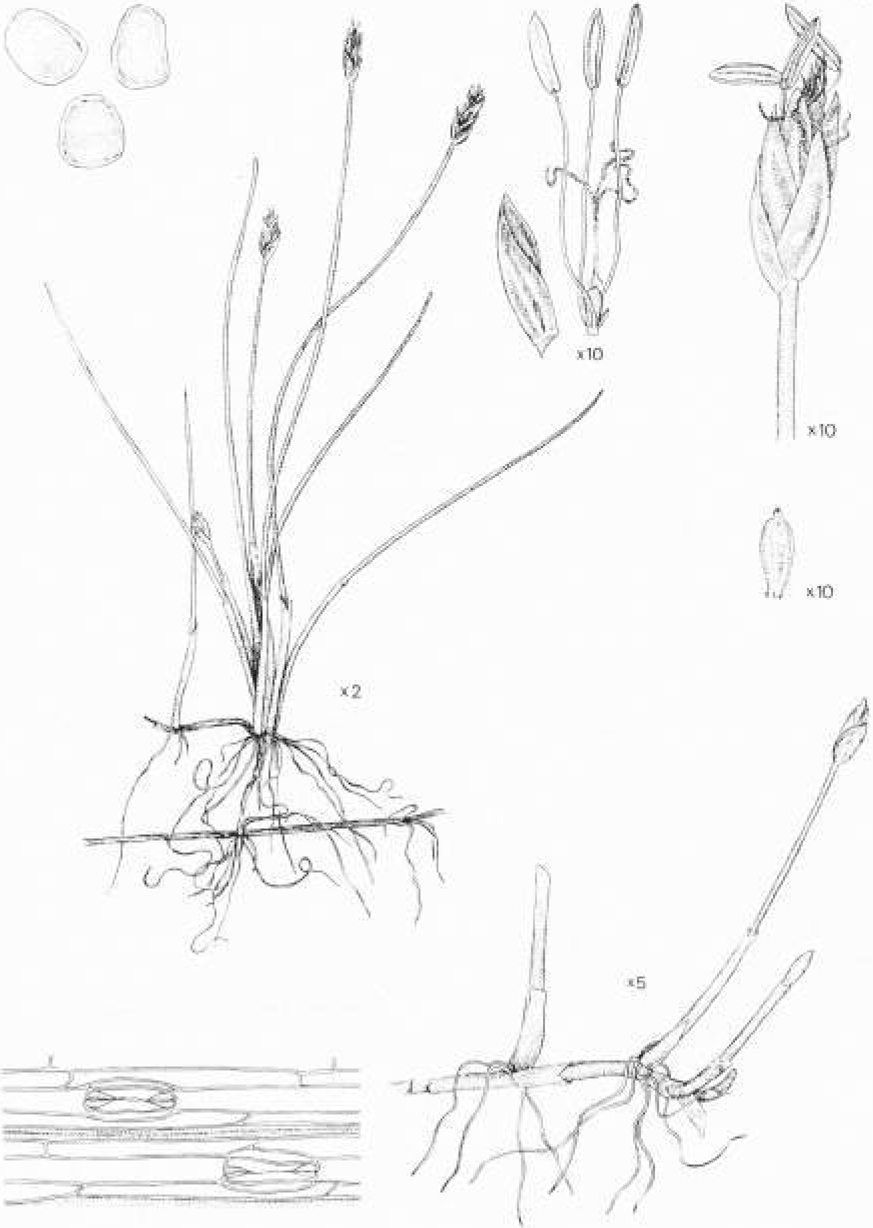
Rhizomes composed of 10—15 mm long internodes of successive shoot generations, *filiform*, with a spongy periphery and a wiry center with vascular bundles: *at each node an assimilating shoot and a sheath-like leaf in the axil of which a new shoot generation is produced;* from the axil of the basal sheaths of the assimilating shoots new assimilating shoots develop, and a cluster of shoots is formed at each node of the rhizome. *Basal sheaths of the culms greenish to reddish, membranaceous; orifice oblique.*

Culms filiform (0.1—0.4 mm in diameter), 2—10 cm high, when submerged sometimes up to 20—30 cm; collenchyma strands weak, 4—8 (—12) cell rows between them; commonly two cell layers, one somewhat palisadic, the other parenchymatous in the interspaces between the vascular bundles. *The number of vascular bundles commonly 4, resulting in 4-angled green to deep green culms,* when submerged semi-translucent and normally barren. Cell walls thin, straight or moderately undulated. Stomatal guard cells with convex short ends, and the subsidiary cells of about the same length or shorter, resulting in ± convex ends of the stomata; stomatal length 32—52 μ.

Spikes 2—5 (—7) mm, in the prefloral stage somewhat compressed and fusiform, later oblong-ovoid, in deeper water often reduced and most of the culms barren. *Basal glumes amplexicaul,* rather short (length 1.5—2.3 mm, width 0.7—1.3 mm), *reddish-brown to dark brown, with a broad, greenish midrib and hyaline, silvery margins, normally with a flower in its axil. Fertile glumes* (1.5—) 1.7—2.2 (—2.4) mm, ovate to lanceolate, somewhat obtuse to acutish, when submerged pale brownish to greenish, otherwise *reddish-brown to dark brown, with a greenish midrib and hyaline, silvery margins.* The total number of flowers 4—12 (—16); receptacle density 32—45 fruits per cm of the rachis. (The exactness of this value is low as the racheae are shorter than 5 mm.)

Thecae pale yellow and 0.7—1.3 mm. Pollen grains ± rounded or sack-shaped; pollen length 32—40 μ, width 28—32 (—36) μ.

XVI



ELEOCHARIS ACICULARIS

Achene shape obovate to oblong in outline; length 0.8—1.1 mm, width 0.4—0.5 mm; colour shining white or yellowish, rarely brownish, with a white, marked reticulation of about 8—10 longitudinal ribs and a fine and close transverse striation. Styles normally trifid. *Style base, though small, prominently developed, ± necked, conical-shaped;* length and width 0.1—0.2 mm. Bristles up to 4, slender and shorter or as long as the achenes, often rudimentary; barbs short, adpressed and ± retrorse.

Chromosome number $2n = 20$. (Specimens from c. 25 localities have been studied.)

E. acicularis often forms more or less closed mats in wet clayish or sandy soils without other dense vegetation. It occurs along the margins and in the bottoms of small ponds, lakes and rivers, but also in brackish bays along the Baltic Sea to a depth of more than one metre. When deeply submersed, it remains vegetative.

It is known from almost all parts of Scandinavia below timberline, but it may be more or less rare, especially northwards. It is sporadically distributed in Denmark, and occurs mostly near the coasts in Iceland.

The general distribution of *E. acicularis* is circumpolar. It occurs throughout most of Europe; it is known from large parts of the USSR, from Arkhangelsk in the north to Crimea and the Caucasus in the south, and eastwards from Siberia to Kamchatka. In North America it is distributed from Alaska to western Greenland southwards to northern Florida and Mexico.

Gametophytes of Equisetum ramosissimum Desf. subsp. ramosissimum. I. Structure and Development

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ABSTRACT

The gametophytes of *Equisetum ramosissimum* Desf. subsp. *ramosissimum* occur on the east bank of the river Yamuna in Delhi. They are reddish-green, compact, and cushion-like, and are available from November to February. The gametophytes are male, female or bisexual and grow by a peripheral meristem. A vertical section shows 3 regions — (*1*) the upper part consisting of erect lobes and arising from a (*2*) middle prostrate system of parenchymatous cells and (*3*) the lower portion bearing numerous unicellular, smooth-walled rhizoids.

Spores were grown on Moore's medium to study germination and details of development of the gametophyte. The gametophytes raised in vitro were also male, female and bisexual but their morphology was very different from those growing in vivo. The former were flimsy, erect and much branched.

The sex organs differentiate in the peripheral meristem and show eusporangiate type of development. Each antheridium is surrounded by a single jacket layer and contains numerous multiciliate, spirally-coiled spermatozoids which are liberated through a pore formed by the separation of cover cells. The archegonia normally contain 2 equal or unequal neck canal cells, a single ventral canal cell and the egg. Occasionally some archegonia show the presence of 2 well-differentiated ventral canal cells. Just before fertilization the 2 neck canal cells and the ventral canal cell degenerate to form a canal. Fertilization is affected by the entrance of the spermatozoid into the egg through its anterior end after casting off its cilia. Numerous archegonia become fertilized but only a few form mature sporophytes.

INTRODUCTION

The genus *Equisetum*, the sole living representative of the *Equisetales*, consists of 30 species which are distributed all over the world barring Australia and New Zealand. The plants are homosporous but the gametophytes of the different species are reported to be unisexual or both unisexual and bisexual.

The earlier literature pertaining to the structure, development and sexuality of the gametophyte has been critically reviewed by HAUKE (1963). An analysis of the literature shows that the findings are not unanimous regarding the following features: (*a*) formation of rhizoids, (*b*) development of antheridia (whether eusporangiate or leptosporangiate), (*c*) mechanism of sperm liberation and (*d*) presence of a single or 2 distinct neck canal cells in the archegonium.

The present work was undertaken to investigate thoroughly the above mentioned features and also to study the detailed structure of the gametophyte, development of sex organs and the process of fertilization in the locally occurring *E. ramosissimum* DESF. subsp. *ramosissimum*. Observations on the effects of environmental and nutritional factors on the sexuality of the gametophytes will be published elsewhere.

MATERIAL AND METHODS

The gametophytes were collected from the east bank of the river Yamuna (Delhi). They appear from the end of November and persist up to late February. The gametophytes were fixed in medium chrom-acetic acid (10 per cent aqueous acetic acid, 7 cc; 10 per cent aqueous chromic acid, 10 cc; distilled water, 83 cc; JOHANSEN 1940). The material was kept in the fixative for 18 to 20 hours followed by washing in running tap water for 12 to 16 hours. The washed material was gradually changed to 70 % ethyl alcohol. The gametophytes were treated with 10 % hydrofluoric acid for 7 days and then thoroughly washed in 70 % alcohol. The treated material was dehydrated in the alcohol-xylol series, and imbedded in paraffin. The imbedded material was soaked in water for 2 weeks before sectioning. The gametophytes were sectioned at a thickness of 10 to 13 microns and were stained with safranin-fast green or iron-haematoxylin.

The structure of mature spermatozoids was studied from permanent slides made in the following way: a drop of water containing living spermatozoids was placed on a slide and fixed over fumes of glacial acetic acid. The slide was dried, stained in an aqueous solution of crystal violet, dehydrated in alcohol-xylol series and mounted in canada balsam.

Since it was difficult to study the early developmental stages of spore germination from samples collected from soil, it was considered useful to culture the spores in vitro. CASTLE (1953) had earlier used Moore's medium successfully for in vitro studies on *Equisetum arvense*. The same medium was therefore used in the present study.

Mature but undehisced cones were collected and stored at 4°C in wax paper bags. They were surface-sterilized with chlorine water for 15 minutes with frequent shaking. The peltate sporangiophores were separated from the cone axis and washed with sterile water under aseptic conditions. A single sporangium was isolated from the cone with the help of a sharp blade and was planted on the medium. Stages in the germination of spore were observed from temporary water mounts of portions of agar removed from the surface of the medium with the help of a sterilized scalpel. In the beginning, germinated spores were removed daily for observation, but when young sporelings were formed, they were taken out at intervals of 3 or 4 days. For a detailed study of the gametophytes (grown in vitro) permanent whole mounts were prepared either in tertiary-butyl alcohol series or after clearing (FOSTER 1949) and mounting them in canada balsam.

The nutrient medium used for in vitro studies contained the following (in mg/l): NH_4NO_3 (500), KH_2PO_4 (200), $MgSO_4 \cdot 7H_2O$ (200), $CaCl_2 \cdot 2H_2O$ (100), $MnSO_4 \cdot 4H_2O$ (3.0), H_3BO_3 (0.5), $ZnSO_4 \cdot 7H_2O$ (0.5), $CuSO_4 \cdot 5H_2O$ (0.025), $CoCl_2$ (0.025), $NaMoO_4 \cdot 2H_2O$ (0.025), H_2SO_4 (0.0005), $FeC_6O_5H_7 \cdot 5H_2O$ (10.0), and sucrose (5000).

The liquid medium was jelled with 0.8 % 'Difco' Bacto-agar and the pH was adjusted to 5.8. Twenty ml of the medium was dispensed into each of the culture tubes (15.2×2.4 cm) and plugged with non-absorbent cotton wrapped in cheese cloth. The tubes containing the medium were sterilized by autoclaving at 1 kg pressure/sq.cm for 15 minutes.

The cultures were maintained at a temperature of 25±2°C and a relative humidity varying between 55 to 60 %. The intensity of light was around 15 ft-c. and the duration 11 hours daily.

SPORE GERMINATION AND DEVELOPMENT OF GAMETOPHYTE

The spores of *Equisetum* are globular, surrounded by a coat which is made up of four layers namely, intine, exine, middle layer and pseudoelaters. The pseudoelaters are two spirally coiled, ribbon-like structures, having spoon-shaped ends (Fig. 1 A). The presence of numerous chloroplasts in the spore gives it a green colour. On the basis of germination tests, the maximum period of spore viability was found to be 8 or 9 days after maturation.

On Moore's basal medium spores germinate 2 or 3 days after planting. In the initial stages the spore swells up considerably, the middle layer breaks and the pseudoelaters are cast off (Fig. 1 B). The division of the spore nucleus is followed by the laying down of a wall which separates a smaller lenticular rhizoidal cell from the larger prothallial or gametophytic cell (Fig. 1 B). The latter contains numerous chloroplasts and oil droplets, whereas the rhizoidal cell has fewer cell inclusions. Further morphogenetic changes occur only in the gametophytic cell, the rhizoidal cell merely elongates to form the first rhizoid. The planes of division in the gametophytic cell are variable. The following patterns are commonly observed:

1. The division is transverse and the first wall may be laid down close to the rhizoidal cell (Fig. 1 C) or away from it (Fig. 1 D). The upper prothallial cell elongates (Fig. 1 E, H), and divides further to give rise to a uniseriate filamentous gametophyte (Fig. 1 H, I).

2. The first division in the gametophytic cell occurs after it has considerably elongated (Fig. 1 F, G).

3. The first division in the prothallial cell (Fig. 1 J, M) is vertical; of the resulting cells only one (Fig. 1 K, L), or both (Fig. 1 M, N) may take part in the formation of the gametophyte.

The subsequent divisions in all the above mentioned types are extremely variable and the developmental pattern of one gametophyte seldom resembles that of another. The rhizoidal cell may elongate at the 2-celled stage of the gametophyte or it may remain unchanged even when the gametophyte is multicellular. The second rhizoidal cell may differentiate when the gametophyte is only 4 or 5-celled, or at a much later stage. In a multicelled gametophyte new rhizoidal cells are formed by the unequal division of the superficial gametophytic cells (Fig. 1 O, Q). The smaller cell is densely cytoplasmic and elongates to form a rhizoid. The young filamentous gametophyte first grows by an apical cell but soon it organizes into a meristematic tip (Fig. 1 P).

Three sexually different types of gametophytes can be distinguished by their external morphology. Males are light green, with smooth and fleshy branches (Fig. 1 R); females are deep green, with much dissected, thin branches (Fig. 1 S) and the bisexuals show fleshy, male branches arising in between much dissected, thin, female branches (Fig. 1 T).

Fig. 1. Spore germination and development of gametophyte in vitro (*am*, apical meristem; *an*, antheridia; *cp*, chloroplasts; *mb*, male branch; *ml*, middle layer; *pc*, prothallial cell; *pe*, pseudoelaters; *rc*, rhizoidal cell; *rh*, rhizoid; *ri*, rhizoidal initial. All diagrams are from whole mounts.) — A. Mature spore before germination. ×143. — B. Germinated spore. The middle layer and the pseudoelaters are cast off. ×143. — C, D. First division in the prothallial cell; in C wall has been laid close to the rhizoidal cell whereas in D it is away from it. ×143. — E, H, I. Progressive stages in the development of a filamentous gametophyte. ×143. — F, G. Young sporelings; prothallial cell has elongated before division in F; the prothallial cell has divided in G. ×143. — J, M. Vertical division in the prothallial cell has formed two unequal or equal cells. ×143. — K, L. Gametophytes in which only one prothallial cell is participating in development. ×143. — N. Young gametophyte in which both the prothallial cells are developing. ×143. — O. Same as N, bearing two rhizoids. Note the apical meristem and rhizoidal initial. ×60. — P. Apical portion of a young gametophyte enlarged. ×143. — O. Portion of the gametophyte showing a rhizoidal initial formed by the unequal division of a gametophytic cell. ×143. — R. Male gametophyte. ×4. — S. Female gametophyte. ×4. — T. Bisexual gametophyte. ×4.

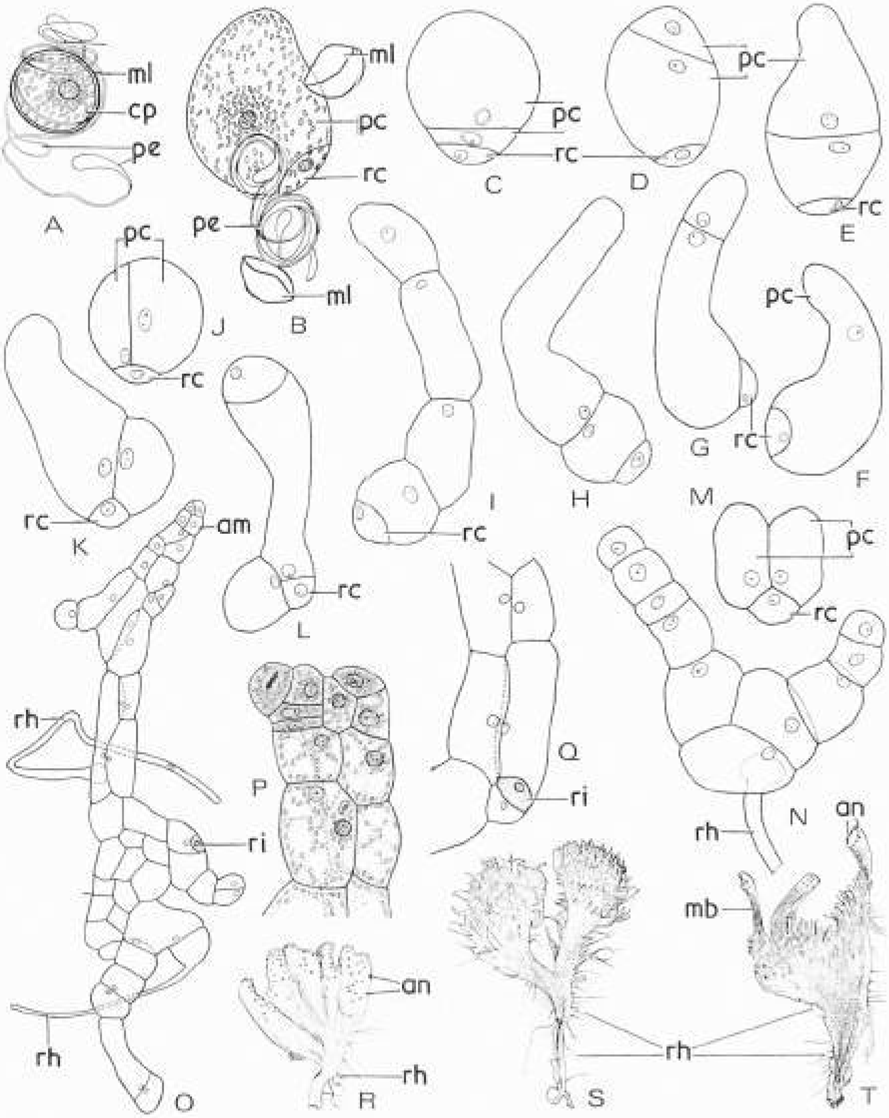
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Fig. 1.

The gametophytes raised in vitro are morphologically different from those occurring in nature. The latter are dorsiventral, compact, cushion-like (Fig. 2 A) and reddish-green or green in colour. The anatomy of the gametophyte collected from nature is described below:

A vertical section through the gametophyte shows 3 zones: (*1*) An upper, lobed, dark-green erect system; (*2*) a middle, light-green prostrate system, and (*3*) a lower, colourless rhizoid-bearing portion. The rhizoids keep the gametophytes firmly attached to the substratum and consequently, they cannot be easily removed from the soil.

The growth of the gametophyte takes place by a peripheral meristem (Fig. 3 A). The meristematic cells appear as inverted pyramids or as elongated columns in longisection (Fig. 3 C) and these cells are usually packed with chloroplasts (Fig. 3 B, C). The derivatives of the meristematic rim differentiate into the green lobes, tissues of the prostrate system, sex organs and many sterile cells. The last mentioned contain fewer chloroplasts and do not divide further.

The early development of the lobes is variable and may take place in the following ways:

(*a*) The inverted pyramid-like cell (lobe initial) divides obliquely to form two cells (Fig. 3 D). The lower cell adds to the thickness of the prostrate system and the upper cell undergoes two transverse divisions followed by a longitudinal division in the terminal cell alone (Fig. 3 E, F). Later divisions occur in various planes (Fig. 3 G). Rarely, only transverse divisions take place in the upper cell, resulting in the formation of a long uniseriate filament (Fig. 3 H).

(*b*) After the two-celled stage, the first division in the upper cell is transverse and the two cells divide longitudinally (Fig. 3 I).

(*c*) The first division in the upper cell is longitudinal, forming two cells followed by transverse and longitudinal divisions (Fig. 3 J, K). Further divisions are irregular and result in a massive branched lobe (Fig. 3 L). The lobes vary in height and reach up to 12 cells. The cells are uninucleate and are packed with chloroplasts. A fully formed lobe is a much branched structure with a narrow lower part and a broad, expanded upper part (Fig. 3 L, M). In some cells the chloroplasts degenerate and a red pigment accumulates (Fig. 2 B).

The prostrate system of the gametophyte consists of a compact tissue of 6 to 10 layers of thin-walled parenchymatous cells. The cells of the

Fig. 2. Gametophyte (*an*, antheridia; *dc*, darkly stained cells). — A. A female gametophyte growing on river bank enlarged to show its habit. ×6. — B. A superficial cross-section of the gametophyte showing irregular outline of the lobes. The darkly stained cells show degenerated chloroplasts. ×143. — C. Cross-section through a male gametophyte showing antheridia distributed along the periphery. ×28.

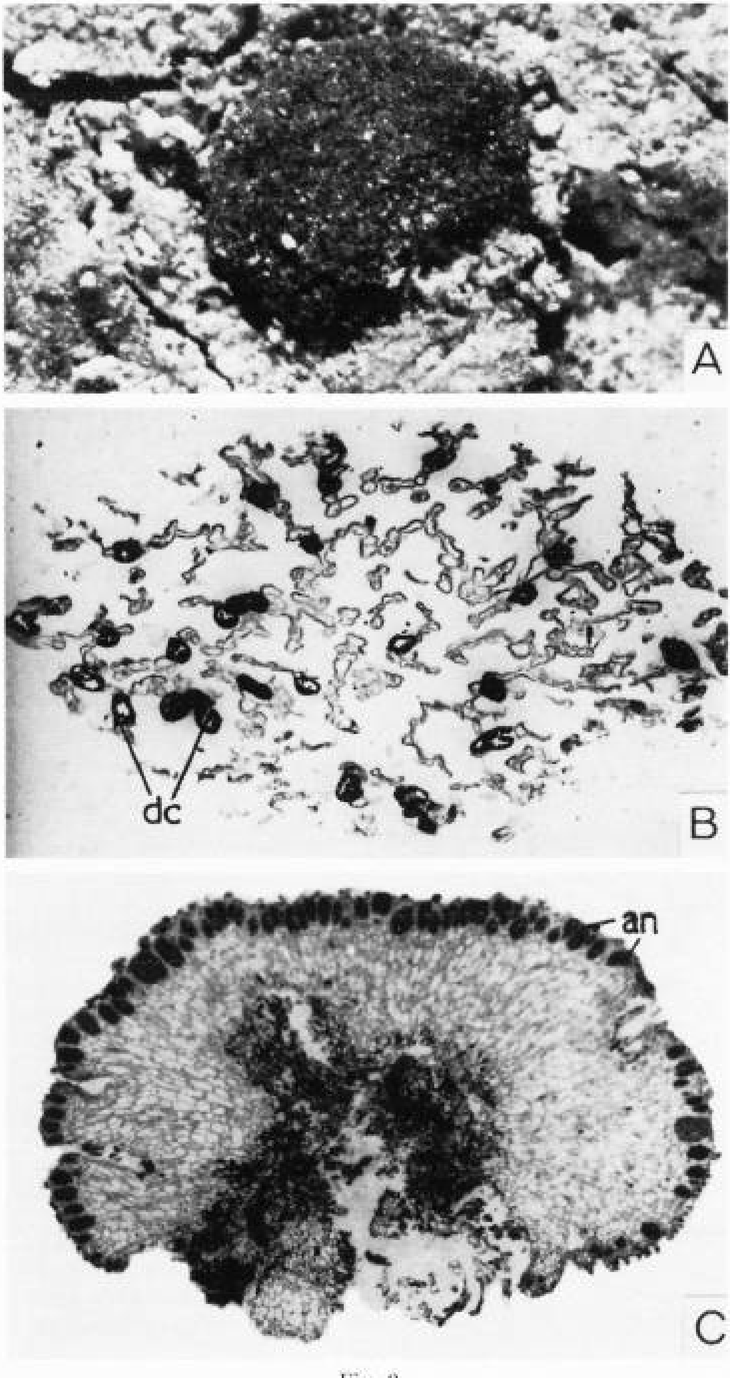

Fig. 2.

upper layer contain numerous chloroplasts and starch grains whereas the cells belonging to the lower part of the cushion are devoid of them. At maturity the cells of the prostrate system develop fibrous thickenings (Fig. 3 N), and they also accumulate oil droplets and starch grains (Fig. 3 O).

From the lower epidermis of the gametophyte certain cells grow out into rhizoids (Fig. 3 P—S). The rhizoidal initial contains a large nucleus and numerous starch grains (Fig. 3 P). As the initial elongates downwards, its nucleus moves into the protuberance. In a fully-formed rhizoid the cytoplasm along with its nucleus occupies the tip (Fig. 3 S). The mature rhizoid is nearly 1 cm long, smooth-walled and has a swollen base (Fig. 3 S).

Occasionally the gametophytes show a tuber-like structure on the ventral surface. The cells of this tuber are parenchymatous but densely packed with starch grains.

ANTHERIDIUM

The antheridia are produced all along the periphery of the gametophyte (Fig. 2 C). As new antheridia are produced by the meristem the older ones are pushed towards the centre. The antheridia are, for the most part, embedded in the tissue of the gametophyte and are surrounded by short, multicellular lobes (Fig. 4 I). In a mature gametophyte, the apical portions of antheridia can be easily recognized (as raised, yellowish green spots) with the help of a magnifying glass. If a mature antheridium is punctured with a needle, numerous spermatozoids ooze out in a white mass.

Fig. 3. Gametophyte (*ag*, archegonium; *c*, recently divided cell; *cp*, chloroplast; *li*, lobe initial; *mm*, meristematic margin; *ol*, oil droplets; *sr*, sterile cell; *t*, terminal cell.) — A. T.s. gametophyte showing peripheral meristem. ×29. — B. Enlarged view of a portion of the meristem from A; a recently divided cell can be seen (*c*). ×314. — C. Same as B, showing lobe initials (*li*) and sterile cells (*sr*). ×314. — D. Division of the lobe initial by an oblique wall. ×314. — E—G. Stages in further development of the lobe. ×314. — H. Uniseriate lobe. ×314. — I. Young lobe showing an anticlinal wall in the upper and the lower cell. ×314. — J—L. Irregular divisions in the lobes; figure L shows a narrow lower part and an expanded upper part. ×145. — M. Cross section of upper part of a mature lobe showing irregular outline. ×145. — N. Surface view of wall of a mature cell of the prostrate system showing thickenings. ×559. — O. A portion of the prostrate system; the cells are packed with oil droplets (*ol*) and starch grains. ×167. — P—S. Progressive stages in the development of rhizoids. P—R ×537; S ×202.

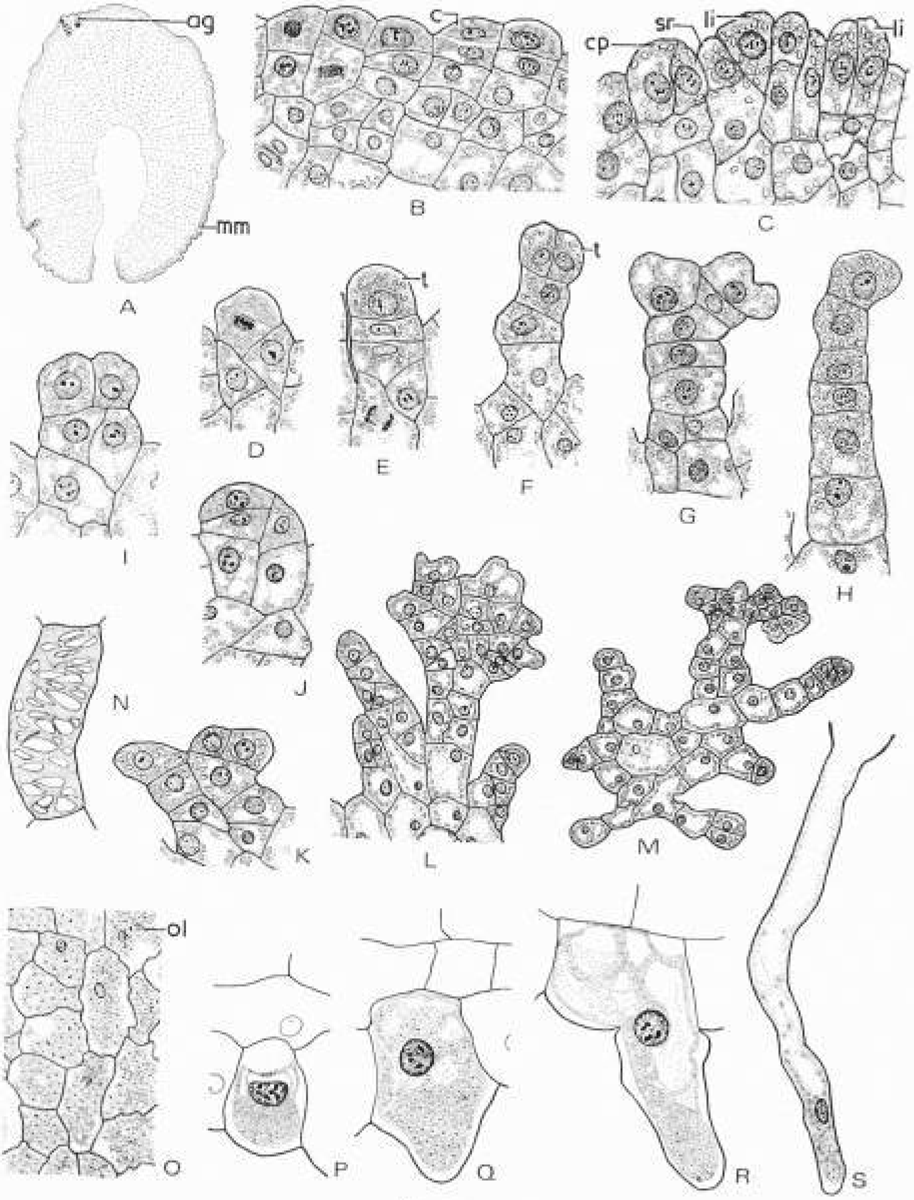

Fig. 3.

Some of the superficial cells of the meristematic margin become densely cytoplasmic; they show a large nucleus and act as antheridial initials (Fig. 4 A). Each initial divides periclinally into an outer cover initial and an inner primary androgonial cell (Fig. 4 B). The latter undergoes a periclinal division (Fig. 4 C) which may be followed by another division in the same plane (Fig. 4 D) or at right angles to it (Fig. 4 E). The cover initial undergoes anticlinal divisions to form a single-layered roof of the antheridium (Fig. 4 F—H). The jacket of the antheridium differentiates from the surrounding cells of the gametophyte. The subsequent divisions in the androgonial cells are irregular and result in a compact tissue of spermatocytes (Fig. 4 F—H). Thus the development of the antheridium is of the eusporangiate type.

Each androgonial cell (Fig. 4 J) divides mitotically and forms two spermatocytes which develop into spermatozoids (Fig. 4 K—P). During the metamorphosis of a spermatocyte into a spermatozoid, a large vacuole appears in the cytoplasm (Fig. 4 K); the nucleus enlarges and gradually assumes a crescent shape (Fig. 4 L). During this change the vacuole disappears, the cytoplasm contracts slightly from the wall and a mucilaginous layer develops around the former (Fig. 4 L—N). Meanwhile the blepharoplast becomes distinguishable as a faint arc-like structure within the concavity of the nucleus (Fig. 4 L). The nucleus of the spermatocyte has a characteristic reticulate appearance with a broad posterior and a narrow anterior end (Fig. 4 L, M).

The nucleus becomes curved and slender, the blepharoplast becomes coiled and develops numerous cilia (Fig. 4 N, O). Gradually the nucleus

Fig. 4. Antheridia (*ac*, androgonial cell; *bp*, blepharoplast; *c*, cytoplasm; *ca*, cilia; *ci*, cover initial; *cs*, cytoplasmic sheath; *cv*, cover cell; *gr*, granule; *jc*, jacket cells; *l*, lobe; *ml*, mucilaginous layer; *n*, nucleus; *p*, pore; *pa*, primary androgonial cell; *se*, spermatocyte; *sz*, spermatozoid.) — A. Antheridial initial. ×513. — B. Initial has divided to form an upper cover initial and a lower primary androgonial cell. ×513. — C, D. First and second periclinal division in the primary androgonial cell respectively. ×513. — E. Anticlinal wall formation in the lower androgonial cell. ×513. — F—H. Progressive stages in the formation of an antheridium. F ×513; G, H ×347. — I. L.s. portion of gametophyte showing two antheridia surrounded by short lobes. ×174. — J. Androgonial cell with a prominent nucleus. ×1047. — K. Young spermatocyte with a prominent vacuole. The nucleus has changed its shape. ×1047. — L. The nucleus of the spermatocyte has become crescent-shaped. ×1047. — M. Dorsal view of a spermatocyte. ×1047. — N, O. Stages in the metamorphosis of a spermatocyte to a spermatozoid. ×1047. — P. Mature spermatozoid. ×1047. — Q. L.s. through the upper part of antheridium; note the formation of a pore between cover cells. ×307. — R. L.s. mature antheridium showing a mass of spermatozoids being discharged through the pore. ×159.

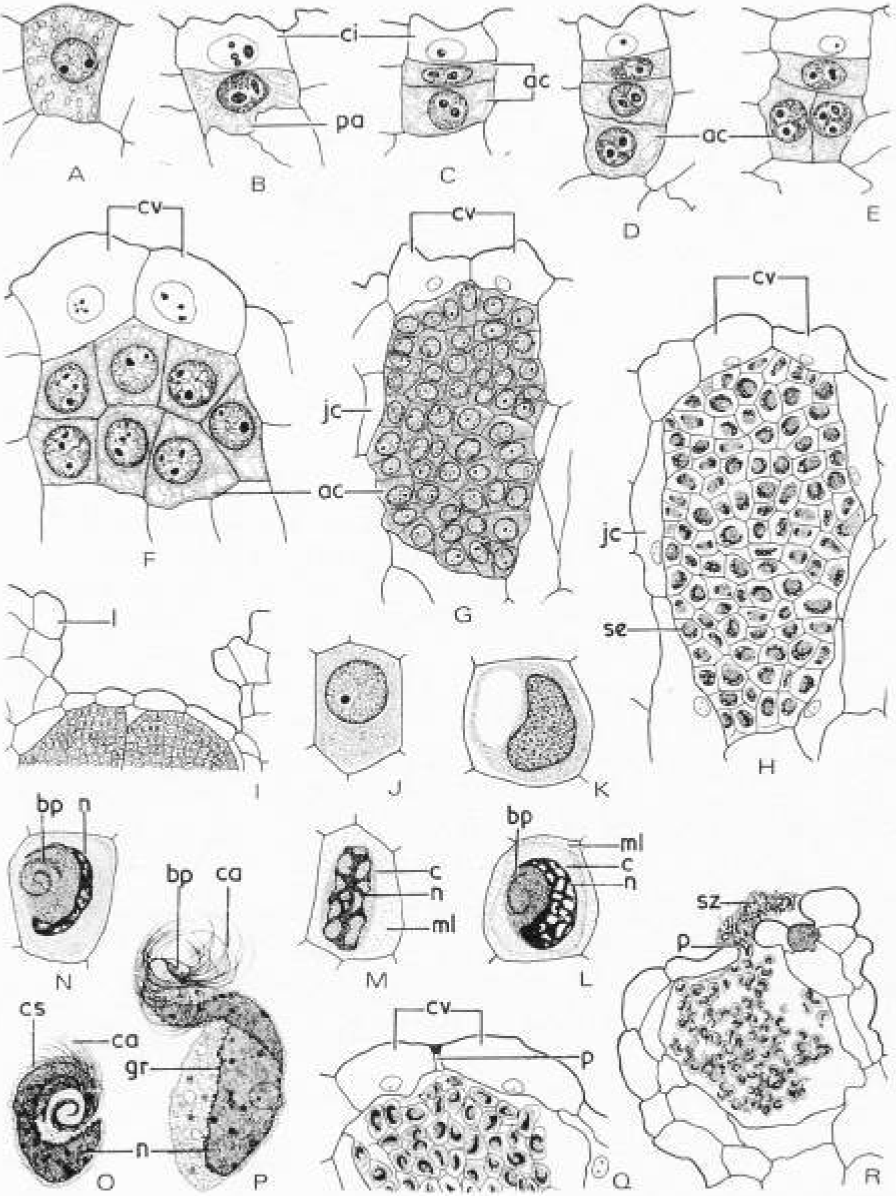
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Fig. 4.

loses its reticulate nature and changes into a densely staining, homogeneous, coiled body (Fig. 4 P). The spermatocytes now start separating from each other but the surrounding wall of individual spermatocytes can still be seen (Fig. 4 Q, R). The mucilaginous layer around the cytoplasm absorbs moisture and swells up. Due to the pressure exerted, the cover cells separate along the median line and a lenticular opening is formed (Fig. 4 Q). The spermatocytes come out in a mass through this pore (Fig. 4 R). When a portion of gametophyte containing mature antheridia is placed in a drop of water, the antheridia dehisce and a mass of spermatocytes is released. After 10 to 15 minutes the spermatozoids start moving within the cells in a clockwise manner. Very soon the wall of the spermatocyte breaks and the spermatozoid slips out of the cell, starts lashing its cilia and moving in characteristic spirals. The greater part of the cytoplasm is left in the cell and only a sheath persists around the nucleus (Fig. 4 O).

The mature spermatozoid is spirally coiled; its nucleus occupies the greater part of the body. A spiral blepharoplastic band which bears numerous cilia is situated at the anterior end (Fig. 4 P). Occasionally a cytoplasmic vesicle is found attached to the spatula-like posterior part of the spermatozoid. Many darkly-stained bodies or granules are seen scattered around the nucleus but are specially concentrated on its concave side (Fig. 4 O, P).

It has been often observed that 2 or 3 antheridial initials differentiate adjacent to each other without intervening sterile cells (Fig. 5 A). Each of these initials develops into an antheridium containing normal spermatozoids (Fig. 5 B—H). At maturity even though the adjacent antheridia coalesce to form a common chamber by the dissolution of the separating walls, the identity of each antheridium can still be made out (Fig. 5 I).

ARCHEGONIUM

The archegonial initials can be recognized soon after the formation of the erect lobes of the gametophyte. The initials differentiate all along the margin of the gametophyte as superficial cells of the meristematic rim. They can be distinguished from the surrounding cells by the presence of a large nucleus, dense cytoplasm, and absence of chloroplasts (Fig. 6 A). The activitiy of the peripheral meristem results in the enlargement of the gametophyte and differentiation of additional arche-

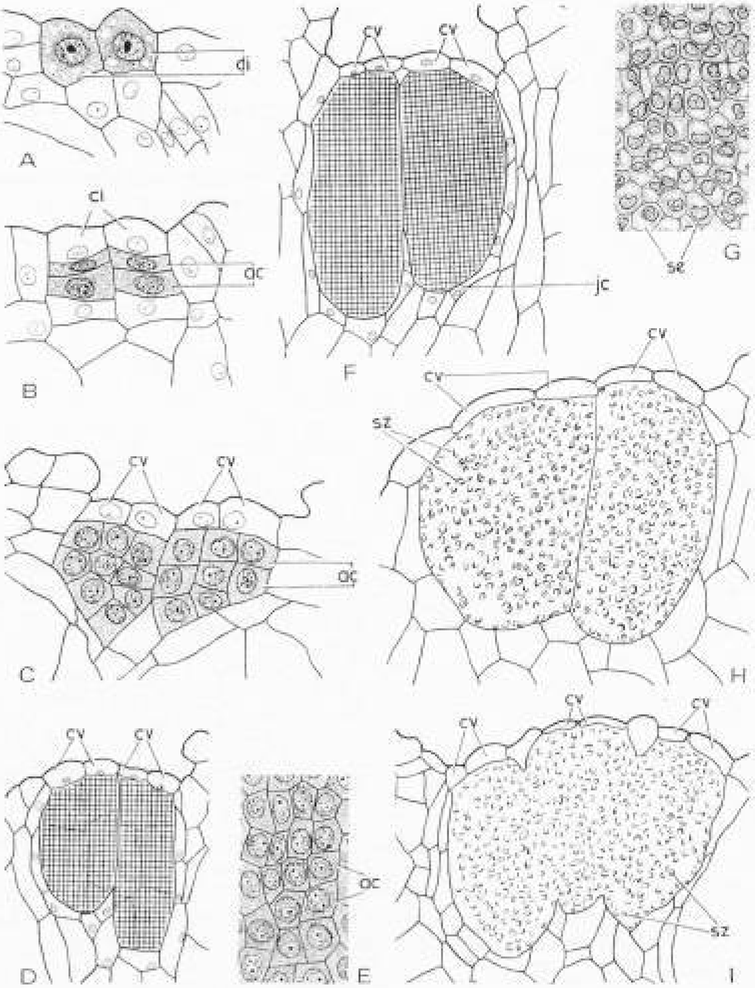

Fig. 5. Antheridia (*ac*, androgonial cells; *ci*, cover initials; *cv*, cover cells; *di* antheridium initials; *jc*, jacket cell; *se*, spermatocytes; *sz*, spermatozoids.) — A. Portion of gametophyte showing a pair of superficial antheridial initials. ×288. — B—D. Developmental stages of anterhidia. B, C ×288; D ×124. — E. A portion from D enlarged to show the androgonial cells. ×288. — F. L.s. antheridia at an advanced stage. ×124. — G. A portion from F magnified to show a mass of spermatocytes. ×288. — H. Antheridia containing numerous spermatozoids. ×124. — I. L.s. mature antheridia. The separating walls between adjacent antheridia have disorganized resulting in the formation of a common chamber. The cover cells are still intact. ×124.

gonial initials. Thus the older archegonia occur towards the centre and younger ones towards the periphery of the gametophyte (Fig. 6 L).

By the laying down of a periclinal wall, the archegonial initial divides into an outer primary neck cell and an inner central cell (Fig. 6 B). A very sudden and characteristic change in the primary neck cell is the accumulation of chloroplasts (Fig. 6 B). The primary neck cell undergoes anticlinal divisions (Fig. 6 C) followed by vertical division in both the daughter cells to form a tier of four cells. The first periclinal division in the central cell gives rise to an outer primary neck canal cell and an inner primary ventral cell (Fig. 6 D). The latter divides earlier than the former (Fig. 6 E) to form the ventral canal cell and the egg cell (Fig. 6 F). Starch grains now appear in all the 3 cells of the axial row (Fig. 6 F). Their nuclei are somewhat oval with prominent nucleoli. The primary neck canal cell then divides and forms 2 neck canal cells (Fig. 6 K) either by an obliquely vertical wall to form 2 unequal neck canal cells (Fig. 6 G), or by a vertical wall resulting in 2 equal boot-shaped cells (Fig. 6 H). When the neck canal cells are unequal the lower one appears to be wedge-shaped while the upper is somewhat rectangular and fills the greater part of the neck of the archegonium.

Fig. 6. Archegonia (*c*, neck canal; *cc*, central cell; *cp*, chloroplast; *eg*, egg; *l*, lobe; *mm*, meristematic margin; *nc*, neck cell; *nk*, neck; *nl*, neck canal cell; *pn*, primary neck cell; *pnc*, primary neck canal cell; *pvc*, primary ventral cell; *vc*, ventral canal cell.) — A. Portion of the gametophyte showing superficial archegonial initial. ×363. — B. The initial has divided to form a primary neck cell and a central cell. ×363. — C. Anticlinal division in the primary neck cell. ×363. — D. The central cell has divided to form primary neck canal cell (*pnc*) and the primary ventral cell (*pvc*). ×363. — E. Nucleus of the primary ventral cell in division. ×477. — F. L.s. young archegonium showing primary neck canal cell, ventral canal cell and the egg. ×363. — G. An oblique wall has been laid in the primary neck canal cell. ×363. — H. Archegonia showing two parallel neck canal cells. ×363. — I. Mature archegonium showing four tiers of neck cells. ×363. — J. Cross-section upper part of the neck showing four neck cells filled with chloroplasts. ×477. — K. Transection through the middle part of the archegonium showing 2 neck canal cells. ×477. — L. Part of female gametophyte showing the sequence of development of archegonia. The youngest is towards the periphery (→) whereas the mature is towards the centre in between the lobes. ×278. — M. Cross-section of an archegonium through the region of the venter showing egg. ×477. — N. L.s. archegonium showing two ventral canal cells formed by the periclinal division of the original ventral canal cell. The primary neck canal cell has not yet divided. ×503. — O. Same as N, but the primary neck canal cell has divided longitudinally. ×329. — P. Archegonium in which the original ventral canal cell has divided longitudinally. ×329. — Q. Archegonium with an elongated neck containing neck canal cells. ×329.

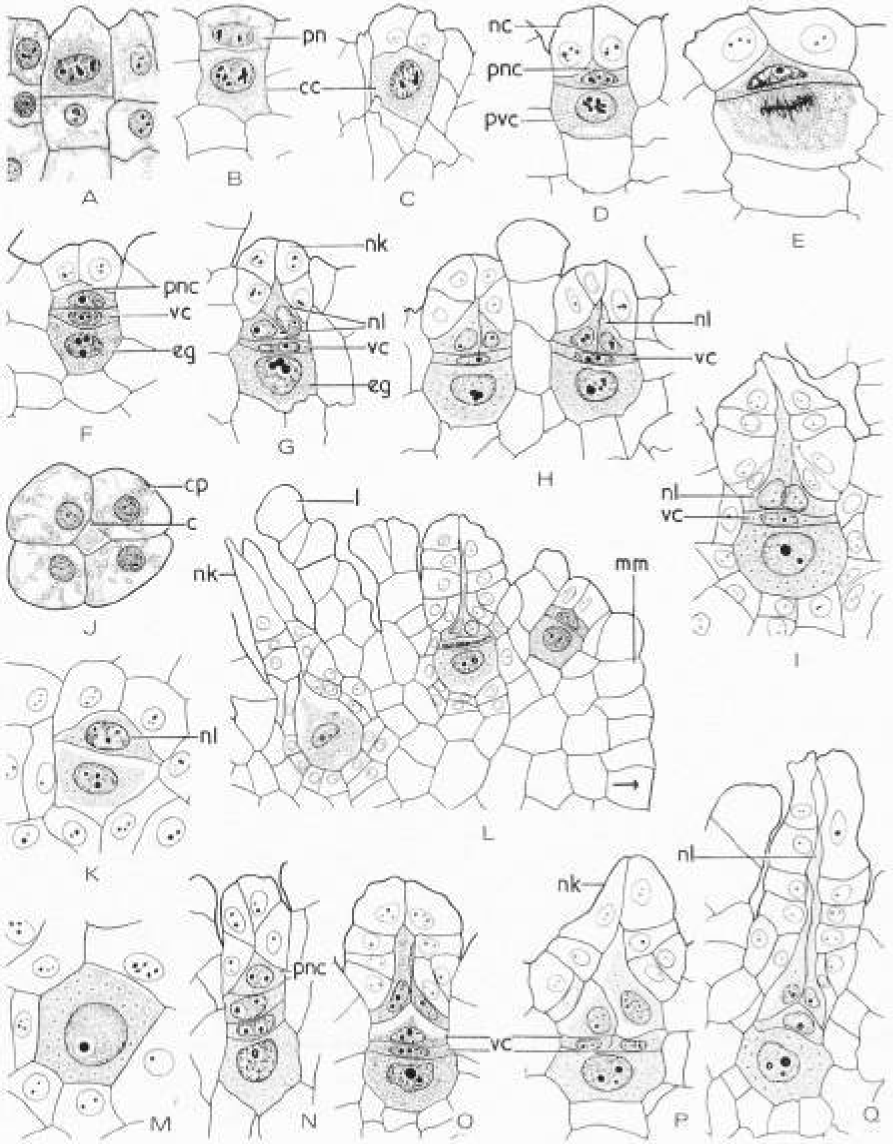
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Fig. 6.

These 2 types of wall formation in the primary neck canal cell occur with equal frequency and both may be seen in the same gametophyte. Further development of the archegonium is accompanied by the flattening of the ventral canal nucleus, whereas the egg nucleus increases in size and becomes spherical (Fig. 6 M).

Simultaneous with the division of the primary neck canal cell, divisions in the single tier of neck cells ensue, resulting in the formation of a neck consisting of 3 or 4 tiers of cells (Fig. 6 I), each tier having 4 cells (Fig. 6 J). The cells of the uppermost tier of the neck are somewhat elongated and larger in size. Originally all the neck cells contain chloroplasts, but those of the uppermost tier lose them after some time. The mature archegonium consists of a venter, embedded in the tissue of the prostrate system, and a neck protruding in between the erect lobes of the gametophyte (Fig. 6 L).

Occasionally some abnormal archegonia were encountered. They were either intermingled with normal archegonia or occurred isolated in the same gametophyte. Of the abnormalities observed, the presence of 2 ventral canal cells was the most common (Fig. 6 N, O). Sometimes this condition was observed in all the archegonia borne by a gametophyte. The presence of superimposed neck canal cells was also noted in some instances. Very rarely a longitudinal division occurred in the ventral canal cell (Fig. 6 P). Figure 6 Q represents an archegonium in which the neck is abnormally long.

FERTILIZATION

The cells lining the venter undergo a few divisions prior to fertilization (Fig. 7 A, D). The ventral canal cell disintegrates and this is accompanied by the degeneration of the neck canal cells (Fig. 7 A). The cells of the upper tier of the neck separate from each other so as to form a canal (Fig. 7 B). The egg cytoplasm which is packed with starch grains (Fig. 7 E—H) receedes from the wall of the venter but occasionally it protrudes into the base of the neck (Fig. 7 D). The spermatozoids enter the archegonium at this stage and the neck becomes almost closed.

Many spermatozoids enter the archegonium (Fig. 7 C) through the canal of the neck. Sometimes, however, only one spermatozoid gains entry (Fig. 7 E, F). Once the spermatozoid reaches the egg, its cilia become undiscernible, although the cytoplasmic sheath can still be made out (Fig. 7 H). The sheath is often visible even after the spermatozoid has entered the egg cytoplasm (Fig. 7 G).

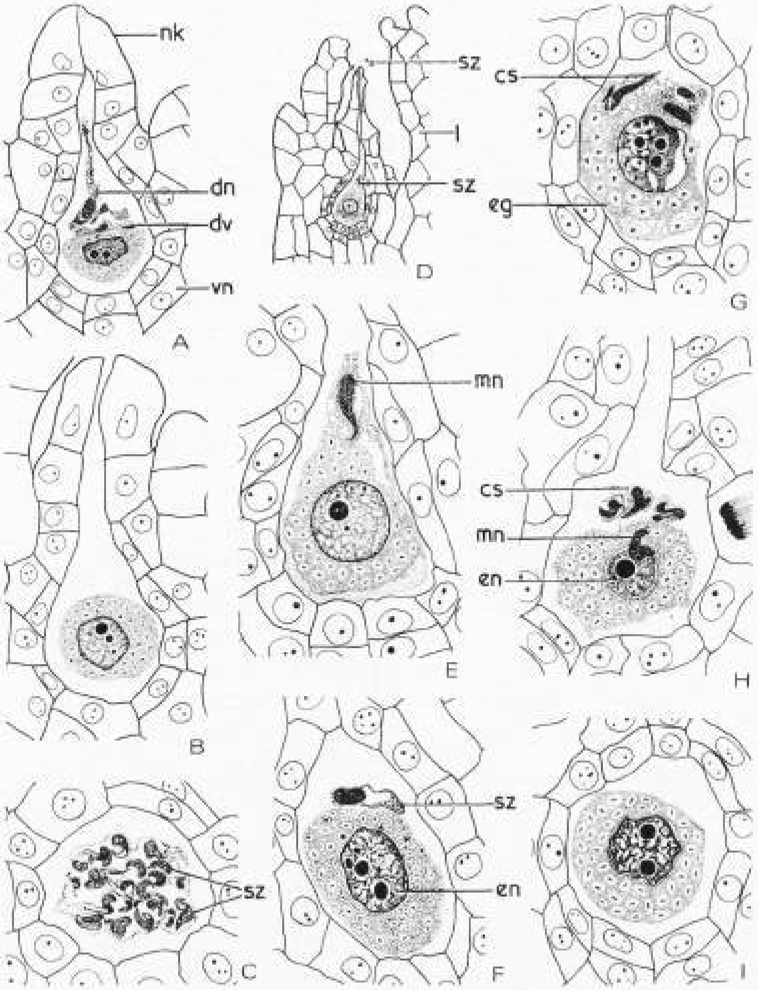

Fig. 7. Archegonia (*cs*, cytoplasmic sheath; *dn*, degenerating neck canal cells; *dv*, degenerating ventral canal cell; *eg*, egg; *en*, egg nucleus; *l*, lobe; *mn*, male nucleus; *nk*, neck; *sz*, spermatozoid; *vn*, venter.) — A. L.s. archegonium before fertilization. The neck canal cells and the ventral canal cell have degenerated. The cells of the venter have divided before fertilization. ×293. — B. Stage later than that in A. Mark the opening of neck. ×336. — C. Cross-section upper part of the venter containing numerous spermatozoids. ×528. — D. An archegonium showing only one spermatozoid in the egg; a few are seen outside the neck. ×133. — E. Lower portion of an archegonium showing entry of spermatozoid into the egg through the anterior end. ×528. — F. T.s. venter showing an egg and a single spermatozoid lying by its side. ×528. — G. Egg showing several spermatozoids in its cytoplasm. ×528. — H. Fusion of male and female nuclei; the nucleus of the spermatozoid is still in a coiled condition. ×528. — I. Cross-section of the venter with zygote. ×400.

Although several spermatozoids enter the egg cytoplasm (Fig. 7 H), only one fuses with the egg nucleus (Fig. 7 H). The spermatozoid may lose its original spiral shape and straighten out after entering the egg cytoplasm (Fig. 7 E) or it may remain coiled until the fusion of the nuclei (Fig. 7 H).

At the time of fertilization the membrane of the egg nucleus is very thin. The chromatin is in the form of granules (Fig. 7 H). Several archegonia in a gametophyte become fertilized but all the zygotes do not develop into mature embryos. The zygotes contain numerous starch grains and the fertilized nucleus shows an uneven outline (Fig. 6 I). The growth of a female gametophyte continues and it produces fresh archegonia even after a few have been fertilized and young sporophytes have been formed. In a bisexual gametophyte, however, new archgonia and antheridia are not formed after fertilization.

DISCUSSION

The structure of the gametophyte and development of sex organs in the various species of *Equisetum* have been studied by several authors (KASHYAP 1914, WALKER 1921, SETHI 1928 and MAHABALE 1945). Although, the structure of the gametophyte is more or less uniform in the different species there are some features which are distinct to this species. These will be discussed below:

While studying the structure and development of the gametophyte of *E. debile*, KASHYAP (1914) described the presence of a primary tubercle stage, similar to that found in *Lycopodium cernuum*. Tuber-like structures were occasionally observed by SETHI (1928) and by the present authors on the ventral surface of the gametophyte. The cells of this region are parenchymatous and are packed with starch grains. Anatomically this tuber-like structure is quite different from the primary tubercle of *Lycopodium cernuum*.

The histological structure of the gametophyte of the present species is essentially similar to that already described for *E. debile* var. *pashan* by MAHABALE (1945). However, in the material observed by us, the cells of the middle region of the mature gametophytes showed the presence of oil droplets and fibrous thickenings.

MILDE (1867) described that the rhizoids arise as small papillae from the epidermis which elongate gradually and are then cut off by a cross wall. DUVAL-JOUVE (1864) stated that rhizoids develop as small papillae but no cross walls separate them. Our observations confirm DUVAL-JOUVE's finding.

The development of green, erect lobes of the gametophyte has not been studied in detail by the earlier workers.

The occurrence of 2 or 3 antheridia without the intervening sterile cells, and also the frequent presence of abnormal archegonia with 2 ventral canal cells have also been reported for the first time.

KASHYAP (1914)) observed female or bisexual gametophytes in *E. debile*. SETHI's (1928) account of the life history of the same species indicates that the gametophytes are bisexual as well as unisexual. In *E. ramosissimum* subsp. *ramosissimum* (present material) also male, female and bisexual gametophytes occur in nature. The bisexual gametophytes are protogynous as also noted by KASHYAP (1914), SETHI (1928) and MAHABALE (1945). WALKER's (1921) report that the antheridia and archegonia continue to develop in the gametophytes of *E. laevigatum* until one or more sporophytes attain a considerable size does not seem to be true in the present material. We have noted that although the female gametophytes continued to grow and produce more archegonia even after fertilization of a few archegonia, and formation of young sporophytes, the antheridia fail to differentiate continuously.

CAMPBELL (1918) wrote that in *E. telmateia* antheridia develop in the manner typical of eusporangiate ferns or have their origin from a single papillate cell. The development of antheridia is of the eusporangiate type in the present species as reported by earlier workers also in other species of *Equisetum* (CAMPBELL 1918, SETHI 1928).

Four different views for the liberation of spermatozoids from a ripe antheridium have been suggested in the literature: (*1*) by the separation of 2 or more cover cells in *E. pratense* (GOEBEL 1905) and in *E. telmateia* (CAMPBELL 1918), (*2*) by the degeneration of the entire outer wall of the antheridium in *E. laevigatum* (WALKER 1921), (*3*) by throwing off a triangular opercular cell from the roof of the antheridium in *E. arvense* (CAMPBELL 1918, FOSTER & GIFFORD 1959) and (*4*) by the separation of 6 to 8 crown cells capping the antheridium found in *E. fluviatile* (SLADE 1964). In *E. ramosissimum* subsp. *ramosissimum* spermatozoids escape from a mature antheridium through a pore formed by the separation of the cover cells along the median line. The presence of an opercular cell has never been observed.

The archegonium in the present material contains an egg, a ventral canal cell and 2 equal or unequal neck canal cells. However, KASHYAP (1914), WALKER (1921) and BOWER (1935) reported the presence of a single neck canal cell in *E. debile* and *E. laevigatum*. Since the primary neck canal cell divides quite late, it is likely that these authors examined only young archegonia in which the primary neck canal cell had not yet divided.

The egg nucleus does not show the presence of a membrane during fertilization (SETHI 1928). In the material examined by us, a definite but thin nuclear membrane has always been observed. SETHI (1928) further reported that the spermatozoid bodily enters the egg cytoplasm. In the gametophytes of the present material the spermatozoids always cast off their blepharoplastic band bearing cilia before they penetrate the egg cytoplasm.

ACKNOWLEDGEMENTS

We are grateful to the late Professor P. MAHESHWARI and to Professor B. M. JOHRI for interest and to Dr H. SINGH and Dr MRIDUL WADHI for critical comments. Thanks are extended to the Council of Scientific and Industrial Research, New Delhi for the award of Research Assistantship to one us (J.C.).

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* Not seen in original.

Pollen Zones at Abisko, Torne Lappmark, Sweden

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ABSTRACT

In pollen diagrams from a mountainous area of Northern Sweden four main pollen zones are distinguished, the limits of which are radiocarbon dated. Diagrams showing the size frequency distribution of *Betula* pollen grains from the different zones are also presented.

INTRODUCTION

Sampling of gyttja and peat for pollen analysis has been carried out in the Torneträsk area, Torne Lappmark, Sweden, for current investigations on the vegetational dynamics of the area, primarily in the mires. The profiles presented in this paper derive from two sites in the Subalpine belt at the mouth of the Abisko Valley. See the topographic maps issued by Rikets Allmänna Kartverk, Stockholm (1 : 100 000).

The investigation area belongs to the mountainous western part of North Scandinavia. The deglaciation of the area has been described by HOLDAR 1957, 1960, the geology of the rocks by KULLING 1965, and a survey of recent vegetation may be found in DU RIETZ 1950 and MÅRTENSSON 1956. The regional variation of mire vegetation has been described by SONESSON 1967. A flora list (vascular plants) has been published by ASPLUND 1950.

SAMPLING SITES

Gp 1, Gp 3: Lake Vuolep Njakajaure, Subalpine belt, 408 m s.m. ca. 68°20′ N. Lat., 18°45′ E. Gr. Gp 1 75—100 m from the southeastern shore, Gp 3 appr. from the middle of the lake (size ca. 500 by 600 m, water depth at least 12.5 m).

Bp 100, Bp 101: mire ca. 500 m SSE. of the outflow of the Abiskojåkk (near the Tourist Hotel), Subalpine belt, ca. 75 by 300 m in size, 360—380 m s.m., ca. 68°20′ N. Lat., 18°45′ E. Gr.

METHODS

For the sediments a Livingstone core sampler (diameter 36 mm), for the peat a Nääs-Odentun core sampler (diameter 25 mm, see NÄÄS & ODENTUN 1958) were used. The sediment sampling was made in winter. Material of the surface mud was obtained by letting the core freeze before sampling. The uppermost sample of the mud (Gp 3, spectrum number 72) comprises ca. 2 cm of the water pillar too.

Bp 100 and Bp 101 derive from a bog like site of the mire. Bp 100 from a hummock and Bp 101 from a depression ca. 100 cm beside and 55 cm below the hummock.

All samples used for the pollen analyses and for the *Betula* measurements were uniformly treated with KOH, HF, HCl, acetolysed and mounted in silicone oil (cf. ANDERSEN 1960, FAEGRI & IVERSEN 1964).

Samples used for the sediment analysis were treated with lactic acid and analysed according to LUNDQUIST 1938. Fifty fields of vision were studied of each slide by means of an ordinary eye-piece micrometer. Concerning the algae found, only the diatoms easily recognized by the magnification used (× ca. 400) were counted.

The ash content in some samples of Gp 3 was determined by ignition. Result (ash weight in per cent of dry matter weight): Spectrum numbers 68 = 62 %, 49 = 61 %, 25 = 71 %, 22 = 46 %, 12 = 56 %.

An X-ray diffraction analysis was made (by Dr. U. REGNELL, Dept. of Mineralogy and Petrology, University of Lund) on one sample of the mineral ground of Gp 3. Pre-treatments with HF, HCl and H_2O_2 reduced the sample from 24.6 g to 0.05 g. The result of the analysis showed a possible though not an exclusive content of graphite.

The radiocarbon datings (made by Mr. S. HÅKANSSON, Radiocarbon Dating Laboratory, University of Lund) were corrected for deviations from the normal C^{13}/C^{12} ratio. It may be noticed, that one sample (Gp 3 spectrum number 15—17) was dated on the NaOH soluble fraction only. Concerning the half-life of radiocarbon, 5730 years, see the discussions in BERGLUND 1966 p. 46.

The pollen diagrams (Figs. 1, 2, and 4) are principally constructed like those in BERGLUND op. cit., the terminology and nomenclature of which are followed too.

The stratigraphic signatures of Bp 100, 101 are based on those of von POST & GRANLUND 1926. The main bryophyte components are indicated by letters: C = *Calliergon trifarium* (WEB. et MOHR.) KINDB., e = *Dicranum* cf. *elongatum* SCHLEICH., f = *Sphagnum fuscum* (SCHIMP.) KLINGGR., w = *S. warnstorfii* RUSSOW, P = *Paludella squarrosa* (HEDW.) BRID., r = *Drepanocladus revolvens* (SM.) WARNST., s = *Scorpidium scorpioides* (HEDW.) LIMPR., T = *Tomenthypnum nitens* (HEDW.) LOESKE. A * designates frozen peat. The sum of calculation of "B" does not comprise *Rubus chamaemorus*. Pollen grains of this species are, however, frequent especially on the levels 15—90 cm and 160—180 cm. "Other sperm." means mainly *Gramineae*.

"Quercetum mixtum" (QM, Gp 3) means the sum of *Quercus*, *Ulmus* and *Tilia*, *Tilia* being least frequent. They are all evenly distributed through the profile.

Table 1. Flora list of Gp 3.

Spectrum number	Species	Number of grains
71	*Epilobium* sp.	1
70	*Astragalus* cf. *frigidus*	1
69	*Saxifraga aizoides*	1
	Pinguicula sp.	1
68	*Corylus avellana*	1
67	*Rhamnus frangula*	1
66	*Ranunculus* sp.	2
65	*Ranunculus* sp.	1
	Saxifraga aizoides	1
64	*Rubus chamaemorus*	1
63	*Saxifraga aizoides*	2
62	*Ranunculus* sp.	1
61	*Pinguicula* sp.	1
58	*Parnassia palustris*	1
57	*Plantago maritima*, annulate[1]	1
55	*Ranunculus* sp.	1
53	*Dryas octopetala*	1
52	*Ranunculus* sp.	1
51	*Saxifraga aizoides*	1
49	*Plantago maritima*, annulate[1]	1
	Saxifraga aizoides	1
47	*Calluna vulgaris*	1
	Galium sp.	1
	Saxifraga aizoides	1
46	*Plantago maritima*, annulate[1]	1
45	*Saxifraga oppositifolia*	1
	Arenaria type	1
39	*Plantago media*	1
38	*Rubus* sp.	1
37	*Ranunculus* sp.	1
36	*Nymphaea* sp.	1
34	*Rubus* sp.	1
31	*Ranunculus* sp.	1
	Rubus chamaemorus	1
30	*Sorbus aucuparia*	2
29	*Plantago maritima*, annulate[1]	2
	Ranunculus sp.	1
22	*Saxifraga aizoides*	1
19	*Corylus avellana*	1
15	*Galium* sp.	1
12	*Rubus* sp.	1
10	*Rubus* sp.	1
6	*Melampyrum* sp.	1
4	*Corylus avellana*	1
2	*Sorbus aucuparia*	1
1	*Polypodium vulgare*	1

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[1] See ANDERSEN 1961.

Table 1 comprises the species of Gp 3 not especially accounted for in the diagram, except the species of QM and those undetermined.

The "*Betula nana* type" was determined on estimations of size, height of the pores and thickness of the wall (Gp 1 and Bp 100, 101) or on estimations of the relative height of the pores only (Gp 3).

The reliability of determining between the *Betula* species by using pollen has recently been discussed by BIRKS (1968, see also references given to earlier literature). For the taxonomy of the genus *Betula* in Fennoscandia, see HYLANDER 1966.

The measurements of *Betula* pollen (Figs. 3 a—3 b) were made with a Leitz "Schraubenmikrometer-Okular". In each sample studied 400 grains were measured.

Some of the abrupt shifting in the pollen curves may be due to an obvious destruction/corrosion of *Pinus* pollen. This concerns among others Gp 3 spectrum numbers 34, 28, 20.

DESCRIPTION OF SEDIMENTS

Gp 1

Depth below lake level (m)	Stratum number	Description
4.45—5.15	5	Clayey fine detritus gyttja, greyish green, non-elastic.
5.15—5.90	4	Slightly clayey fine detritus gyttja, greyish dark-green, distinctly elastic and stratified.
5.90—6.68	3	Clayey fine detritus gyttja.
6.68—6.73	2	Greenish greyey clay.
6.73—	1	Greyish clay.

Gp 3

Depth below lake level (m)	Stratum number	Description
12.50—13.80	6	Clayey fine detritus gyttja, greyish green, non-elastic. Green algae frequent (i.a. *Pediastrum* and *Botryococcus*).
13.80—15.00	5	Slightly clayey fine detritus gyttja, greyish dark-green, distinctly elastic and stratified. Green algae less frequent. *Pinus* needle at 14.55.
15.00—15.45	4	Clayey fine detritus gyttja, greyish dark-green, elastic and somewhat stratified. Green algae infrequent (but rather common between 15.30—15.45).
15.45—15.58	3	Slightly clayey fine detritus gyttja, stratified. Green algae infrequent.
15.58—15.65	2	Greenish greyey clay.
15.65—	1	Greyish clay.

POLLEN ZONES (PRELIMINARY DIVISION)

T 1

Low values of *Pinus* and *Alnus*, high values of *Betula*. *Hippophaë* frequent, *Ericales* infrequent.

Zone boundary T 1/T 2. Distinctly rising *Alnus* and *Juniperus* curves. Decreasing *Hippophaë*. — Zone boundary radiocarbon dated to ca. 7000 B.C.

T 2

Low values of *Pinus*, high values of *Betula*, *Alnus* and *Juniperus*. *Ericales* infrequent.

Subzone a. Relatively low values of *Alnus*. High values of *Juniperus* and *Gramineae*. In the beginning of the subzone *Pinus* is increasing and *Betula* markedly decreasing.

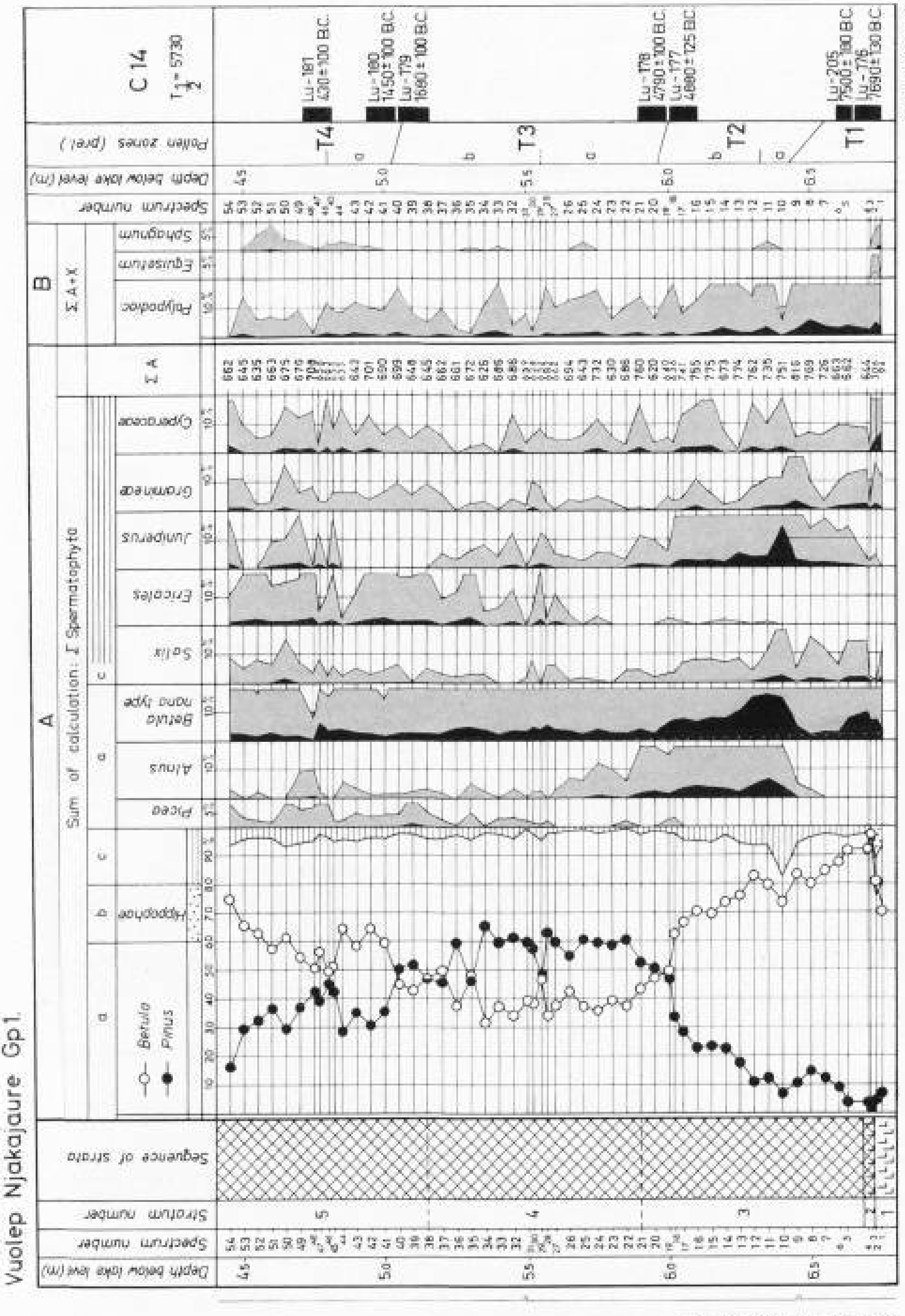

Fig. 1. Pollen diagram from the vicinity of southeastern shore of Lake Vuolep Njakajaure. Depth of water 4.15 m.

Subzone b. High values of *Alnus* and *Juniperus*, low values of *Gramineae*.

Zone boundary T 2/T 3. Distinctly rising *Pinus* and decreasing *Betula* curves. — Zone boundary radiocarbon dated to ca. 4800 B.C.

T 3

The frequencies of *Pinus* generally about equal to or higher than those of *Betula*. Decreasing *Alnus*. Beginning of the continuous *Picea* curve. Increasing *Ericales*.

Subzone a. *Picea* only sporadic. Low NAP. Still relatively high frequencies of *Alnus*.

Subzone b. Continuous *Picea* curve. Increasing NAP.

Zone boundary T 3/T 4. Distinctly decreasing *Pinus* and increasing *Betula*. — Zone boundary radiocarbon dated to ca. 1500 B.C.

T 4

The frequencies of *Betula* higher than those of *Pinus* and increasing. *Alnus* still lower than in the preceding zone. Increasing NAP. Relatively frequent *Ericales*.

The subzoning has been made according to the temporary increases of *Pinus* and decreases of *Betula*.

Subzone a. Relatively low values of *Pinus*, high of *Betula*.

Subzone b. Ditto.

Subzone c. Ditto.

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My wife, ANITA, Mr. NILS ENGLESSON and Mr. BENGT NIHLGÅRD have assisted during field-work.

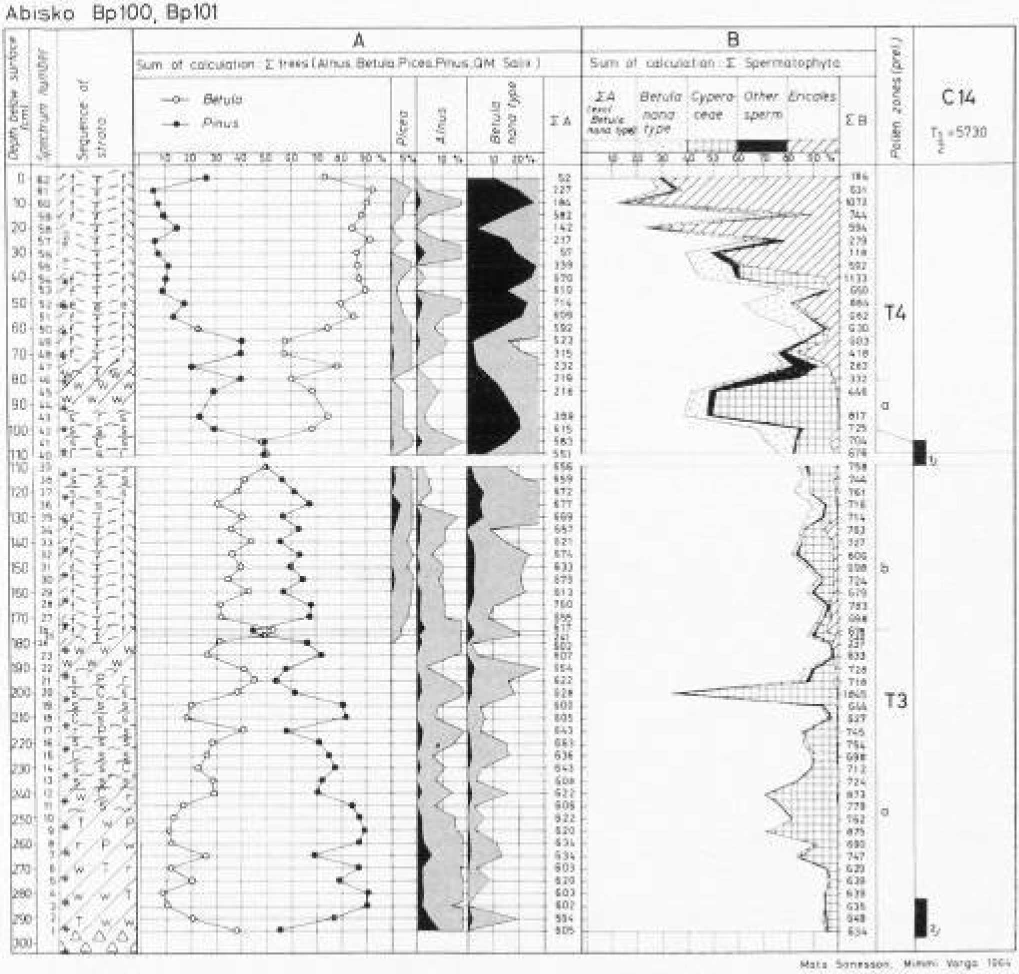

Fig. 2. Pollen diagram from mire NE Abisko Tourist Hotel. For symbols, see p. 492. 1) Lu-229: 540 ± 100 B.C. (N.B. The sample symbol has been incorrectly drawn in the diagram. It should lie between 95 and 115 cm. The sample is unexpectedly young.). 2) Lu-228: 4510 ± 100 B.C.

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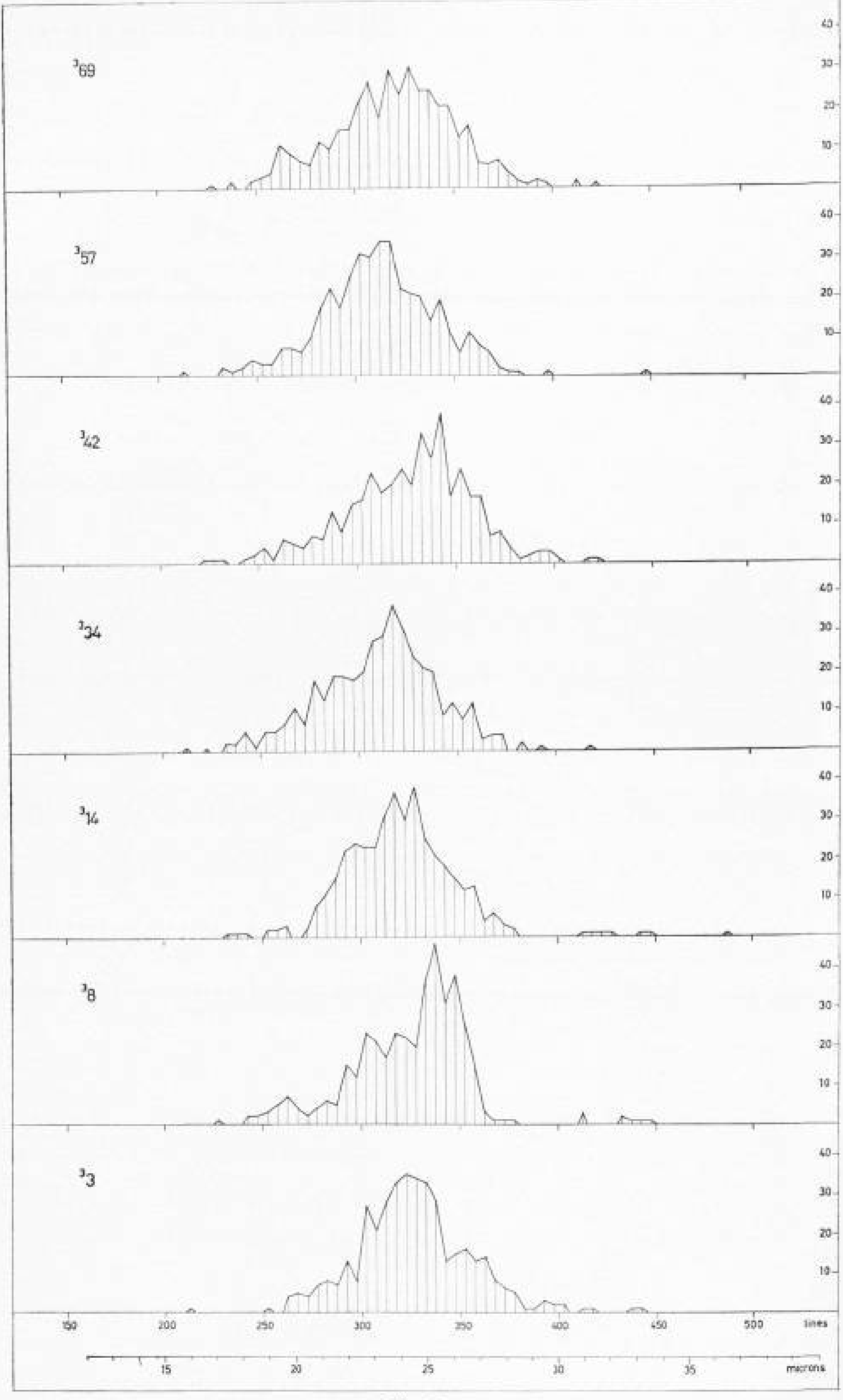
To all mentioned I wish to express my sincere gratitude.



³69
³57
³42
³34
³14
³8
³3
10
20
30
40
150
200
250
300
350
400
450
500
lines
15
20
25
30
35
microns

Fig. 3 a.

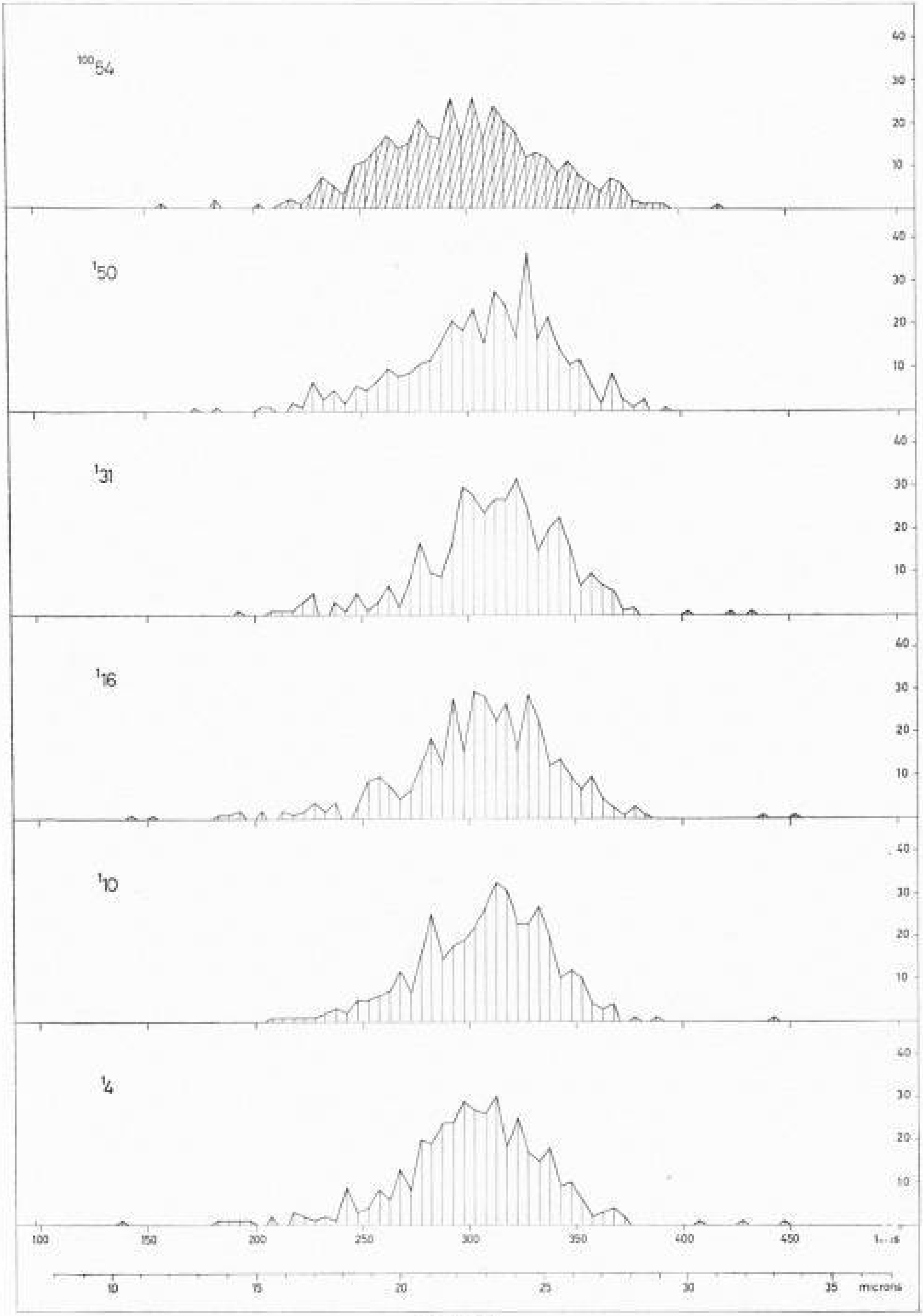


Fig. 3 b.

Fig. 3 a—b. Frequency curves for grain diameter of *Betula* in different spectra of Gp 3 (a, left) and Gp 1, Bp 100 (b, right). 400 grains measured of each sample.

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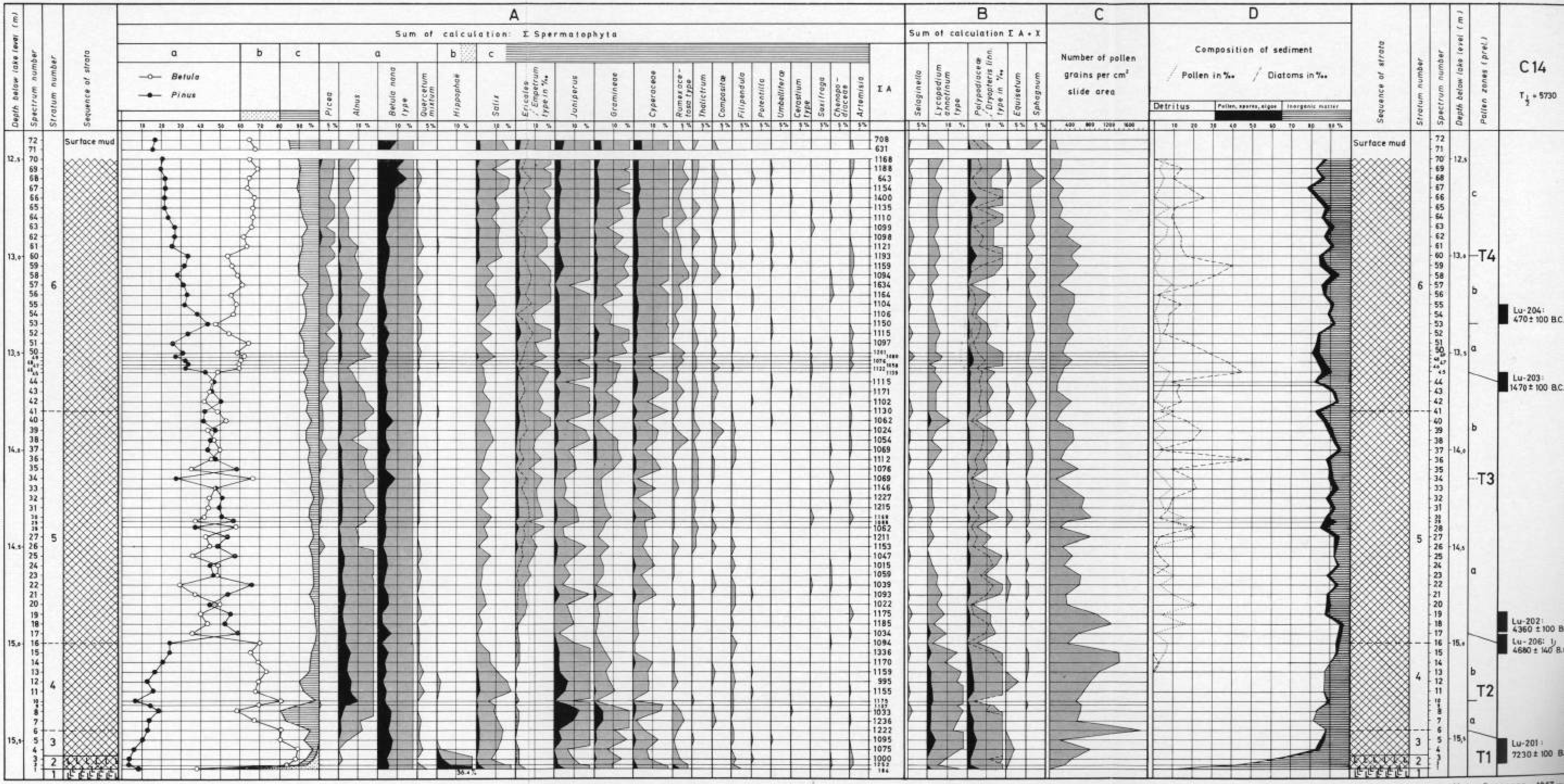
Fig. 4. Pollen diagram from appr. the middle of Lake Vuolep Njakajaure. Depth of water 12.5 m. 1) dated on the NaOH soluble fraction only.

Fig.

Vuolep Njakajaure Gp 3.



Mats Sonesson 1967—

Distributional-Type Spectra in Greenland Montane Localities

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ABSTRACT

Species in 71 montane localities have been analysed to find what species reached the greatest altitudes, and to find the variations in the biological distributional-type of the species that reached any selected altitude. It was found that the primary division of the species into high-arctic, low-arctic, etc., applied equally well to either changes in altitude or latitude in the areas investigated.

The altitudinal ranges of vascular species occurring in three montane regions of Greenland have been investigated with a view to discovering the maximum altitudes attained by individual species and the altitudinal ranges of the various biological distributional-types represented in the flora.

The species were recorded from an inland area on the south-east coast near Angmagssalik (104 species at 27 localities up to a maximum altitude of 2300 m) by Gribbon (1963, 1968) and Stocken (1966), and from two coastal areas on the mid-west coast near Sukkertoppen (126 species at 19 localities up to 1680 m) and Umanak (124 species at 25 localities up to 1850 m) by Gribbon (1965, 1967). Previous data on montane localities in mid-west Greenland was limited to 11 localities up to 1600 m studied by Böcher (1963).

Vascular species in Greenland have been divided by Böcher, Holmen and Jakobsen (1959) and Böcher (1963) between 11 different biological distributional-types determined by the climatic and environmental differences existing throughout Greenland. The types are: (1) A, arctic widely distributed; (2) H, high arctic; (3) AC, arctic widely distributed continental; (4) M, medium arctic; (5) L, low arctic; (6) LO, low arctic oceanic-montane; (7) LC, low arctic continental; (8) B, boreal; (9) BS, boreal sylvicolous-hygrophilous; (10) BC, boreal continental; and (11) BO, boreal oceanic. — Another larger grouping is arctic (A, H, AC, M),

Table 1. Highest Altitude Species.

Altitude (m)	Species (and type)
H [1]	*Papaver radicatum* (A)
(H—100)	*Saxifraga cernua* (A), *Saxifraga nivalis* (A)
(H—200)	*Saxifraga caespitosa* (A), *Cerastium arcticum* (A), *Luzula spicata* (L), *Silene acaulis* (A), [2] *Erigeron eriocephalus* (M), *Antennaria* sp.
(H—300)	*Draba nivalis* (A), *Oxyria digyna* (A), *Minuartia rubella* (A), *Saxifraga oppositifolia* (A), [3] *Carex nardina* (M), *Luzula confusa* (A), *Poa glauca* (A), *Salix herbacea* (LO), *Chamaenerion latifolium* (A), [2] *Saxifraga tricuspidata* (AC), [2] *Campanula uniflora* (M)
(H—400)	*Trisetum spicatum* (A), *Potentilla nivea* (LC), *Ranunculus pygmaeus* (A), *Cardamine bellidifolia* (A), *Salix arctophila* and *glauca* (L)
(H—500)	*Polygonum viviparum* (A), [2] *Erigeron humilis* (M)

[1] H is the highest point at which vascular plants were found in each of the three regions; it is slightly lower than the highest points visited.

[2] in two western regions only

[3] highland species only

low arctic (L, LO, LC) and boreal (B, BS, BC, BO). — Those species which occur commonly within 500 m of the highest point examined in the three areas are listed in order in Table 1. They are all characteristic arctic species, chiefly of the A-type, which indicates their similar response to the climatic conditions associated with either altitudinal or latitudinal changes. Species belonging to other distributional-types play an increasingly important role at lower altitudes.

Table 2 gives the distributional-type spectra for species with a continuous range from sea level to their upper limit: highland species, omitted in Table 2 (a), are given in Table 2 (b). The total number of species in any selected altitude range is obtained by addition of the relevant columns in Tables 2 (a) and (b).

The conclusions to be made from these Tables are:

1. A-type species, which alone reached the highest localities, must have the biological capability to tolerate the greatest climatic extremes and disadvantages. They are unlike the members of the other distributional-types whose occurrence at high altitudes does seem to depend to a greater degree on locally favourable microclimatic and soil conditions, for example a sheltered southerly aspect and a stable soil with adequate water supply and drainage. The number of species particularly of the A-type can be surprisingly large under favourable high altitude conditions.

Table 2 a. Distributional-type spectra of continuous range species.

Type	Region	Angmagssalik (66°N, 36°W)							Sukkertoppen (65°N, 52°W)					Umanak (71°N, 52°W)						
	Altitude Range (m)	0 50	650 950	950 1250	1250 1550	1550 1850	1850 2150	2150 2300	0 50	400 850	850 1150	1150 1450	1450 1700	0 50	50 350	350 650	650 950	950 1250	1250 1550	1550 1850
(1)	A	16	16	16	15	13	10	7	17	14	13	7	1	19	18	18	18	18	18	3
(2)	H	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—
(3)	LC	3	1	1	1	1	1	—	6	6	2	—	—	17	17	14	12	8	4	—
(4)	M	1	—	—	—	—	—	—	1	—	—	—	—	7	6	5	5	4	3	—
(5)	L	10	6	5	3	1	—	—	25	16	11	1	—	25	17	12	9	6	5	—
(6)	LO	25	21	12	11	5	3	2	37	27	14	3	—	15	12	8	3	2	2	—
(7)	LC	1	—	—	—	—	—	—	7	4	2	—	—	7	5	4	3	2	—	—
(8)	B	5	2	2	2	—	—	—	11	4	1	1	—	5	2	—	—	—	—	—
(9)	BS	2	—	—	—	—	—	—	11	1	—	—	—	—	—	—	—	—	—	—
(10)	BO	1	1	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—

Table 2 b. Distributional-type spectra of highland species.

(1)	A	—	3	3	3	2	2	1	—	3	3	2	—	—	1	3	3	4	4	—
(2)	H	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	2	2	2	—
(3)	LC	—	3	3	4	2	2	—	—	2	3	1	—	—	1	1	1	1	1	—
(4)	M	—	3	3	5	2	—	—	—	3	2	1	—	—	1	1	1	2	3	—
(5)	L	—	7	5	6	4	3	—	—	—	2	—	—	—	—	—	—	—	—	—
(6)	LO	—	3	2	2	1	1	—	—	2	—	—	—	—	—	—	—	—	—	—
(7)	LC	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
(8)	B	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

2. Arctic species (A, H, AC, M) reached the highest localities, low arctic species (L, LO, LC) extended throughout all except the highest localities, and boreal species (B, BS, BO) were restricted to the lowest localities. The altitudinal distribution therefore reflects the latitudinal ranges of these species.

3. (A, H, AC, M) species increased in number and frequency on moving north from Sukkertoppen to Umanak and there was a corresponding decrease in the number of (L, B, etc.) species.

4. The average rate of decrease in species number at the higher localities of all three regions was about 5 species per 100 m. Table 1 gives the species responsible for the decrease rate at the highest localities, while the species existing at lower altitudes can be determined from the species lists of GRIBBON, etc.

5. The maximum upland development of vegetation, comprising a large number of both continuous and highland range species, occurred at a higher altitude in the climatically more-continental area at Angmagssalik than in the oceanic-montane coastal areas at Sukkertoppen and Umanak. An optimal altitude range for both the continuous range and highland species occurred at a certain altitude related to the position of local glacierization in each area. A coastal area had more species than an inland area at the same latitude.

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Distribution and Substrate in the South African Genus Aspalathus L. (Leguminosae)

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ABSTRACT

Recent observations on the ecology and distribution, with enumerated collections made in South Africa 1965—66, are presented for a great part of the genus *Aspalathus* as a complement to the revision of this genus published in the series Opera Botanica. The species treated are mostly confined to the southwestern parts of the Cape Province. Certain distribution maps are given, and the distributions are discussed in relation to the geological formations and their soils. The soil type has great influence on the selection of species, and the distribution areas of most of the studied species fall within the areas of particular types of substrate, and accordingly within the areas of geological formations as far as these form particular soils. Other factors, however, are naturally also of great importance. Some species are ecologically tolerant or heterogeneous.

INTRODUCTION

The species of *Aspalathus* have been treated in Opera Botanica and Botaniska Notiser (see literature list). The genus was subjected to a further study during a period of field work between July 1965 and March 1966, when I was accompanied by Mr. A. STRID. The results have been included in the parts of my revision published after that, but for the species presented in earlier publications substantial distributional and ecological additions remained to be made. DAHLGREN & STRID is abbreviated "D. & S." A complete set of our collections is deposited in Lund (LD) while a less complete set will be deposited in the Compton Herbarium, National Botanic Gardens, Kirstenbosch (NBG). With reference to literature, DAHLGREN is abbreviated "D."

A preliminary report on the dependence of *Aspalathus* species on the substrate was given in D. 1963 b pp. 220—221.

Additions to the Knowledge of the Distribution and Ecology in Aspalathus Species

Subgenus Purpureipetala R. DAHLGR.; D. 1963 b p. 107. — Type species: *Aspalathus nigra* L.

Aspalathus forbesii HARV.; D. 1961 a p. 61 ff. — On marine deposits near the coast. Dominant in sand dunes at the E base of Cape Hangklip Mt. (D. & S. no. 3933), where it is an effective sand binder.

A. submissa R. DAHLGR.; D. 1961 a p. 53 ff. — Concentrated to the southern regions with clayey soil and often growing in clay collected in fissures of shales (Bokkeveld Series), in a vegetation of fynbos often with *Elytropappus*. Collected by us in Robertson Div. near De Hoop Farm some miles NE of Robertson (D. & S. no. 3463) on shaley ground, but also frequent in shale fissures ca. 5 miles NNE of Villiersdorp, Caledon Div. (D. & S. nos. 3374—3376). Map: Fig. 6 E.

A. nigra L.; D. 1961 a p. 41 ff. — Common mainly in rhenosterbos or rhenosterbos-fynbos transition in the southern divisions (numerous collections), and occurring mostly on fine-grained substrate. It is found on limestone hills in Bredasdorp Div., e.g. near Ouplaas (D. & S. no. 3650), and in Caledon Div., ca. 1 mile S of Stanford (D. & S. no. 3665). — The species is represented by up to 70 cm tall forms with relatively large flowers (cf. forms under "B" in D. 1961 a p. 48) in Burger's Pass W of Montagu (D. & S. no. 3476). Similar tall-grown forms occur on clayey ground in the Gydo Pass region, Ceres Div. (D. & S. nos. 3984, 3990, and 4123).

A. globulosa E. MEY.; D. 1961 a p. 57 ff. — Very frequent locally in almost pure sand, together with *A. forbesii* (see above), at the E base of Hangklip Mt., Caledon Div. (D. & S. no. 3934), and also found in marine sand, e.g., near Betty's Bay, same div. (D. & S. no. 3928).

A. cephalotes THUNB.; D. 1961 a p. 27 ff. — Ssp. *cephalotes* occurs in rather moist and shaded kloofs, in relatively tall fynbos, e.g. in the innermost part of Jonkershoek Valley, Stellenbosch Div. (D. & S. no. 4079). It is distinctly different from ssp. *violacea* R. DAHLGR., which usually grows in more open habitats (e.g. D. & S. no. 4094 from the Jonkershoek Valley). Specific rank for the two taxa may prove justified, but further investigations are desirable. Ssp. *violacea*, which is common in the southwestern divisions, has been collected by us in Du Toit's Kloof, Worcester Div. (D. & S. no. 3447).

A. cerrhantha ECKL. & ZEYH.; D. 1961 a p. 20 ff. — Found in fynbos ("false fynbos" sensu ACOCKS 1953), often in somewhat grassy habitats (e.g. D. & S. no. 2957 from the Knysna region).

Subgenus Triplobractea R. DAHLGR.; D. 1963 b p. 108. — Type species: *Aspalathus triquetra* THUNB.

A. triquetra THUNB.; D. 1961 b p. 88 ff. — Grey-pubescent forms treated under "K" in D. op. cit. p. 100, which also correspond to "*A. propinqua* E.

MEY.", were found on a shale band on the SW slopes of Cedarberg Tafelberg, Clanwilliam Div. (D. & S. no. 4432). Such forms appear relatively distinct from other forms with green and sparsely hairy leaves in the same mountains. The latter forms at least occasionally grow in sand. The specific problem in *A. triquetra* requires further investigations.

A. galeata E. MEY.; D. 1961 b p. 106 ff. — Found mainly in sand (weathered from T.M.S. sandstone). Common locally in the Grey's Pass area and in the Algeria Valley (Clanwilliam Div.).

A. grandiflora BENTH.; D. 1961 b p. 115 ff. — An eastern outpost was collected on steep slopes in the central part of Garcia's Pass, Riversdale Div. (D. & S. nos. 2573 and 4637), where the ca. 100—130 cm tall shrubs had bright-yellow petals, contrary to forms in, e.g., the Keeromsberg Mts., where the petals are cream-coloured. — Other recent records: Montagu Div.: Lower slopes of Naudesberg, Koo, 1959, BARKER no. 9180 (LD, NBG) and Robertson Div.: Dassieshoek Peak, Langeberge nr. Robertson, 1961, ESTERHUYSEN no. 29100 (BOL, LD). The former of these collections is said to have cream-coloured petals, the latter deep-yellow ones. Map in Fig. 2 A.

Subgenus Aspalathus; D. 1963 b p. 109 ff.

A. desertorum BOL.; D. 1965 p. 73 ff. — Regionally common in and around Gydo Pass, Ceres Div. (D. & S. nos. 3985, 3993, and 4125), in compact clay of the Bokkeveld Series together with, e.g., *Cliffortia ruscifolia* and *Elytropappus*. The pods are shown in Fig. 2 I.

A. aculeata THUNB.; D. 1963 a p. 29 ff. — Generally on clayey soil, probably mainly of the Malmesbury Beds, but sometimes on sandy ground (cf. D. 1963 a p. 31). To the rather numerous finds of this species in the southwestern divisions may be added one on the NE slopes of the Paardeberg Mt., Malmesbury Div. (D. & S. no. 4102). Map in Fig. 3 F.

A. acanthiloba R. DAHLGR.; D. 1963 a p. 42 ff. — Previously known only from Pringle Bay, Caledon Div. Collected by us also along the pass leading up to the Stenbras Water Works (D. & S. nos. 3312 and 4490), in sand mixed with stones (T.M.S). This locality is situated ca. 2 miles S of Gordon's Bay and a few miles N of the first collections.

A. araneosa L.; D. 1963 a p. 46 ff. — Growing in sand. A peripheral record of this regionally common southwestern species is: Malmesbury Div.: Paardeberg, NE side nr. the "Nooitgedacht" farm (D. & S. no. 4103).

A. pigmentosa R. DAHLGR.; D. 1963 a p. 53 ff. — Locally abundant in sand, e.g. in the E part of Du Toit's Kloof, Worcester Div. (D. & S. nos. 3454 and 3458).

A. rubiginosa R. DAHLGR.; D. 1963 a p. 56 ff. — In sand weathered from T.M.S. sandstone (D. & S. no. 3145 from the E part of Du Toit's Kloof was found on a sandy road bank).

A. ciliaris L.; D. 1963 a p. 63 ff. — Numerous recent collections of this common southern species mainly agree with the outlines of variation already given for the respective populations (op. cit.). The species almost constantly grows on sandy substrates. On the N base of Soetanysberg (W of Cape Agulhas), Bredasdorp Div., up to 1 m tall, erect specimens occur in sandy basins between limestone outcrops (D. & S. nos. 3774—3775). Similar, but lower specimens have been found on windswept limestone slopes near Agulhas village close to the sea (D. & S. no. 3401). These are widely different from forms in, e.g., the Baardscheerdersbosch region, where the calyx lobes and leaflets are relatively broad and short ("*A. robusta*").

A. millefolia R. Dahlgr.; D. 1963 a p. 88 ff. — Not distinguished as a species until 1963 and largely overlooked. Rather common, however, in the rudiments of natural vegetation of the rhenosterveld regions in Caledon—Riversdale Divs. The following additional records clarify the distribution considerably (see map in Fig. 2 A). The habitat is clayey ground (cf. *A. ciliaris*) often with gravel or on shales. The shrublets are decumbent—ascending, with branches up to > 50 cm long.

Caledon Div.: Lebanon, gentle mt. slopes; alt. ca. 900 m. 1967, Kruger no. 538 (LD). — Bredasdorp Div.: Ca. 2 miles E of Kathoek, base of hill. 1965, D. & S. no. 4183 (LD). — Swellendam Div.: Nr. Fairview, ca. 5 miles NE of Malagas. 1965, D. & S. no. 4599 (LD). — Hill nr. Platkop, ca. 10 miles NE of Malagas on rd. to Heidelberg. 1965, D. & S. no. 4601 (LD). — Hill ca. 4 miles E of Swellendam. 1965, D. & S. no. 3850 (LD). — S slopes of Ertjiesvlei Berg, ca. 6 miles N of Heidelberg. 1965, D. & S. no. 4606 (LD). — Riversdale Div.: 5 miles from Riversdale along rd. to Corente River. 1965, D. & S. no. 2599 (LD).

A. spicata Thunb.; D. 1963 a p. 93 ff. — Numerous recent collections made give no substantial addition to previous knowledge of distribution and variation. Ssp. *neglecta* (Salter) R. Dahlgr. has been collected at the bottom of Viljoen's Pass, Caledon Div. (D. & S. no. 3714). Close clumps of ssp. *cliffortioides* (Bol.) R. Dahlgr. of the Tradu Pass population illustrated in op. cit. Fig. 31 were refound on steep slopes at the N end of this pass (D. & S. no. 4903). A form corresponding to that in Fig. 32 in D. 1963 a was found in local abundance on clayey flats ca. 1 mile W of Potberg Farm (W end of Potberg) (D. & S. no. 3632). The variation in ssp. *cliffortioides* is considerable and there seems to be connections to *A. ciliaris*, which might deserve further studies.

A. confusa R. Dahlgr.; D. 1963 a p. 117 ff.; D. 1966 p. 54. — Distinct from *A. spicata*, and growing on clayey shale bands below Pakhuis Peak in the summit area of Pakhuis Pass (D. & S. no. 4470), together with, e.g., *A. nudiflora* Harv.

A. linguiloba R. Dahlgr.; D. 1963 a p. 127 ff. — Confined mainly to marine sand in the southwestern divisions. Recorded, e.g., from the following relatively eastern localities, which slightly extend the distribution.

Caledon Div.: In sand nr. the seashore at Betty's Bay. 1965, D. & S. no. 3999 (LD). — Bredasdorp Div.: Flats S of Soetanysberg nr. Asfontein. 1965, D. & S. no. 4542 (LD). — 8 miles N of Struisbaai. 1965, D. & S. no. 3394 (LD). — Swellendam Div.: In sand, ca. 3 miles ESE of Albertsdale Farm, Potberg area. 1965, D. & S. no. 4585 (LD). This last-mentioned form is grey-puberulent and has relatively short leaves and calyx lobes.

A. cymbiformis DC.; D. 1963 a p. 132 ff. — Mainly on clayey ground (in contrast to *A. linguiloba*). Found on compact clay in Gydo Pass, Ceres Div. (D. & S. nos. 3989 and 4128). — To the numerous previous records from the southwestern divisions may be added a find from the Paardeberg Mt. (D. & S. no. 4110) and one from Old Witzenberg Pass, Witzenberg Mts. (D. & S. no. 4382), Malmesbury and Ceres Divs., respectively.

A. campestris R. DAHLGR.; D. 1963 a p. 145 ff. — Described in 1963 from a rather limited material, and, like *A. millefolia*, largely overlooked previously. It has a considerable southern distribution and is concentrated to the more or less clayey hills and flats with rhenosterbos-fynbos transition south of Riversonderend and Langeberg Mts. Map in Fig. 2 C. New records:

Caledon Div.: Ca. 3 miles SE of Riversonderend on rd. to Klipdale; rhenosterveld on hills, clayey ground. 1966, D. & S. no. 4911 (LD). — Swellendam Div.: Hill nr. Platkop, ca. 10 miles NE of Malagas on rd. to Heidelberg. 1965, D. & S. no. 4602 a (LD). — Ca. 7.5 miles SW of Swellendam; gravel on shales. 1966, D. & S. no. 4778 (LD). — Riversdale Div.: Roadside ca. 12 miles E of Heidelberg, on clay. 1966, D. & S. no. 4781 (LD). — Mossel Bay Div.: 9 miles W of Mossel Bay. 1966, D. & S. no. 4789 (LD).

A. salteri L. BOL.; D. 1963 a p. 150 ff. — Like *A. prostrata* and *pallescens* (mentioned in D. 1967), this is a typical limestone species. It grows on bare limestone rock, such as near Cape Maclear on the Cape Peninsula and on hills W of Baardscheerdersbosch (D. & S. no. 4523) and on limestone flats near Arniston (D. & S. no. 4197), the latter two places in Bredasdorp Div. Map in Fig. 7 H.

A. asparagoides L. FIL.; D. 1963 a p. 158 ff. — A variable species. Erect, up to > 1 m tall forms (similar to those forms described in D. 1963 a p. 163) with relatively long, often almost straight, closely set leaves, branches densely hairy in the upper parts, and sometimes with a partly hairy carina prove to occur in several places in the southwest. Such collections are as follows.

Caledon Div.: Along streamlet just N of Genadendal. 1965, D. & S. no. 2834 (LD). — Black soil at S base of Pilaarkop, Riversonderend Mts., nr. the "Esperance" farm. 1965, D. & S. no. 4221 (LD). — Swellendam Div.: 5 miles E of Zuurbraak. 1965, D. & S. no. 4298 (LD). — Ca. 23 miles W of Heidelberg. 1965, D. & S. no. 2871 (LD). — 14 miles W of Heidelberg along rd. to Swellendam. 1965, D. & S. no. 2367 (LD). — Lower S slopes of Ertjiesvlei Berg, ca. 6 miles N of Heidelberg. 1965, D. & S. no. 4607 (LD).

The "typical" forms of ssp. *asparagoides* are mainly concentrated more to the east, and have been collected by us in the Swellendam, Riversdale, Mossel Bay, and Knysna Divs. They are often found on clayey ground, whereas ssp.

rubrofusca (ECKL. & ZEYH.) R. DAHLGR., which is largely even more eastern, is found on ± sandy substrate in so-called "false fynbos" (sensu ACOCKS 1953). A relatively western find of this is D. & S. no. 4879 from the N end of Outeniqua Pass, George Div.

A. opaca ECKL. & ZEYH.; D. 1963 a p. 166 ff. — Commoner in the western parts of the distribution area than known previously (cf. *A. millefolia* and *campestris*, with which *A. opaca* is sometimes associated). Some western finds are as follows.

Caledon Div.: Base of Riversonderend Mts. between the "Casy" and "Happy Valley" farms. 1965, D. & S. no. 3910 (LD). — Riversonderend Mts., nr. base of Pilaarkop at the "Esperance" farm. 1965, D. & S. no. 3812 (LD). — Swellendam Div.: Bontbok Nat. Park, ca. 2—3 miles S of Swellendam. 1965, D. & S. no. 4561 (LD). — Hill nr. Platkop, ca. 10 miles NE of Malagas on rd. to Heidelberg. 1965, D. & S. no. 4602 (LD). — Ca. 1.5 miles S of Barrydale, just N of Tradu Pass. 1965—66, D. & S. nos. 2281 and 4902 (LD). — 14 miles W of Heidelberg, clay. 1966, D. & S. no. 4780 (LD). — Riversdale Div.: 12 miles E of Heidelberg, clayey ground. 1966, D. & S. no. 4782 (LD). — 6 miles from Riversdale on rd. to Corente River, in red clay. 1965, D. & S. no. 2607 (LD).

The collections from Caledon Div. should be referred to ssp. *opaca*, whereas the others mentioned have relatively short calyx lobes and can be classified as ssp. *pappeana* (HARV.) R. DAHLGR. — Forms collected further to the east, in the Uniondale, Knysna, and Humansdorp Divs., correspond to ssp. *opaca* and ssp. *rostriloba* R. DAHLGR. (D. & S. no. 4836). An eastern outpost of the species was collected in Alexandria Div.: 13 miles from Colchester on rd. to Grahamstown (D. & S. no. 4807). It agrees closely with the type of the synonymous species "*A. elongata* E. MEY.", which was recorded erroneously from "? Draakenstein" by DRÈGE (cf. D. 1963 a p. 171). These two collections differ from other populations of ssp. *opaca* in that the relatively large flowers have a glabrous carina.

A. varians ECKL. & ZEYH.; D. 1965 p. 19 ff. — On clayey ground largely of the Malmesbury Beds (map in Fig. 3 D). To previous collections may be added D. & S. no. 3223 from flats at W base of Warmbadsberg (Olifants River Mts.) near Pieterskop, growing on clay with sparse rhenosterbos. The specimens in this place were large and the decumbent branches were up to > 1 m long. The species also grows on flats between Tulbagh Road Stn. and Tulbagh Waterfall (D. & S. no. 3838).

A. ericifolia L.; D. 1965 p. 24 ff. — Ssp. *ericifolia* and ssp. *minuta* R. DAHLGR. normally grow in sand weathered from T.M.S. sandstone. Ssp. *ericifolia* is previously known only sporadically from Caledon Div. Marginal new collections have been made, e.g., at Betty's Bay (D. & S. no. 3533), in Shaw's Mt. Pass (D. & S. no. 3562), at Hemel en Aarde (D. & S. no. 3553), and in the Hagedisberg Pass E of Stanford (D. & S. nos. 3422 and 3729). Decumbent, small-flowered forms of ssp. *ericifolia* occur on flats near Botrivier Vlei in the same division (D. & S. nos. 3330 and 3332). Also a find from Bredasdorp Div.

can be noted: the sand hills ca. 5 miles NE of Baardscheerdersbosch (D. & S. no. 3672). — Ssp. *pusilla* R. DAHLGR. with smaller flowers and much smaller leaflets otherwise prevails in the latter division, and has been collected in mixed rhenosterveld ca. 3 miles WNW of Elim (D. & S. no. 3405), on sand flats ca. 3 miles E of Viljoenshof (D. & S. no. 3772), and ca. 9 miles WNW of Bredasdorp (D. & S. no. 3382). The ecology of this subspecies is somewhat variable and deserves further investigations.

A. muraltioides ECKL. & ZEYH.; D. 1965 p. 35 ff. — Confined to fine-grained clayey substrate, partly or mainly on the Malmesbury Beds (map in Fig. 3 E). The distribution covers part of the western divisions but extends further to the east than known previously. The species is locally abundant in the western divisions, e.g. on the NE side of Paardeberg, Malmesbury Div. (D. & S. no. 4106) and on flats ca. 11 miles N of Malmesbury (D. & S. no. 4106). It may even be subdominant in mixed rhenosterveld on roadsides, such as in the Wellington region (D. & S. nos. 3823 and 3825) and near Gouda (D. & S. no. 3197). It has also been collected in hard clay in Gydo Pass, Ceres Div. (D. & S. 3991) and on flats near Tulbagh Road Stn., Tulbagh Div. (D. & S. no. 3839). An eastern outpost was found in the valley N of Villiersdorp, ca. 15 miles S of Worcester (D. & S. no. 4412).

A. flexuosa THUNB.; D. 1965 p. 39 ff. — Very common in the western divisions and mainly concentrated on ground with clay or a clay-sand mixture, partly, at least, of the Malmesbury Beds. Map in Fig. 3 B. Numerous collections have been made by us in the western regions.

A. rectistyla R. DAHLGR.; D. 1965 p. 43 ff. — Previously known only from a couple of collections on the flats W of Olifants River Mts., Piketberg Div. The species is locally abundant ca. 11 miles NE of Piketberg along the road to Grey's Pass (D. & S. no. 2505), growing in red, clayey soil mixed with sand, and ca. 6 miles from Eendekuil along the road to Porterville (D. & S. no. 3224).

A. hispida THUNB.; D. 1965 p. 46 ff. — The numerous recent collections indicate that there is an ecological difference between the forms treated in D. 1965 p. 53 under "A" and those treated on p. 54 under "B". In the western regions the former are generally tall, spreading, erect, relatively short-leaved, and supplied with pale-yellowish (not violet), glabrous carina petals. They occur mainly on clayey soil. The latter are often lower, more long-leaved, and supplied with ± violet and partly puberulous carina petals. They are found in sand, often in marine sand along the coasts.

Specimens with the former appearance are found, e.g., on the mixed rhenosterveld hills in the southern divisions from Riversonderend in the east to Caledon in the west, e.g. at Riversonderend and in adjacent regions (D. & S. nos. 2717 and 2860—2861), on the shaley hills between Caledon and Napier (D. & S. no. 3424), and on a kopje E of Kathoek (D. & S. no. 3631). Similar forms, but low and subprostrate, although still rigid and spreading, have been found of clayey flats E of Witzenberg, Ceres Div. (D. & S. no. 4370), and N of Malmesbury (D. & S. no. 4348). The latter forms are ± pubescent on the carina and approach the forms under "B" above. The transition is in fact rather gradual. Similar more or less compact forms occur on clayey substrate in the Cedarberg Mountains (e.g., in Pakhuis Pass, D. & S. no. 4467, and on the clayey shale band of Cedarberg Tafelberg, D. & S. no. 4433, where they are almost cushionlike).

Ssp. *albiflora* (ECKL. & ZEYH.) R. DAHLGR. has been found mainly in sand, e.g., near Knysna (D. & S. no. 4664) and near Still Bay, Riversdale Div. (D. & S. no. 4623), in the latter area growing in sand between limestone hills. Very small-flowered forms of *A. hispida*, with short leaves, and transitional between ssp. *albiflora* and ssp. *hispida*, occur in Swellendam Div. (D. & S. nos. 4569 and 4603) on clayey ground in the fynbos-rhenosterbos transition.

A. parviflora BERG.; D. 1965 p. 62 ff. — On clayey ground or on sand mixed with clay, partly on the Malmesbury Beds.

A. calcarata HARV.; D. 1965 p. 70 ff. — Possibly restricted to clayey soil, and locally frequent on clayey flats of Bontbok Nat. Park, ca. 2 miles S of Swellendam (D. & S. no. 4560).

A. macrantha HARV.; D. 1965 p. 76 ff. — On sandy substrate often mixed or covered with black porous soil, in rather tall fynbos communities. Frequent to dominant after fire in the Orange Kloof—Wynberg region on the Cape Peninsula (e.g. D. & S. no. 3358). See DAHLGREN in Fl. Plants of Africa, Plate 1481.

A. rycroftii R. DAHLGR.; see D. 1967 p. 32 ff. — On clayey ground in the Malmesbury region.

A. uniflora L.; D. 1965 p. 81 ff. — Ssp. *uniflora*, regionally common in the western divisions, prefers open, ± clayey habitats. — Ssp. *willdenowiana* (BENTH.) R. DAHLGR. has a southern distribution, only meeting ssp. *uniflora* in some regions. In contrast to ssp. *uniflora*, it prefers sandy soil and more shaded habitats. Certain eastern forms, hitherto included in ssp. *willdenowiana*, may deserve separate taxonomic rank. They have been found by us in Tradu Pass, Swellendam Div. (D. & S. nos. 2663 and 3952) and in Garcia's Pass, Riversdale Div. (D. & S. no. 2572), and are trees up to > 4 m tall with long, pendulous branches bearing sparsely dispersed white—pink flowers or beaked pods. All the western forms of the species have yellow (or partly bright-red) petals, and their pods are beakless. A study of the somewhat transitional forms in Robertson Div. and the western parts of Swellendam Div. is desirable.

A. macrocarpa ECKL. & ZEYH.; see D. 1967 p. 34 ff. and DAHLGREN in Fl. Plants of Africa, Plate 1482.

A. pinea THUNB.; D. 1965 p. 92 ff. — Ssp. *pinea* occurs in sand, usually among large rocks and stones (of T.M.S.) in Tulbagh, Ceres, and Clanwilliam Divs. To the previously given distribution may be added collections from "Scherpenheuwelsberg", a rocky outcrop 3—4 miles NW of Grey's Pass in

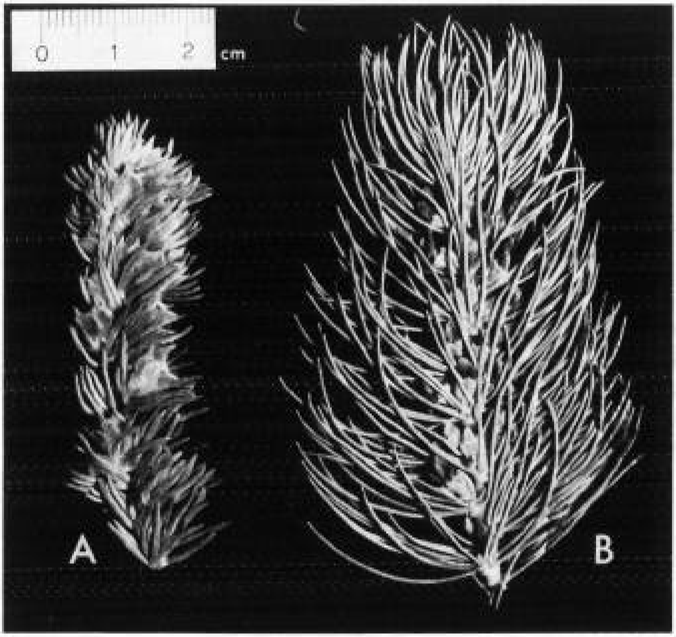

Fig. 1. — A: A supposedly new species of *Aspalathus* from a limestone outcrop north of Blombos, Riversdale Div., DAHLGREN & STRID no. 2359. — B: *Aspalathus longifolia* BENTH., flowering branch end, from the northern part of Garcia Pass, same div., D. & S. no. 2588.

Olifants River Mts. (D. & S. nos. 3238 and 4450). — A new find of the rare ssp. *caudata* R. DAHLGR. was made in Stellenbosch Div.: inner part of Jonkershoek Valley, S-facing slopes, in close *Erica* vegetation (D. & S. no. 4089).

A. filicaulis ECKL. & ZEYH.; D. 1965 p. 102 ff. — Occurs in sand in the southern lowland as well as in the northern mountainous parts of the distribution.

A. sceptrum-aureum R. DAHLGR.; D. 1965 p. 102 ff. — Mainly in a mixed sclerophyll-rhenosterbos community on fine-grained substrate. An additional recent locality is: Ladismith Div.: 0.5 miles N of Ladismith, S of the foothills of Little Swartberge, D. & S. no. 4673.

A. acanthes ECKL. & ZEYH.; D. 1965 p. 114 ff. — On sand or sandstone ground. In the N part of Garcia's Pass, 1—2 miles S of Muiskraal, Riversdale Div., the species grows on a shallow layer of sand resting on horizontal sandstone rock (D. & S. nos. 2575, 3966, and 4895). It has also been collected ca. 9 miles E of Rietvlei, N side of Langeberge, same division (D. & S. no. 2675).

A. hystrix L. fil.; D. 1965 p. 134 ff. — The ecology of this species is somewhat variable. On Anysberg (D. & S. no. 4650) and near Wittepoort (D. & S. no. 4653), Ladismith Div., it may be found in sand and on sandstone. In perhaps most other regions, e.g. near Ladismith, it seems to prefer a more finegrained substrate, and often grows mixed with rhenosterbos.

A. lamarckiana R. Dahlgr.; D. 1965 p. 138 ff. — Found a couple of miles SE of Wittepoort, Ladismith Div., in a rocky valley on the precipices of a sandstone plateau (D. & S. no. 4652). Also *A. hystrix* occurs in this area. The distinctness between these two species seems to be clear.

A. hirta E. Mey.; D. 1965 p. 140 ff. — Widespread, apparently restricted to sandy ground of T.M.S. (map in Fig. 4 B), and often found in relatively dry sclerophyll vegetation, especially at the bases or on the low slopes of the mountains, where it may be dominant locally. Numerous recent collections do not increase the previously known distribution area considerably. Records from Kogman's Kloof (D. & S. no. 2246) and the N side of Langeberge 5—6 miles E of Montagu (D. & S. no. 2257), both in Montagu Div., may be mentioned. — Ssp. *stellaris* R. Dahlgr., like ssp. *hirta*, grows on sandy substrate in fynbos. It is common on the upper slopes of sandstone hills a few miles SW of Uniondale (D. & S. nos. 3000, 3004, and 4855). A somewhat transitional form between the two subspecies is D. & S. no. 4869 from the S slopes of Mannetjiesberg, Kammanassie Mts., at ca. 1410 m altitude.

A. spectabilis R. Dahlgr.; D. 1965 p. 158 ff. — Found in the S part of Tradu Pass, Swellendam Div., at ca. 220 m altitude, near a streamlet (D. & S. nos. 2295, 2662, and 4908). The similar, but much more small-flowered *A. hirta* occurs in the same area (D. & S. nos. 3956 and 4909).

A possibly new species, similar to *A. laricifolia* Berg. ssp. *canescens* (L.) R. Dahlgr. was found by us on a limestone outcrop ca. 5 miles N of Blombos, Riversdale Div. (D. & S. no. 2359). The shrubs were up to 1 m tall, erect, somewhat lanky, and had foliage similar to that of *A. laricifolia* ssp. *canescens*. However, the calyx lobes (only the bud stage was seen) were much larger, cordate, and ± overlapping at the base. Fig. 1 A.

A. chortophila Eckl. & Zeyh.; D. 1965 p. 171 ff. — Occurring mainly on sand and sandstone, but a form from near Maalgat River, 6 miles W of George, (D. & S. no. 4886) was found on a shale slope. This comprised >1 m tall shrubs with sparsely pubescent leaves. Similar but lower forms occur on sandy ground on the hills near Brenton, Knysna Div. (D. & S. no. 4667). To the distribution of the relatively low and short-leaved forms of ssp. *kougaënsis* R. Dahlgr., a find from near Waterkloof, ca. 1.5 miles N of Ladismith may also be added (D. & S. no. 4647).

A. alopecurus Benth.; D. 1965 p. 195 ff. — Growing mainly in sand. Map in Fig. 7 E. The rigid-leaved forms found, e.g., on the N slopes of the Aasvogelberg range in Riversdale Div. (e.g. D. & S. no. 2642), however, grow in stony and sandy soil mixed with clay, or on black, rather fine-grained substrate.

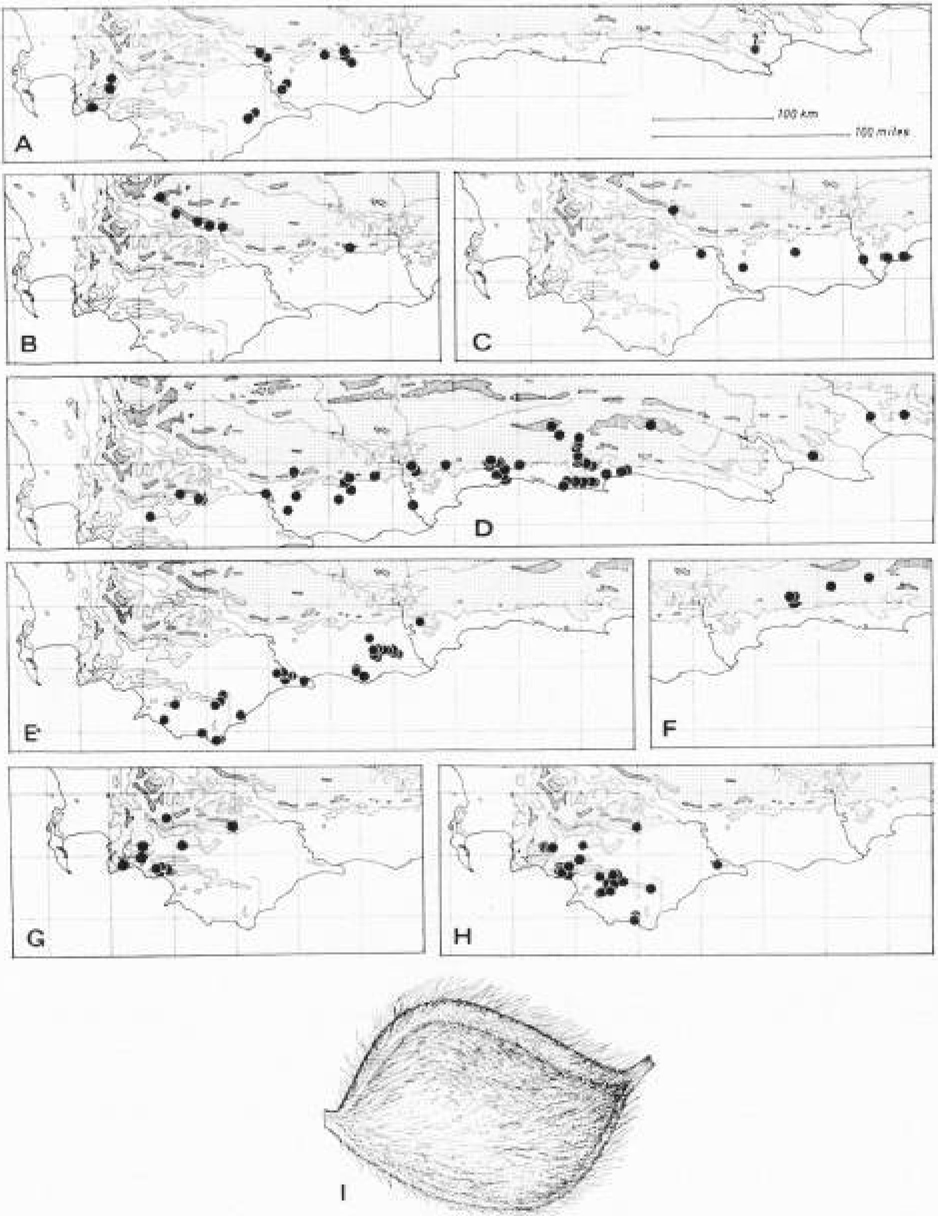

Fig. 2. Documented distributions of: A: *Aspalathus millefolia* R. DAHLGR. — B: *A. grandiflora* BENTH. — C: *A. campestris* R. DAHLGR. — D: *A. opaca* ECKL. & ZEYH. — E: *A. incurvifolia* WALP. — F: *A. glabrescens* R. DAHLGR. — G: *A. ramulosa* E. MEY. — H: *A. caledonensis* R. DAHLGR. — I: Pod of *Aspalathus desertorum* BOL., DAHLGREN & STRID no. 4125 from Gydo Pass, Ceres Div., × 5.

A. glabrescens R. DAHLGR.; D. 1965 p. 217 ff. — Previously known only in a few collections from the Outeniqua Pass region, George Div., where it was rediscovered (D. & S. nos. 2943, 4656, 4878, and 4881). Rather short-leaved forms of the species have been collected in: Uniondale Div.: Ca. 5 miles WSW of Uniondale along rd. to George, in dry fynbos with sparse rhenosterbos. 1966, D. & S. no. 4874 (LD), and George Div.: Ca. 33 miles WSW of Uniondale along rd. to George; low outcrop N. of Outeniqua Mts. opposite Langeberg Peak. 1966, D. & S. no. 4874 (LD). Map in Fig. 2 E.

A. longifolia BENTH.; D. 1965 p. 220 ff. — Previously somewhat incompletely known, occurring in local abundance on slopes ca. half a mile S of Muiskraal, N of Garcia's Pass, Riversdale Div. (D. & S. nos. 2588, 3972, and 4900). The vegetation is partly mixed with rhenosterbos, partly with *Aspalathus hirta* (see above). Fig. 1 B.

A. incurvifolia WALP.; D. 1965 p. 213 ff. — Variable in appearance as well as ecology. Certain forms are very characteristic of *limestone rock* and are found, sometimes abundantly, together with *A. calcarea* R. DAHLGR., on the limestone hills in Bredasdorp and Riversdale Divs. Such collections are: Bredasdorp Div.: Ca. 1 mile NW of Arniston, limestone flats. 1965, D. & S. no. 4199 a (LD). — Hills above Agulhas village, limestone rocks. 1965, D. & S. no. 4202 (LD). — Limestone hill ca. 2 miles NE of Bredasdorp along rd. to Swellendam. 1965, D. & S. no. 4180 (LD). — Riversdale Div.: Ca. 10 miles SE of Riversdale, N of Melkhoutfontein, limestone hills. 1965, D. & S. no. 4616 (LD). — Limestone hills nr. Melkhoutfontein. 1965, D. & S. no. 4619 (LD). — Limestone ridges 3—5 miles N of Blombos. 1965, D. & S. nos. 2358 and 4631 (LD).

Of these, the population in Riversdale Div. is characterized by relatively small pods with short, rather appressed pubescence, the Bredasdorp Div. population by slightly larger pods with more villous pubescence.

Other forms occur on sand or on sandstone rock (or sometimes on slightly clayey ground, viz. near Potberg), often in pure white sand on flats. The accompanying species are also not of a calciphilous selection. Such collections, mainly on sand, are: Bredasdorp Div.: Ca. 5 miles SSE of the Papiesvlei crossroad, SW of Koueberge, rocky sand slopes. 1965, D. & S. no. 3412 (LD). — Low S slopes of Soetanysberg, above Asfontein. 1965, D. & S. no. 4536 (LD). — Rocks on Potberg, above Potberg Farm; ca. 400 m. 1965, D. & S. no. 3642 (LD). — Swellendam Div.: Nr. Koenskraal Farm, ca. 3 miles WSW of Port Beaufort, slopes at base of Potberg. 1965, D. & S. no. 4586 (LD). — Ca. 2 miles from N base of Potberg in the Melkhoutrivier area; clay-sand ground. 1965, D. & S. no. 4582 (LD). — Riversdale Div.: Sand flats ca. 9, 8, 8, 4, and 3 miles W of Albertinia. 1965—66, D. & S. nos. 4683, 2620, 2628, 4784, and 2639, respectively (LD). — Upper part of Aasvogelberg ridge ca. 1.5—2 miles SE of Albertinia. 1965, D. & S. no. 2646 (LD).

Of these collections, the first two mentioned, from Bredasdorp Div., are exceptionally long-leaved and have long woolly pod pubescence. A similar form was previously recorded from near Hagelkraal in the same division (D.

1965 p. 215). The other collections resemble rather much the limestone forms mentioned above, although those in Riversdale Div. have more tail-like branches with numerous flowers and also woollier pubescence than the limestone forms in the same division. A close connection between habitat and appearance is accordingly not found in the species. The species turned out to be commoner than thought from previous collections. Map in Fig. 2 E.

A. caledonensis R. DAHLGR.; D. 1960 p. 284 ff. (under the name "*A. argentea* L."). — Restricted to often white sand or sandstone gravel weathered from T.M.S. sandstone, and found in the main parts of Caledon and Bredasdorp Divs. (map in Fig. 2 G). The ± lanky specimens may reach more than 120 cm in height in undisturbed habitats. The species was collected by us, e.g. on the Onrust Mt. (D. & S. no. 3655), near and on the Hermanus Mt. (D. & S. nos. 3345 and 3897), near Mosselrivier (D. & S. no. 3555), and on Shaw's Mt. (D. & S. no. 3907), all in Caledon Div. — In Bredasdorp Div. it has been collected, e.g., near Baardscheerdersbosch (D. & S. nos. 2129 and 3683), on the W as well as E end of Bredasdorp Mt. range (D. & S. nos. 2138 and 3388), and on the S slope of Soetanysberg (D. & S. no. 4534).

A. oblongifolia R. DAHLGR.; D. 1960 p. 289 ff. — In sand, sometimes on the lower slopes of sandstone mountains, as near Pringle Bay (D. & S. no. 3939), sometimes on sand flats, as E of Gt. Hangklip Mt. (D. & S. no. 3936), Caledon Div.

A. intervallaris BOL.; D. 1960 p. 292 ff. — Growing in sand. Near Betty's Bay, Caledon Div., this rare species can be found in pure marine sand (D. & S. no. 4318) associated with *A. retroflexa* L. It is decumbent and more slender than the previous two species. The branches may be up to > 1 m long and more branched than known from the material at hand before 1965.

A. quadrata L. BOL.; D. 1960 p. 294 ff. — Not seen by me, but collected in 1962 by Dr. J. G. LEWIS. (L. no. 5923) on sand flats ca. 6 miles W of Albertina, Riversdale Div., where it flowered in October.

A. vulpina R. DAHLGR.; D. 1960 p. 297 ff. — Rediscovered on a hill at the N end of Garcia's Pass, Riversdale Div. (D. & S. nos. 2582 and 3970), growing in shallow sand mixed with stones on horizontal sandstone rock.

A. ramulosa E. MEY.; D. 1960 p. 190 ff. — Like *A. caledonensis*, this species grows in grey or white sandstone gravel or sand weathered from T.M.S. sandstone. Commoner in the mountains in the western parts of Caledon Div. than known before. Besides several collections from Klein River Mts. and its connective ridge towards Babylons Tower Mts. (D. & S. nos. 3884, 3659, 3554, and 3896) it has been collected as far north as on the Donkerhoek Mt., above the Boskloof farm at ca. 650 m altitude (D. & S. no. 3924). See map in Fig. 2 H.

A. sericea BERG.; D. 1960 p. 201 ff. — Similarly restricted to sand. Ssp. *sericea* often grows on flats with marine sand near the seacoasts in the southwestern divisions. The forms recorded from Montagu Div. morphologically correspond rather to ssp. *sericea* than ssp. *aemula* (E. Mey.) R. Dahlgr. as the petal pubescence is sericeous rather than villous and the petals are relatively narrow. However, they differ from the other forms of the species in the leaves, which have three relatively small, equally large leaflets. Such a form was found by us at the N base of Langeberg Mts., ca. 6 miles ESE of Montagu (D. & S. no. 2256). Ssp. *aemula* grows in sand, often among large boulders, on mountain slopes, in several places together with *A. pinea* Thunb.

A. altissima R. Dahlgr.; D. 1960 p. 209 ff. — Growing in sand, generally on rocky slopes or in association with rocky outcrops (of T.M.S. sandstone). In the mountain pass above Elandskloof, E of Citrusdal, Clanwilliam Div., it grows even in fissures of sandstone rock, reclining over the steep slope with lanky stems up to 2 m tall (D. & S. no. 2547).

A. quinquefolia L.; D. 1960 p. 235 ff. — Confined to sand, ssp. *virgata* (Thunb.) R. Dahlgr. being a most characteristic and often dominant constituent of the vegetation on the marine-sand flats in the western as well as eastern divisions. This subspecies is also found on sand accumulated in the mountains in the western divisions, and is rather common, e.g., in the Olifants River and Cedarberg mountain ranges. Of numerous recent collections, a find in sand at the N base of Langeberg Mts. 5—6 miles ESE of Montagu may be noted (D. & S. no. 2251).

A. tridentata L.; D. 1960 p. 213 ff. — Some recent finds have been made east of the previously known distribution area: Bredasdorp Div.: Ca. 1 mile W of Potberg Farm, flats W of Potberg. 1965, D. & S. no. 4190 (LD). — Swellendam Div.: 3—4 miles E of Swellendam, hills mostly with fynbos. 1965, D. & S. nos. 2377 and 3949 (LD). — Bontbok Nat. Park, 2—3 miles S of Swellendam. 1965, D. & S. no. 4554 (LD). — Of these, the forms near Swellendam have features of ssp. *staurantha* (Eckl. & Zeyh.) R. Dahlgr. and are, at least sometimes found on clayey soil.

The ecology of this complex species as a whole is variable. Ssp. *tridentata* is usually found in sand or sandstone gravel weathered from T.M.S. sandstone. Extreme such habitats are found on poor sandstone gravel or white sand, e.g., on the top ridge of Shaw's Mt., Caledon Div. (D. & S. no. 3898) and on a hill NW of Elim, Bredasdorp Div. (D. & S. nos. 4216 and 4920). Ssp. *staurantha*, on the contrary, is mainly concentrated in the clayey parts, partly on the Malmesbury Beds, e.g. near Gouda, Tulbagh Div. (D. & S. no. 4969). However, there is not a consistent ecological difference between the two subspecies, and, besides, they are connected by intermediate forms. — Ssp. *fragilis* R. Dahlgr. has been collected by us on compact clay near the top of Uitkyk (=Cedarberg) Pass in central Cedarberg Mts. (D. & S. nos. 4265 and 4437), whereas ssp. *rotunda* R. Dahlgr. at least occasionally grows in sand.

A. villosa Thunb.; D. 1960 p. 301 ff. — Occurs in white sand in the mountains of the western divisions.

A. bodkinii BOL. and *A. comptonii* R. DAHLGR.; D. 1960 p. 304 ff. — Both have been collected in Cedarberg Mts. N of Algeria Valley, and the species are apparently mutually distinct (D. & S. nos. 4486 and 4285, respectively).

A. ternata (THUNB.) DRUCE and *A. dasyantha* ECKL. & ZEYH.; D. 1960 p. 274 ff. — These species occur in marine sand in the western and southern parts of the southwestern divisions respectively. Map in Fig. 7 C.

A. acidota R. DAHLGR.; D. 1960 p. 104 ff. — Occurs in fissures of sandstone rock (T.M.S.). Found by us at the top and somewhat E of the top of Kardouw (=Dasklip) Pass, Piketberg-Clanwilliam Div. border (D. & S. nos. 3213 and 3219) where it comprised shrubs 30—120 cm tall.

A. psoraleoides (PRESL) BENTH.; D. 1960 p. 137 ff. — Previously not known outside the Cape Peninsula, where it has been found in sand, mainly in the southern parts, but also as far north as Muizenberg Mt. — The species was found by us (D. & S. no. 3576) in Caledon Div.: Slope at SW end of Babylon's Tower, ca. 5 miles NE of Hawston, in white sand (weathered from T.M.S. sandstone) on a recently burnt slope. This form agrees well with those on the Peninsula, but the leaves as well as the flowers are relatively large. The species was frequent in a limited area in 1965.

A. marginata HARV.; D. 1960 p. 133 ff. — Found in sand or sometimes in sandstone rock fissures, in Caledon and Bredasdorp Divs. There is great variation in leaf size and pubescence, as described in op. cit. p. 136. Though there is a striking population with rather broad, grey-pubescent leaves in the Elim region (D. & S. no. 4213), the forms W of Cape Agulhas (on the S slopes of Soetanysberg; D. & S. no. 4533) and near Baardscheerdersbosch (D. & S. no. 3678) have smaller green leaves, but the latter form is somewhat intermediate. All these places are in Bredasdorp Div. Sharply spine-tipped, small leaflets and small flowers characterize the population in the W-most part of Caledon Div.

A. stenophylla ECKL. & ZEYH.; D. 1960 p. 120 ff. — Confined to often white sand weathered from T.M.S. sandstone, and growing in low fynbos; chiefly after fire in abundance. — Ssp. *colorata* R. DAHLGR. has been collected by us in some new areas in Caledon Div., e.g. on the summit ridge of Shaw's Mt. (D. & S. no. 3903), near Mispath E of Kogelberg (D. & S. no. 4360), on Eseljagtberg ca. 3 miles NNW of Maraisdal (D. & S. no. 3918), and on Donkerhoek Mt. ca. 1 mile SW of Boskloof (D. & S. no. 3922). The locality near Mispath differed from the others in having fine-grained soil. On top of Houw Hoek Pass there is great variation in leaflet size, pubescence, and colour in the subspecies, partly depending on age, the leaves of the old shoots being relatively small and glabrous, whereas those of the quick-growing shoots of young plants are relatively large, often closely puberulous, and light-green. Genetic variation certainly contributes to the variation further. (D. & S. nos. 4332—4334.)

Lower and more narrow-leaved forms in the Riversonderend Mts. comprise ssp. *stenophylla*. This similarly grows in sand. It has been collected in the Bushman Kloof Pass (D. & S. nos. 3486 and 4229) and on the S slope of Pilaarkop near Riversonderend (D. & S. nos. 3800 and 4236).

Ssp. *garciana* R. DAHLGR., finally, was found in shallow sand on horizontal sandstone rock at the N end of Garcia's Pass, Riversdale Div. (D. & S. nos. 2583 and 3970), and a similar form was also collected in sand N of Tradu Pass, ca. 1 mile S of Barrydale, Swellendam Div., but was not in flower.

A. aspalathoides (L.) R. DAHLGR.; D. 1960 p. 114 ff. — This occurs in sand or sandstone gravel (T.M.S.) throughout the distribution area. Young, closely lanate specimens have been collected near Palmiet River Mouth (D. & S. no. 3565), in Klein River Mts. (Maanschijnkop, D. & S. no. 3890), and in the NE part of Zondagskloof (D. & S. no. 3740). It is probable that these represent merely the juvenile stage and that the later developed leaves are more rigid, sparsely hairy, and light green.

A. cytisoides LAM.; D. 1960 p. 160 ff. — Found on sandstone (T.M.S.) rock or in sand generally in association with sandstone in typical fynbos communities. The distribution is relatively wide and ranges between the Hottentotsholland Mts. and the E part of Riversonderend Mts. (D. & S. no. 2153). Forms with white-puberulous leaves on the branch ends (resembling the forms previously described in Tulbagh Div.) have been found in the N part of French Hoek Pass (D. & S. no. 4011) in Paarl Div. and also in Viljoen's Pass (D. & S. nos. 3570 and 4428) and near Grabouw (D. & S. no. 3782) in Caledon Div. Other forms, with relatively small greenish leaves prevail in the Villiersdorp area (D. & S. nos. 2823 and 4003) in Caledon Div.

A. rugosa THUNB.; D. 1960 p. 165 ff. — This species similarly grows in sand and especially ssp. *rugosa* often among sandstone boulders.

A. bracteata THUNB.; D. 1960 p. 313 ff. — A highly variable species occurring on different types of substrate. One short-leaved, rather distinct population, characterized, e.g., by several-ovuled ovaries, grows on compact clay or in fissures of horizontal shales. It was treated under the letter "F" and illustrated in Fig. 108 in D. 1960. One representative of this has been collected 6 miles N of Wellington (D. & S. no. 663) previously. It was collected by us also near Wellington (D. & S. no. 4113) and 4 miles N and 4 miles S of Hermon (D. & S. nos. 3126 and 3826, respectively). — Other forms of *A. bracteata* were found mainly on sand, e.g. in Cedarberg Mts. (D. & S. no. 4552) or on rocks, e.g. near Tulbagh Waterfalls (D. & S. no. 3828). — Prostrate forms with flat leaflets up to 1 mm broad (forms corresponding to those treated under the letter "G" in op. cit.) grow in sand at the S spur of Schurfteberg and near the top of Gydo Pass in Ceres Div. (D. & S. nos. 4133, 4137, and 4397).

A. patens R. DAHLGR.; D. 1960 p. 331 ff. — Found on the very top of Mannetjiesberg, at ca. 1,800 m altitude, growing in sandy soil (T.M.S.) between rocks, mainly among *Erica*. The branches were partly prostrate and the ground temporarily traversed by filtering water. The mist on this level certainly also contributes to a humid climate. (D. & S. no. 4866). See D. 1968 c p. 11 and Fig. 1 A.

A. lanata E. MEY.; D. 1960 p. 336 ff. — This species seems to prefer chiefly clayey ground. In the upper part of Pakhuis Pass, Clanwilliam Div., it grows associated with *A. nudiflora* HARV., on hard, compact clay or on shales (D. & S. nos. 4469 and 4473).

Subgenus Ecklonella R. DAHLGR.; D. 1963 b p. 212. — Type species: *A. diffusa* ECKL. & ZEYH.

A. diffusa ECKL. & ZEYH.; D. 1960 p. 343 ff. Found on shelving sand slopes with a rich water supply. May be rather frequent locally in places recently burnt.

Relation between Substrate and Distribution Areas in Aspalathus, a Discussion

The great dependence of the floristic composition on the different kinds of substrate in the Riversdale area was stressed and analyzed in detail by MUIR (1929). — ACOCKS (1953) classified and mapped the vegetation types in South Africa with due consideration to the soils. However, hardly any attempts have been made previously to correlate the distributions of a considerable number of species in any genus of South African plants with the soils or geological formations.

From the account above and from the distributional and ecological comments presented in especially the later parts of "Revision of the genus Aspalathus" (see literature list), it is obvious that most species are confined to, or at least chiefly concentrated to, particular soils.

Certain variable species, such as *Aspalathus spinosa* L., *acuminata* LAM., *divaricata* THUNB., *tridentata* L., and *bracteata* THUNB., are ecologically eurytopic. However, also within these species there are biotype groups (which may be classified as ecotypes) which may be ecologically very characteristic (such as *A. divaricata* THUNB. ssp. *horizontalis* R. DAHLGR. which grows on clay, whereas most other forms of the species are confined chiefly to sand and sandstone).

As the soils are largely dependent upon the geological formations, we may expect that species in their distribution might coincide partly with the distributions of geological formations. However, the condition in nature is often not as simple as that. Each geological formation may contain constituents of different kinds and form soils of different types. The Table Mountain Series (T.M.S.) of the Cape System, e.g., consists mainly of sandstone and sand, but also of shales and clay weathered from shales. Different geological formations may also form somewhat similar soils (such as certain of the clayey loams weathered from shales of different, especially the Bokkeveld, series of the Cape System and the clayey beds of the Malmesbury System). Therefore plant species in their distributions cannot always be expected to fall entirely within the distributions of the soils of geological formations.

Moreover, the geological formations are sometimes very complicated and divided so that the details can hardly be reproduced on a small-sized map. With all these factors in mind, an attempt is still made here to compare the distributions of the soils of some geological formations with the documented distributions of various species of *Aspalathus* (see Figs. 3—7). General knowledge of the substrate on which the species thrive is necessary for this comparison.

The comparison presented below does not imply that the species mentioned are entirely dependent on the formations under which they are enumerated, but rather that their distributions seem to be dependent on some kind of substrate formed of the geological formation concerned. Besides on the substrate, there is naturally also a great dependence on other conditions, such as precipitation (cf. the map and discussion in D. 1963 d pp. 434—436), altitude, competition, and dispersal in connexion with the evolutionary history of the species.

Reservations must be made for the great discrepancies between distribution of suitable substrate and distribution of actual plant species in regions largely cultivated with crops, such as the Malmesbury Flats and the southern regions with Bokkeveld deposits, which are largely dominated by wheat plantations. In addition, the collected material of many *Aspalathus* species is insufficient for a comprehension of the distribution area.

A clear and often abrupt change in the vegetation — and thus in the selection of species — within a limited area where altitude, climate, and rainfall are essentially the same can be studied, e.g., in the Riversdale Division, where the species growing in sand (such as *Aspalathus quinquefolia* ssp. *virgata*, *A. hispida* ssp. *albiflora*, *A. arenaria*) are replaced by others on the limestone rocks or in the limestone clay (*A. candidula*, *calcarea*, *sanguinea*). On the clayey soils of the Bokkeveld Series (somewhat further inland) we find, e.g., *A. steudeliana* and *zeyheri*, but none of the former species.

Similarly, in a limited mountainous area, such a sharp difference between the selection of species can be studied near Gydo Pass, Ceres Division. In the pass itself the soil consists largely of compact clay (Bokkeveld Series). Here one can find *Aspalathus pedicellata*, *desertorum*, *nigra*, *intricata*, and *pallidiflora*. On the slopes with sand, poor in nutrients and weathered from the

T.M.S. sandstone, near the top of the same pass at the southern spur of Schurfteberg, we find entirely different species, such as *A. sericea* ssp. *aemula*, *A. pinea* ssp. *pinea*, *A. aurantiaca*, *A. filicaulis* and *A. villosa*.

In each of these areas the vegetation naturally varies considerably, especially with regard to the relative frequency of the species, depending on the exposure and steepness of the slopes and other conditions which bring about differences in light, temperature, moisture of the air, access of water in the ground, competition, etc. Nevertheless, the selection of species gives clear evidence of the soil type.

With the above-mentioned restrictions we may accordingly proceed to study some regionally important geological formations and the distributions of species partly or entirely falling within these formations.

The maps showing the distribution of geological formations are redrawn from the two sheets of the geological map prepared and drawn by the Geological Survey, Pretoria; the geological data of this map were compiled by F. C. TRUTER and P. J. ROSSOUW.

The distribution maps of *Aspalathus* species selected for comparison with the distributions of geological formations are preferably ones with relatively wide areas, but not too great an amplitude of geological variation. They are also selected in order to represent as diverse patterns as possible, but local endemics or species with very restricted distribution areas have been omitted largely, although they represent a large proportion, in fact the majority, of the species.

Malmesbury Beds and Similar Soils (map in Fig. 3 A)

The Malmesbury Beds, of Precambrian age, covering parts of the southwestern lowlands and undulating landscape, are sometimes considered to represent a separate system, the Malmesbury System, sometimes classified under the Transvaal System (as by DU TOIT 1954 p. 167); sometimes it is considered considerably younger than that system and close in age to the Nama System. There is also disagreement as to its distribution, the lowlands east of a line Piketberg—Wellington, the Tulbagh Valley, a strip in the Breede River Valley, and the Klipheuwel Beds being sometimes referred to the Loskop System, as in the maps of the Geological Survey of South Africa (the latter regions ///-hatched in the map of Fig. 3). Beds partly of the Malmesbury System, partly of the Nama System, occupy the flats of the Vanrhynsdorp Basin north of the Olifants River.

The strata are arenaceous clay-slates or fine-grained argillaceous quartzites alternating with phyllite, quartzite, ferruginous quartzite, dark felspatic grit, and occasionally conglomerate, limestone, etc. Thick

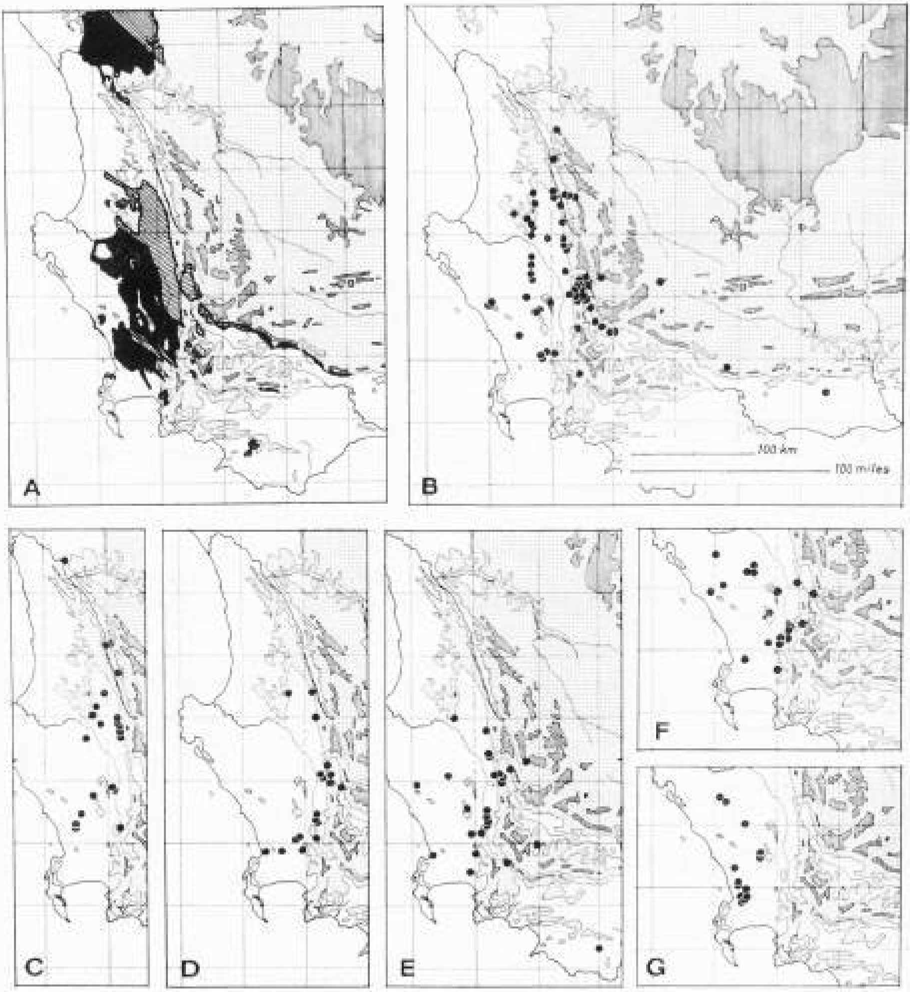

Fig. 3. — A: Distribution of the Malmesbury Beds and related soils. Malmesbury Beds black, soils sometimes referred to the Loskop System ▨-hatched, beds of the Nama System ▨-hatched. — B: *Aspalathus flexuosa* THUNB. — C: *A. wurmbeana* E. MEY. — D: *A. varians* ECKL. & ZEYH. — E: *A. muraltioides* ECKL. & ZEYH. — F: *A. aculeata* THUNB. — G: *A. acanthophylla* ECKL. & ZEYH.

bands of crystalline limestone occur interbedded with dark slates locally, e.g. at Piketberg, Moorreesburg and Saron. (DU TOIT 1954 p. 167.)

The soils formed from the Malmesbury (? and Loskop) System(s) are sandy clay loams often with gravel, white quartz pebbles and occasionally with ferruginous concretions (VAN DER MERWE 1940 pp. 276—277). The vegetation is mainly sclerophyllous, and, like the ground of the Bokkeveld Series (see below), contains a substantial amount of *Elytropappus rhinocerotis*. The precipitation of the western lowland is considerably less than in the adjacent sandstone ranges to the east (cf. map in D. 1963 d p. 434). The clay loams are of a similar kind to those of the Bokkeveld Series in the southern divisions, but relatively few *Aspalathus* species are in common between the two regions. Species bound to clay are also found associated with shale bands of the Table Mountain Series. The lowlands of the Malmesbury (and similar) Beds are largely cultivated, which reduces considerably the distribution areas of the species concerned.

Species largely found on clay loams in the areas of the mentioned formations are the following.

Aspalathus aculeata THUNB. (occasionally in sand) — *A. rycroftii* R. DAHLGR. — *A. cymbiformis* DC. (many forms) — *A. varians* ECKL. & ZEYH. (map in Fig. 3 D) — *A. ericifolia* L. ssp. *puberula* (ECKL. & ZEYH.) R. DAHLGR. — *A. flexuosa* THUNB. (map in Fig. 3 B) — *A. muraltioides* ECKL. & ZEYH. (map in Fig. 3 E) — *A. rectistyla* R. DAHLGR. — *A. hispida* THUNB. (certain forms) — *A. parviflora* BERG. — *A. tridentata* L. ssp. *staurantha* (ECKL. & ZEYH.) R. DAHLGR. — *A. arida* E. MEY. ssp. *procumbens* (E. MEY.) R. DAHLGR. — *A. spinosa* L. (certain forms) — *A. acanthophylla* ECKL. & ZEYH. (map in Fig. 3 G) — *A. glabrata* R. DAHLGR. — *A. wurmbeana* E. MEY. (map in Fig. 3 C) — *A. recurva* BENTH. (certain forms) — *A. cuspidata* R. DAHLGR. — *A. divaricata* THUNB. ssp. *horizontalis* R. DAHLGR. — *A. bracteata* THUNB. (certain forms).

The Cape System, Table Mountain Series (T. M. S.) (map in Fig. 4 A)

Consisting mainly of sandstones and quartzites, whitish in colour and moderately coarse-grained. Shales and conglomerates are rare, the former mainly in two strata (Lower and Upper Shales). The soils are sandy, mainly acid, and grey-brown to dark-brown in colour. Steep slopes are generally devoid of soils, shelving slopes often covered with sand with various amounts of organic material, beneath which there is a white sand layer resting on the rock. The T.M.S. is the dominant member of the Cape Folded Belt as far east as Port Elizabeth and the only member of the system in Pondoland and Natal. (DU TOIT 1954 and VAN DER MERWE

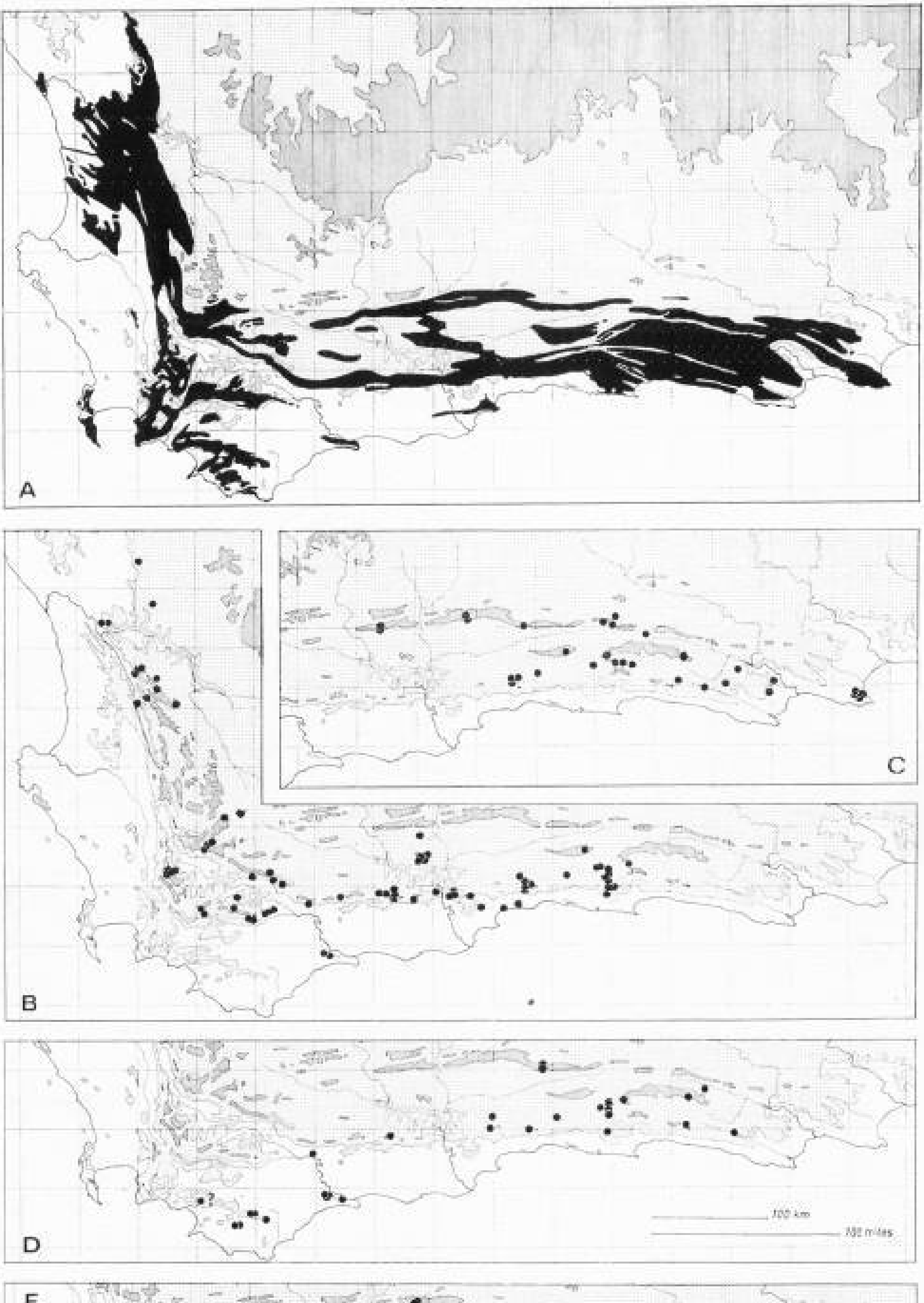

Fig. 4. — A: Distribution of the Table Mountain Series, Cape System, consisting mainly of sandstone, sandstone gravel, and sand. — B: *Aspalathus hirta* E. MEY. — C: *A. collina* ECKL. & ZEYH. — D: *A. aciphylla* HARV. — E: *A. rubens* THUNB.

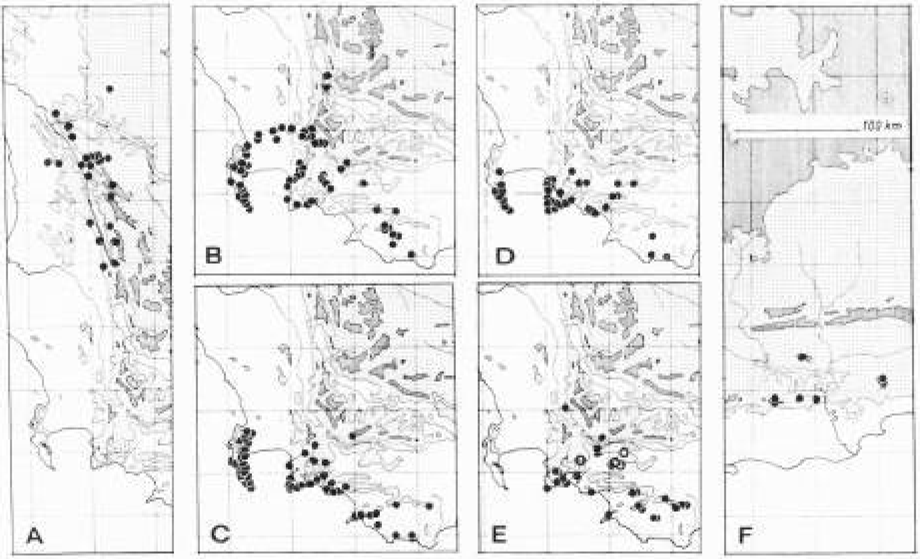

Fig. 5. — A: *Aspalathus vulnerans* Thunb. — B: *A. abietina* Thunb. — C: *A. callosa* L. — D: *A. fusca* Thunb. (dots) and *A. subulata* Thunb. (rings). — E: *A. serpens* R. Dahlgr. — F: *A. granulata* R. Dahlgr.

1940.) Members of *Proteaceae* and *Restionaceae* are common on the T.M.S.

There are many species in the genus which appear, from soil and distribution, to be partly or entirely confined to the T.M.S. The following may be enumerated, classified according to D. 1963 d. Maps are found in the respective parts of the revision.

Aspalathus cephalotes Thunb. (forms) — *A. galeata* E. Mey. — *A. chenopoda* L. — *A. acanthiloba* R. Dahlgr. — *A. araneosa* L. — *A. pigmentosa* R. Dahlgr. — *A. rubiginosa* R. Dahlgr. — *A. ciliaris* L. (most forms) — *A. spicata* Thunb. — *A. incurva* Thunb. — *A. macrantha* Harv. — *A. uniflora* L. ssp. *willdenowiana* (Benth.) R. Dahlgr. — *A. pinea* Thunb. — *A. filicaulis* Eckl. & Zeyh. (most forms) — *A. acanthes* Eckl. & Zeyh. — *A. hirta* E. Mey. (map in Fig. 4 B) — *A. laricifolia* Berg. (at least most forms) — *A. chortophila* Eckl. & Zeyh. (most forms) — *A. caledonensis* R. Dahlgr. (map in Fig. 2 H) — *A. oblongifolia* R. Dahlgr. — *A. intervallaris* Bol. (also in marine sand) — *A. vulpina* R. Dahlgr. — *A. ramulosa* R. Dahlgr. (map in Fig. 2 G) — *A. sericea* Berg. ssp. *sericea* — *A. altissima* R. Dahlgr. — *A. quinquefolia* L. (also largely on marine sand) — *A. tridentata* L. (forms of at least of ssp. *tridentata*) — *A. argyrella* MAC OWAN — *A. acidota* R. DAHLGR. (on rocks) — *A. borboniifolia* R. DAHLGR. — *A. rupestris* R. DAHLGR. (on rocks) — *A. fasciculata* (THUNB.) DRUCE — *A. polycephala* E. MEY. — *A. psoraleoides* (PRESL) BENTH. — *A. marginata* HARV. — *A. stenophylla* ECKL. & ZEYH. — *A. aspalathoides* (L.) R. DAHLGR. — *A. cytisoides* LAM. (often on rocks) — *A. rugosa* THUNB. — *A. decora* R. DAHLGR. — *A. capensis* (WALP.) R. DAHLGR. — *A. carnosa* BERG. — *A. excelsa* R. DAHLGR. — *A. capitata* L. (often on rocks) — *A. fusca* THUNB. and *A. subulata* THUNB. (on rocks; map in Fig. 5 D) — *A. callosa* L. (map in Fig. 5 C) — *A. aciphylla* HARV. (map in Fig. 4 D) — *A. collina* ECKL. & ZEYH. (map in Fig. 4 C) — *A. citrina* R. DAHLGR. — *A. granulata* R. DAHLGR. (map in Fig. 5 F) — *A. spinosa* L. (only certain forms) — *A. longipes* HARV. (certain forms) — *A. gerrardii* BOL. (in Natal) — *A. vermiculata* LAM. — *A. retroflexa* L. (most forms) — *A. batodes* ECKL. & ZEYH. (often on rocks) — *A. juniperina* THUNB. (most forms) — *A. rubens* THUNB. (map in Fig. 4 E) — *A. ulicina* ECKL. & ZEYH. — *A. vulnerans* THUNB. (map in Fig. 5 B) — *A. aristifolia* R. DAHLGR. — *A. glossoides* R. DAHLGR. — *A. divaricata* THUNB. (most forms) — *A. serpens* R. DAHLGR. (map in Fig. 5 E) — *A. aurantiaca* R. DAHLGR. — *A. microphylla* DC. (most forms) — *A. attenuata* R. DAHLGR. — *A. patens* R. DAHLGR. — *A. crenata* (L.) R. DAHLGR. (most forms) — *A. lanceifolia* R. DAHLGR. — *A. cordata* (L.) R. DAHLGR. — *A. barbata* (LAM.) R. DAHLGR. — *A. diffusa* ECKL. & ZEYH. — *A. linearis* (BURM. FIL.) R. DAHLGR. ssp. *linearis* and ssp. *pinifolia* (MARL.) R. DAHLGR.

These species occur mainly on sand, sandstone gravel or sandstone rock. In addition, within the T.M.S., there are some species found mainly on the shale bands in clayey soil, such as *A. nudiflora* HARV., *A. confusa* R. DAHLGR., *A. pedicellata* HARV., *A. wittebergensis* COMPT. & BARNES, and forms of *A. triquetra* THUNB. s. lat., but such species do not seem to be particularly bound to the T.M.S., rather to shales on the whole within the mountains (i.e., also in the Bokkeveld and Witteberg Series).

The Cape System, Bokkeveld Series (map in Fig. 6 A)

When typically developed consisting of five dominant argillaceous (shaly) layers separated by thinner layers of sandstone and quartzites (DU TOIT 1954 p. 250). The softer strata consist of bluish, blackish or greenish shales, some micaceous flagstones, and soft felspatic sand-

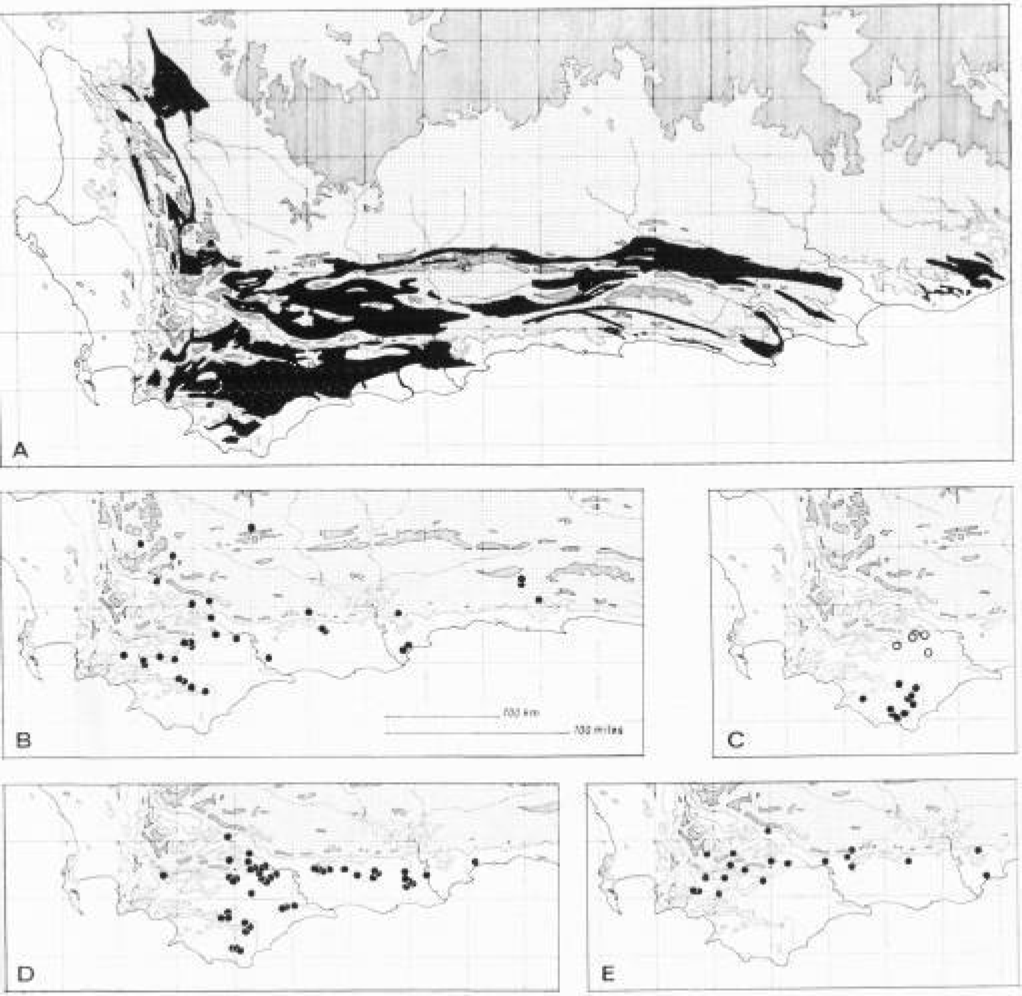

Fig. 6. — A: Distribution of the Bokkeveld Series, Cape System, consisting largely of shales and clay loams. — B: *Aspalathus alpestris* (Benth.) R. Dahlgr. — C: *A. pycnantha* R. Dahlgr. (dots) and *A. incompta* Thunb. (rings). — D: *A. steudeliana* Brongn. — E: *A. submissa* R. Dahlgr.

stones, but no limestone. These strata are easily weathered, and the products form considerable beds of relatively fertile soils chiefly in the valleys and lowlying parts. The soils formed are usually greyish-brown to light-brown, somewhat basic clay loams, in the surface layer often with quartz and shale fragments. The vegetation is poor in proteaceous and restionaceous representatives; characteristic are instead *Elytropappus* and *Cotyledon* (DU TOIT 1954 p. 252). The Caledon—Riversdale region, which is a rolling landscape, is largely cultivated, which results in very restricted distribution patterns for the wild species concerned. MUIR (1929) classified this area as the chief part of his "Rhenosterveld".

Species occurring on the clay loams or sometimes on shales mainly in the southern regions are as follows.

Aspalathus submissa R. DAHLGR. (map in Fig. 6 E) — *A. nigra* L. (many forms) — *A. millefolia* R. DAHLGR. (map in Fig. 2 A) — *A. campestris* R. DAHLGR. (map in Fig. 2 C) — *A. asparagoides* L. FIL. (certain forms) — *A. opaca* ECKL. & ZEYH. ssp. *pappeana* (HARV.) R. DAHLGR. — *A. hispida* THUNB. (certain forms of ssp. *hispida*) — *A. calcarata* HARV. — *A. burchelliana* BENTH. — *A. candicans* AIT. (at least partly) — *A. pinguis* THUNB. (forms). — *A. steudeliana* BRONGN. (map in Fig. 6 D) — *A. smithii* R. DAHLGR. — *A. zeyheri* (HARV.) R. DAHLGR. — *A. pycnantha* R. DAHLGR. and *A. incompta* THUNB. (map in Fig. 6 C) — *A. biflora* E. MEY. (certain forms) — *A. alpestris* (BENTH.) R. DAHLGR. (map in Fig. 6 B) — *A. linearis* (BURM. FIL.) R. DAHLGR. ssp. *latipetala* R. DAHLGR. (partly).

Other species occurring on clayey ground mainly in the mountains probably often grow on substrate of the Bokkeveld Series, e.g. populations of *A. pedicellata* HARV., *A. lanifera* R. DAHLGR., *A. nudiflora* HARV., and *A. desertorum* BOL.

Also the main parts of Little Karroo are covered with Bokkeveld deposits; but no *Aspalathus* species occur in typical Karroo vegetation, only along its border, such as *Aspalathus spinosa* L. ssp. *glauca* (ECKL. & ZEYH.) R. DAHLGR.

The Cape System, Witteberg Series (not mapped here)

Distributed over relatively wide areas east of the Cedarberg and north of the Anysberg—Swartberg Mountains, including the Swartruggens and Witteberg Mountains bordering the Karroo. The series consists of white, fine-grained quartzites with micaceous shales. Some *Aspalathus* species are found in the area of the Witteberg Series, but few are restricted entirely to it. Thus, e.g., *A. joubertiana* ECKL. & ZEYH. and *A. hystrix* L. FIL. occur also in other series of the Cape System. *A. wittebergensis* COMPT. & BARNES and *A. intricata* COMPT. are found on clayey ground but likewise occur outside the series. The Witteberg Series also dominates the system in the Grahamstown region, Albany

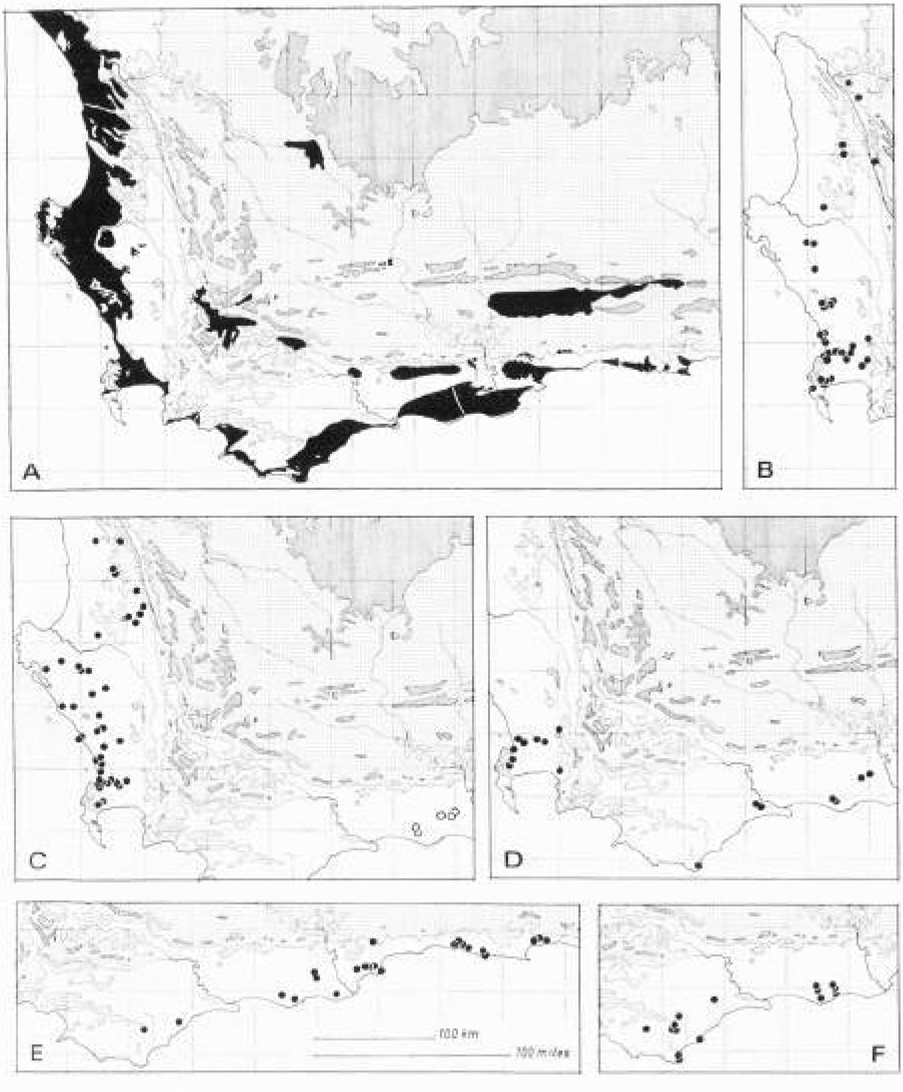

Fig. 7. — A: Distribution of Tertiary—Recent deposits, in the south and west mainly marine sand, frequently, especially in the south, also limestone rocks. — B: *Aspalathus albens* L. — C: *A. ternata* (THUNB.) DRUCE (dots) and *A. dasyantha* ECKL. & ZEYH. (rings) — D: *A. tylodes* ECKL. & ZEYH. — E: *A. alopecurus* BENTH. — F: *A. calcarea* R. DAHLGR. — G: *A. sanguinea* THUNB. — H: *A. salteri* L. BOL.

Division, together with the Bokkeveld Series. Here we find *A. frankenioides* DC., forms of *A. chortophila* ECKL. & ZEYH., and the more restricted *A. argyrophanes* R. DAHLGR. and *A. teres* ECKL. & ZEYH., the last-mentioned species of which occurs near Port Elizabeth, on the T.M.S.

Cretaceous and Tertiary to Recent Deposits (map in Fig. 7 A)

Most of these deposits, viz. those of the western and southern lowlands near the coast are marine. They may be divided into the southern and western ones. Along the coast from Cape Agulhas and eastwards there is a narrow strip of white dunes consisting of shifting sand; beyond these there are limestone ridges which are sometimes very prominent and may extend ca. 10 miles inland. The sand is loose and rests on a hard limestone layer. Sometimes a grey-brown, loose sand soil is formed. Beyond the limestone ridges, further inland, there are regionally flats of almost pure sand. The limestone ridges bear a particular selection of calcicolous sclerophyll (fynbos) species, among which there are many narrow-endemics. West of Cape Agulhas to Stanford these formations consist of a relatively thin layer of whitish sand over solid limestone layers, a condition greatly similar to that in the Saldanha Bay region in the west.

On the western flats the sand covers limestone in the Saldanha Bay region, but clay further inland and southwards, e.g. in the Hopefield region. The coastal regions north of the Great Berg River are dry and covered with sand often mingled with broken shells; regionally the sand is mixed with clay.

Species occurring on marine sand in the southern and western regions (Coastal Macchia sensu ACOCKS 1953 p. 128) are:

Aspalathus globulosa E. MEY. — *A. forbesii* HARV. (sometimes on limestone ridges) — *A. linguiloba* R. DAHLGR. (also on T.M.S. sand) — *A. hispida* THUNB. (certain forms) — *A. alopecurus* BENTH. (at least certain forms; see map in Fig. 7 E) — *A. incurvifolia* WALP. (most forms on limestone, see p. 516) — *A. sericea* BERG. ssp. *sericea* (also on T.M.S. sands) — *A. quinquefolia* L. (most forms; also on T.M.S. sand, especially in NW) — *A. heterophylla* L. FIL. [especially ssp. *lotoides* (THUNB.) R. DAHLGR.] — *A. ternata* (THUNB.) DRUCE and *A. dasyantha* ECKL. & ZEYH. (vicarious; see map in Fig. 7 C) — *A. tylodes* ECKL. & ZEYH. (see map in Fig. 7 D) — *A. arenaria* R. DAHLGR. — *A. spinescens* THUNB. (most forms) — *A. albens* L. (map in Fig. 7 B) — *A. acutiflora*

R. DAHLGR. — *A. retroflexa* L. [mainly ssp. *bicolor* (ECKL. & ZEYH.) R. DAHLGR.] — *A. divaricata* THUNB. ssp. *divaricata* (certain forms) — *A. biflora* E. MEY. ssp. *longicarpa* R. DAHLGR. — *A. angustifolia* (LAM.) R. DAHLGR. (certain forms).

In addition, there are the following species which are more or less obligately restricted to limestone ridges and are thus decidedly calcicolous. They are all southern.

Aspalathus prostrata ECKL. & ZEYH. — *A. salteri* L. BOL. (map in Fig. 7 H) — *A. pallescens* ECKL. & ZEYH. — *A. laricifolia* BERG. ssp. *laricifolia* (very particular forms) — *A. incurvifolia* WALP. (most forms) — *A. sanguinea* THUNB. (map in Fig. 7 G) — *A. candidula* R. DAHLGR. — *A. aciloba* R. DAHLGR. — *A. calcarea* R. DAHLGR. (map in Fig. 7 F) — *A. crassisepala* R. DAHLGR. (most forms) — *A. repens* R. DAHLGR.

More detailed remarks on the species, accounts on species not easily ordered under any of the paragraphs above, and insufficiently known or somewhat controversial species fall outside the frame of the present, rather introductory account. There are indeed, as mentioned above, also variable species occurring on different types of substrate.

It should be obvious from the previous discussion, however, that there is a great need for careful records of the soils on which the collected plants are found. Disjunctions of the kind found in *Aspalathus tylodes* ECKL. & ZEYH. — as well as regional, somewhat puzzling absence of species — may be best explained on the basis of substrate requirements.

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A Critical Survey of European Taxa in Ulvales, II
Ulva, Ulvaria, Monostroma, Kornmannia

By Carl Bliding

Borås, Sweden

ABSTRACT

Of the genus *Ulva* eight species have been described on living material; their reproduction and development were followed in culture during some generations. The delimitation of the species on the basis of anatomy and life history has been checked by cross-breeding experiments, since in *Ulvaceae* only the fertilization between intraspecific gametes gives rise to developable zygotes.

Two new species are described, *Ulva scandinavica* and *Ulva rotundata*, the former from the west coasts of Sweden and Norway, the latter from the Mediterranean Sea and the Atlantic coasts of Tenerife and northernmost Norway. A new combination, *Ulva gigantea*, is established with *Phycoseris gigantea* KÜTZING as basionym.

Monostroma blyttii (ARESCHOUG) WITTROCK, which, together with *obscurum*, *fuscum* and *splendens*, composes subgenus *Ulvaria* of *Monostroma* THURET sensu J. AGARDH — has isomorphic generations of monostromatic plants with rhizoidal cells; the uniseriate germling later becomes tubular to sackshaped and opens at the extreme end to a monostromatic plant. In view of ontogeny and anatomy these taxa of *Monostroma* are included in the genus *Ulvaria* RUPRECHT 1851 under the names *Ulvaria obscura* (KÜTZING) GAYRAL and *Ulvaria obscura* var. *blyttii* (ARESCHOUG) BLIDING.

Monostroma oxyspermum (KÜTZING) DOTY, *M. orbiculatum* THURET and *M. wittrockii* BORNET have small differences between themselves in regard to anatomy and development. They are monostromatic plants with rhizoidal cells, asexual without alternation of generations. Their ontogeny fully agrees with that of *Ulvaria obscura* var. *blyttii*. Consequently these taxa, too, have been removed from *Monostroma* and transferred to *Ulvaria* under the same specific name, *oxysperma*, consisting of two varieties, *oxysperma* and *orbiculata*, the former with forma *wittrockii*.

The closely related genera *Enteromorpha*, *Ulva* and *Ulvaria* constitute the natural family *Ulvaceae*.

The genera *Capsosiphon* and *Percursaria* have been removed from *Ulvaceae*, the former to *Capsosiphonaceae* CHAPMAN and the latter to a new family, *Percursariaceae*.

Monostroma bullosum (ROTH) THURET, *M. grevillei* (THURET) WITTROCK and *M. arcticum* WITTROCK have an anatomy, ontogeny and development, that exclude their belonging to the family *Ulvaceae*. Sexual species (*bullosum* and *grevillei*) have heteromorphic generations; the zygote remains one-celled, growing into a cyst producing zoospores; the zoospore germinates into a prostrate disc, from which the macroscopic plant upheaves. The asexual species (*arcticum*) has no alternation of generations; the neutral, 2-flagellate swarmers develop into prostrate systems, from which new macroscopic plants arise.

The former *Monostroma leptodermum* KJELLMAN agrees much with *Blidingia* regarding anatomy, swarmers and life history and has been proposed as the type species of a new genus, *Kornmannia*. The removal to *Kornmannia* of *Monostroma zostericola* TILDEN and of *zostericola* TILDEN sensu YAMADA and TATEWAKI is discussed. Attention is called to the fact that *Blidingia* and *Kornmannia* differ from *Monostroma* THURET in some important features and may certainly be brought together to a separate family of *Ulvales*. Here these genera are placed as divergent genera of *Monostromataceae* KUNIEDA ex SUNESON.

New family: *Percursariaceae*; new genus: *Kornmannia*; new species: *Ulva scandinavica*, *Ulva rotundata*; new comb.: *Ulva gigantea*, *Ulvaria obscura* var. *blyttii*, *Ulvaria oxysperma* var. *oxysperma*, *Ulvaria oxysperma* var. *oxysperma* forma *wittrockii*, *Ulvaria oxysperma* var. *orbiculata*, *Kornmannia leptoderma*, *Kornmannia zostericola*.

INTRODUCTION AND ACKNOWLEDGEMENTS

The present work has been carried out on material collected partly at the European biological stations visited in 1952—1962 (an account of them is given in BLIDING 1963 p. 5) and partly when visiting the following places:

in 1964, 2/3—23/3 Tenerife, the Canary Islands; 27/4—10/5 Station Biol., Roscoff, France; 21/5—1/6 and 21/9—10/10 Zool. Stat. Kristineberg, Sweden.

in 1965, 10/4—1/5 Rhodes and Symi in the Aegean Sea, Greece; 28/5—5/6 and 10/9—14/9 Zool. Stat. Kristineberg.

in 1966, 3/4—2/5 Lab. Arago, Banyuls s/m, France; 13/7—3/8 Tromsö Museum and Biol. Stat., Tromsö, Norway.

For the field work at the Labor. Arago, Banyuls, and at Tromsö financial aid was received from the Swedish Council of Natural Science.

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I have had the privilege of studying Herb. Agardhiorum in the Botanical Museum, Lund, and other herbarium material has been lent to me by Naturhist. Riksmuseum, Stockholm; Inst. of Systematic Botany, Uppsala; Inst. of Marine Botany, Gothenburg; Rijksherbarium, Leiden; Botanical Museum, Copenhagen; British Museum (Nat. Hist.), London; Botanical Inst., Univ. of Vienna; Botanical Inst., Ac. Sc., Leningrad.

Professor GEORGE F. PAPENFUSS has kindly given me advice and information about some nomenclatural questions (regarding *Entermorpha prolifera*

in Part I and regarding *Ulva fusca* and the typification of *Monostroma* THURET in Part II).

My cordial thanks are due to the Editor of Botaniska Notiser, Dr. ROLF DAHLGREN and to the Curator of the Botanical Museum, Lund, Dr. OVE ALMBORN, for helpful service, and I wish to express my deep gratitude to Mr. STEN LIDÉN, Borås, for translating the English text and to Dr. T. HEDBERG, Borås, for revision of the Latin text.

Systematic Part

The nomenclature in the genera *Monostroma* and *Ulvaria* and the use of the family name *Monostromataceae* are in accordance with the proposed re-lectotypification of the genus *Monostroma* THURET (vide pp. 587 and 600).

FAM. ULVACEAE (continued from Part I = BLIDING 1963)

Genus Ulva Linnaeus 1753, emend. Thuret 1854

Species lectotypica: *Ulva lactuca* L.

In "Note sur la synonomie des *Ulva lactuca* et *latissima*, L." THURET has excluded from the genus *Ulva* both C. AGARDH's *Ulva lactuca* and the other monostromatic species that make up *Ulva* KÜTZING, and included KÜTZING's *Phycoseris* in *Ulva*. In doing so THURET brought together within the genus *Ulva* species with a parenchymatic, frond-like thallus, built up by two adjacent layers of cells (THURET 1954 a p. 28).

It is an important feature of the genus that the germling in *Ulva* as well as in *Enteromorpha* and *Ulvaria* begins as a single row of cells but soon becomes hollow (BLIDING 1963 p. 7). All the species of *Ulva* described here and also *Ulva conglobata* (YOSHIDA 1965) pass through such a tubular *Enteromorpha*-stage. As soon as the plant is a few mm high the tubular thallus becomes compressed and the walls meet and grow together. Now the *Ulva* plant has reached its final distromatic stage without cavities.

The young plants are at first fastened to the substrate by primary and secondary attaching cells (Fig. 12 E, Fig. 26 D—H) later by tubular prolongations, similar to hyphae of fungi, from cells in the lower part of thallus, the rhizoidal cells, formed in the plant when it is still hollow (Fig. 12 G) and in *Ulva* as a rule even more marked than in *Enteromorpha*. Rhizoidal cells in *Ulva* are multinuclear whereas the other cells have one nucleus (DELF 1912).

Fig. 1. *Ulva lactuca*, Kristineberg. ×0.47.

Most species of *Ulva* are diplohaplonts with isomorphic generations: one gametophyte of male or female plants, one sporophyte of zoospore plants. This development was discovered by Föyn (1929). Only 3 European species without alternation of generations are known up to the present. Their motile reproductive bodies are neutral swarmers, zoosporoids, of the size between gametes and zoospores. In two of these species (*U. scandinavica* and *neapolitana*) the swarmers are 2-flagellate, in the third (*U. olivascens*) they are 2- or 4-flagellate, but of the last

Fig. 2. *Ulva lactuca*. Kristineberg. ×0.47.

mentioned species also gametes and zoospores are reported from one African locality.

The life-cycle without alternation of generations is shared by two non-European species, namely *Ulva linearis* DANGEARD from Morocco (2-flagellate neutral swarmers, DANGEARD 1957) and *U. conglobata* KJELLMAN from Japan (4-flagellate swarmers, YOSHIDA 1965).

All the sexual species described here are anisogamous; in one species (*U. rigida*) the anisogamy is less pronounced, but applies at least to plants within the same population.

Both male and female gametes can easily germinate and develop into a gametophyte plant of its own sex. That is the reason why gamete plants are more common than zoospore plants, especially in forms in strongly exposed localities or in flowing waters where the gametes, at once or soon after swarming out, become negatively phototactic.

The *Ulva* species usually show great intraspecific variation. Specifically distinctive characteristics are checked by cross-breeding studies with special regard to typical or delayed copulation and by culturing the zygotes (BLIDING Part I 1963 pp. 10—12). Essential morphological features are the number of pyrenoids, the arrangement and size of the cells, the thickness of the thallus in different parts of the plant, especially at the margin of the upper part of the lamina and at the base immediately above the rhizoidal zone. Valuable information is also given by the young macroscopic germlings, which in many species have a very characteristic exterior form which is not to be found in the fully developed plant.

1. Ulva lactuca LINNAEUS

Ulva lactuca LINNAEUS 1753 p. 1163 (non sensu C. AGARDH 1817 p. 41, nec sensu KÜTZING 1843 p. 296); THURET 1854 a p. 23 pro parte; KYLIN 1949 p. 17; SUNDENE 1953 p. 140; FÖYN 1955 p. 267. — *Ulva lactuca* [LINNAEUS] THURET; vide PAPENFUSS 1960 p. 314.
Ulva stipitata ARESCHOUG 1850 p. 185.
Ulva crassa KJELLMAN 1877 a p. 44.

Ulva lactuca has a mainly northerly distribution and is the preponderant *Ulva* species from southern Scandinavia up to the Arctic Region. Earlier in this century it was believed to be the only *Ulva* species in this area (KYLIN 1949).

The alga grows in salt and brackish water, mostly in the littoral zone, on stones, rocks or larger algae, but also in the sublittoral zone, at least down to the depth of 15 m, on shells and stones. Fertile specimens of sublittoral forms are as a rule only 10—12 cm high, whereas littoral specimens especially at localities with flowing water, may attain the height of 1 m.

The form of the erect frond varies very much: from *Enteromorpha linza*-like with attenuating base and a crisp and flounce-shaped margin (Fig. 3 A) to a deeply laciniated palmate type (Fig. 1) resembling LIN-

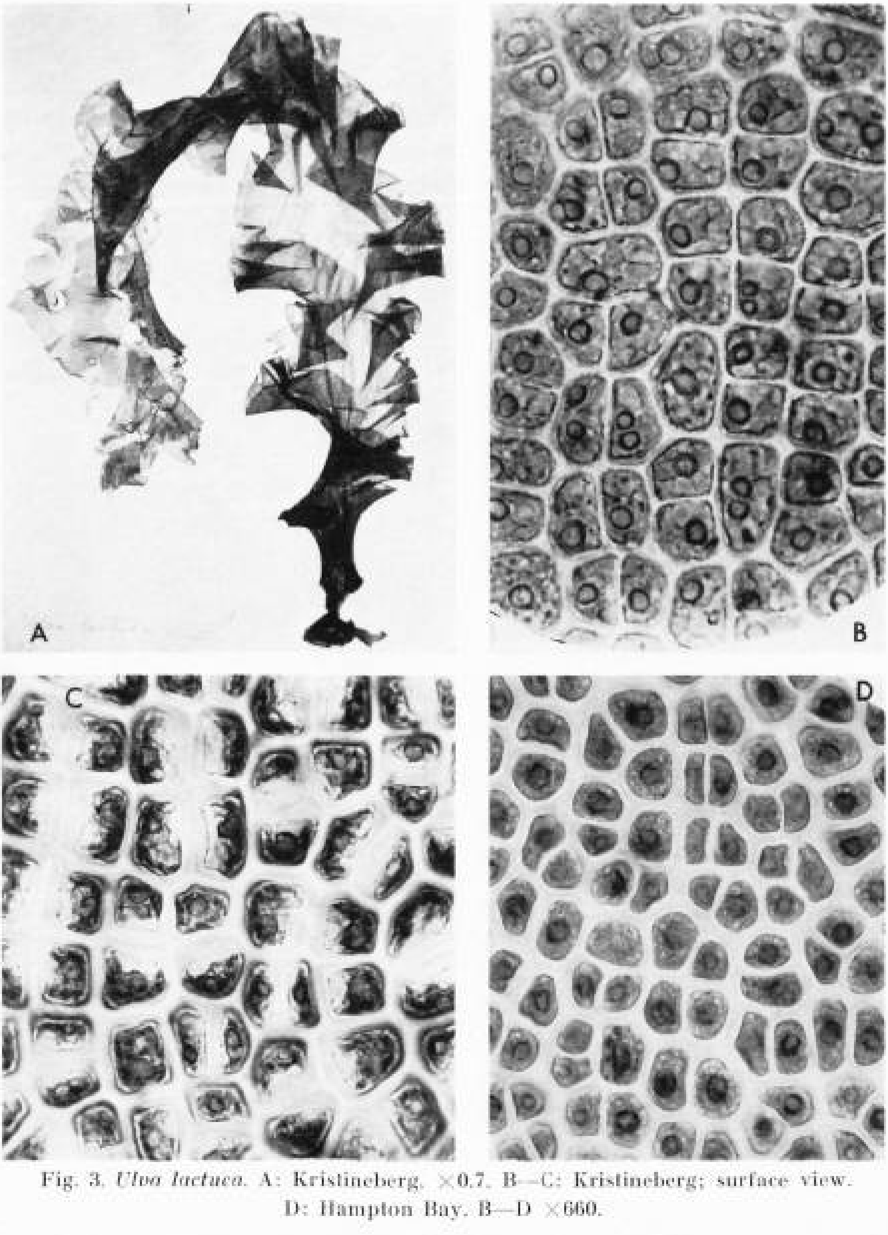


Fig. 3. *Ulva lactuca*. A: Kristineberg, ×0.7. B—C: Kristineberg; surface view. D: Hampton Bay. B—D ×660.

NAEUS' original specimen (PAPENFUSS 1960, pl. 1, fig. 10, right-hand side). As a rule the disc is slightly perforated and specimens with numerous big perforations (Fig. 2) are very rare.

ANATOMY. The margin of the disc always lacks the microscopic tooth-like protuberances that are common in *Ulva rigida*. The cells are more or less well-arranged in slightly curved rows. They usually have a well developed chromatophore with one pyrenoid [only 2—12 % of the cells have 2 (—3) pyrenoids]. The rhizoidal cells form an exception, as they have several pyrenoids. In surface view the cells range from rectangular to quadrangular or rounded, rarely slightly polygonal, fully grown cells averaging the size of 18×13.5 μ (Figs. 3 B—D, 4 A—B).

Thallus is thinnest, about 48 μ (Fig. 4 C), at the margin of the upper part of the disc in spring specimens (April and May on the Swedish West Coast). Here cell lumen has a maximum height of about 16 μ and a maximum breadth of about 11 μ. More centrally in the upper part of the disc the thallus is about 60 μ thick and cell lumen 26 μ high and 18 μ broad (Fig. 4 D).

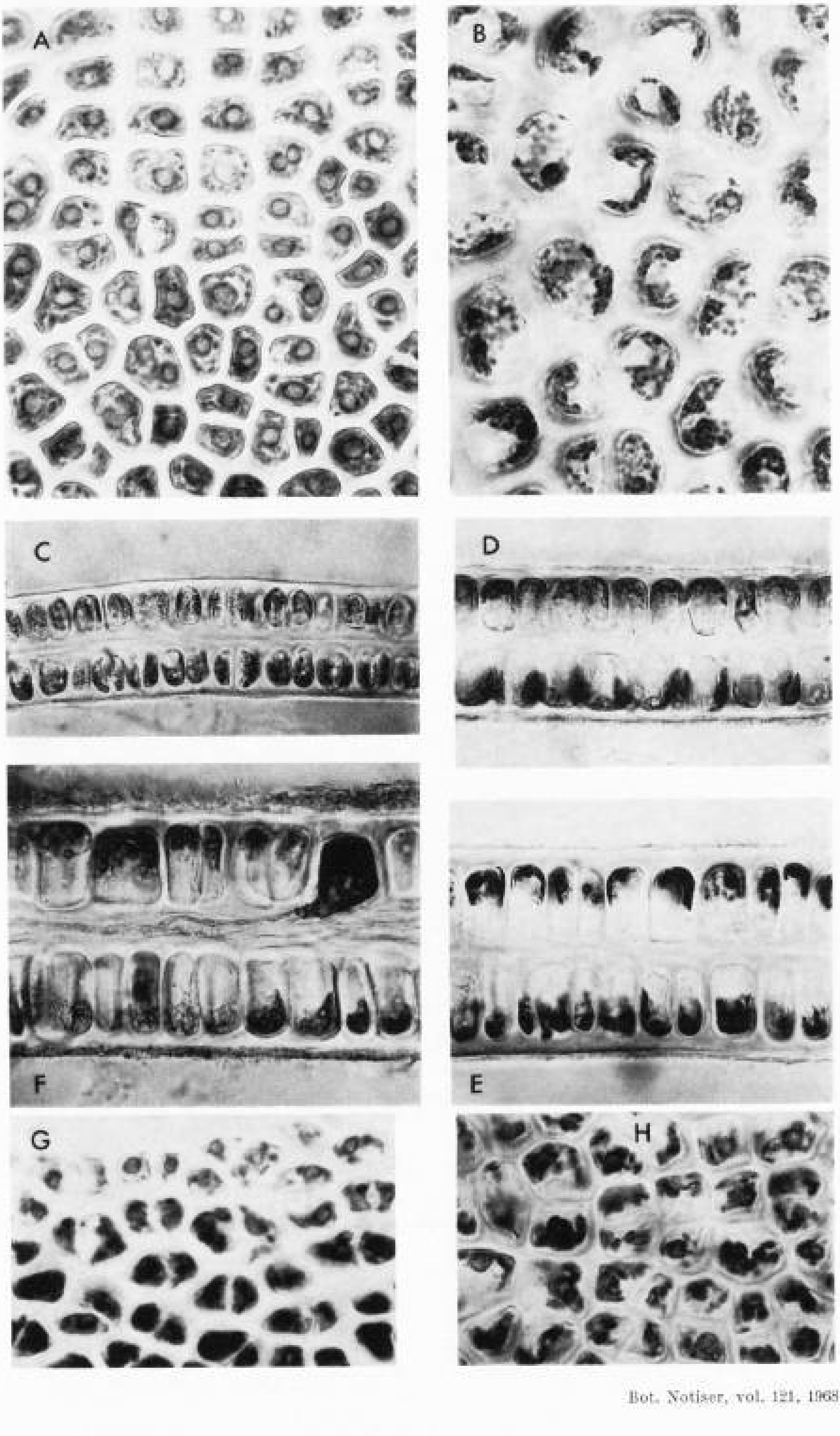
The cross-section of the lower part of the plant (Fig. 4 E) is 80—90 μ with height and breadth of lumen amounting to 27—31 μ and 19—21 μ respectively. In the rhizoidal zone (Fig. 4 F) thallus is about 100 μ thick. In the whole frond above the rhizoidal zone the proportion between the height and the breadth of the cells in my material was varying between 1.4 and 1.5.

REPRODUCTION AND DEVELOPMENT. *Ulva lactuca* has the alternation of generations with three kinds of isomorph plants that is normal in this genus. The male plant is easily recognizable by the reddish yellow colour of the fertile marginal region. In the female plant the corresponding part is greenish yellow, in the zoospore plant dark green. The light yellow colour of the male gametes is due to the fact that, contrary to the female gametes, they do not contain chlorophyll (Levring 1955 p. 40).

The marked anisogamy in *Ulva lactuca* is seen most clearly on comparison between the breadths of the two kinds of gametes. The male gametes just swarmed out are on an average 6.8×2.1 μ, and the female gametes 7.6×3.6 μ (Fig. 5 A—B).

Both ♂- and ♀-gametes also germinate without fertilization and then normally bring forth male and female plants respectively. The zoospores (Fig. 5 C) are 9.7—12.1×5.9—6.8 μ and germinate directly into ♂- and ♀-plants.

Fig. 4. *Ulva lactuca*. A—B: Surface view; Tromsö. C: cross-section, upper part, margin. D: centrally, upper part. E: near the base. F: rhizoidal zone. G: the type specimen of *Ulva stipitata* Areschoug. H: the type specimen of *Ulva crassa* Kjellman. A—B, G—H ×660, C—F ×330.


A
B
C
D
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H

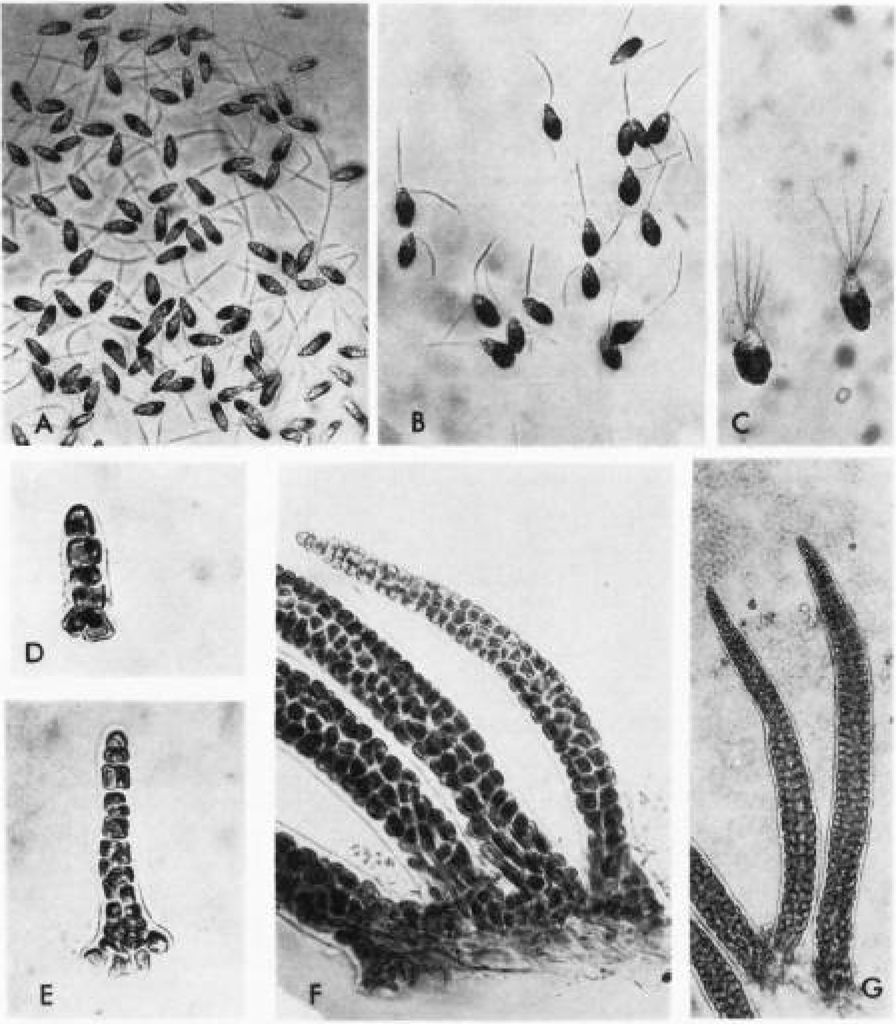
The development of the germling is shown in Fig. 5 D—J. The one-seriate germling becomes tubular through the longitudinal divisions of the cells and their orientation round a cavity which remains until the plant is about 3—4 mm high (Fig. 5 H—I), when the tube begins to be compressed, its walls grow together and the distromatic disc is formed. The young macroscopic plant is for a long time long and narrow (Fig. 5 F—G and Föyn 1955 Fig. 2, upper row), which makes it distinctly different from young germlings of *Ulva rigida* and, above all, from *U. rotundata* (Fig. 22).

LIVING MATERIAL from: Norway, Troms, Tromsö, Juledagsskär and oth. loc. (July and Aug. 1966); Hordaland, Kviturdvikspollen and Nordåsvatn, Strömme bro and oth. loc. (July 1960, Aug. and Oct. 1962). Sweden, Bohuslän, Kristineberg, Strömmarna and oth. loc.; Halland, Varberg. England, Kent, Hampton Bay, Herne Bay (sent by Dr. Price, British Museum).

TAXONOMY. In his important work from 1960 Papenfuss has given an account of the discovery of Linnaeus' type of *Ulva lactuca* and the scientific utilization of the material. Text figure 1 (op. cit. p. 306) shows a cross-section, about 95 μ, of the upper part of the rhizoidal region, and fig. 2 another cross-section, of the area immediately above the rhizoidal zone, where thallus is about 80 μ. In the last-mentioned cross-section the height of cell lumen is about 28 μ, its breadth about 20 μ, the proportion between height and breadth being about 1.4. The accordance of these measurements and the corresponding measurements of living material (see above) is practically complete. It is also probable that Linnaeus' specimen was collected on the Swedish West Coast, in Bohuslän, as Linnaeus (Flora suecica, Ed. 2. 1755 p. 433) gave the locality of *lactuca* in the following words "in Oceano Bahusiense frequens".

Both *Ulva stipitata* Areschoug (1850 p. 185), according to No. 224 in Areschoug Alg. Exs., and *Ulva crassa* Kjellman (1877 p. 44), according to specimen in Naturh. Riksmuseet, Stockholm, conform well to *lactuca* (Fig. 4 G—H). The former taxon is mentioned by Thuret 1854 a p. 23 as a synonym (with a question-mark) for *Ulva lactuca* Linnaeus.

Fig. 5. *Ulva lactuca*. A: ♂-gametes. B: ♀-gametes. C: zoospores. D—E: germlings, the older 2 weeks. F: development of rhizoidal cells. G: plants, 1 month old. H—I section through germlings, ca. 3 mm high. J: young plants ×0.6. A—C ×660. D, H ×330. E, F ×260, G, I ×130.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2. **Ulva rigida** C. Agardh

Ulva rigida C. Agardh 1822 p. 410; Thuret 1854 a p. 24; J. Agardh 1883 p. 168; Feldmann 1937 p. 57 fig. 12 B; Dangeard 1958 a p. 22. — *Ulva rigida* [C. Agardh] Thuret, Papenfuss 1960 p. 314. — *Ulva lactuca* L. var. *rigida* (Ag.) Le Jolis 1863 p. 38; Hamel 1931 p. 45; Newton 1931 p. 77.

Ulva plicata Müller in Flora Danica Tab. 829 sensu Roth 1797 p. 208.

Phycoseris lacinulata Kützing 1849 p. 476. — *Ulva lactuca* L. forma *lacinulata* (Kützing) Hauck 1885 p. 437; Feldmann 1937 p. 55 fig. 10.

Phycoseris gigantea Kützing β *perforata* Kützing 1849 p. 476.

Ulva thuretii Föyn 1955 p. 267.

Ulva rigida is the most common *Ulva* species on the Mediterranean coast as well as on the Atlantic coast from the Canary Islands to the Channel. It is less common further to the north but is still to be found on the west coast of Sweden, where it was first observed in May 1964, in Sälviken near Kristineberg Biological Station, and later in a few places not far from there. In harbours, shallow bays and sublittorally the species is often rankly developed, 1 m high or more, but in extremely exposed localities, for instance in many places on the west coast of Tenerife, it is often only a few cm high. On the Swedish side of the Baltic the species has not yet been found, but it is met with in brackish water in at least some of the pools (étangs) of southern France, where it mostly lies loose in richly perforated specimens (Fig. 6 C), propagating vegetatively.

ANATOMY. *Ulva rigida* already differs from the majority of other *Ulva* species by the fact that the margin of the disc has toothlike, generally microscopic protuberances (Fig. 6 D—E). The cells are fairly well arranged in longitudinal, and sometimes also transverse, rows in the greater part of the thallus, but mostly only slightly ordered or without any order near the base (Fig. 7 D, F). In surface view the cells are rectangular or slightly polygonally rounded, 15—22 × 11—17 μ, with the average measures 18 × 14 μ for the fully grown cell. In the young plant the cells are bigger, about 29 × 16 μ (Fig. 7 B).

Cross-sections (Fig. 8 A—F) show that the thallus in the upper part of the margin is only 38—42 μ thick, in a more central part of the disc 48—76 μ, but at the base much thickened, especially in sublittoral forms (Fig. 8 E—F), with cross-sections up to 200 μ.

It is furthermore particularly characteristic of the species that the marginal cells in the upper part of the plant are ball-shaped (Fig. 8 A—B), of a height of about 21 μ, whereas the cells in the lower part are very high, up to 70 μ, and tapering at the top (Fig. 8 D—F).

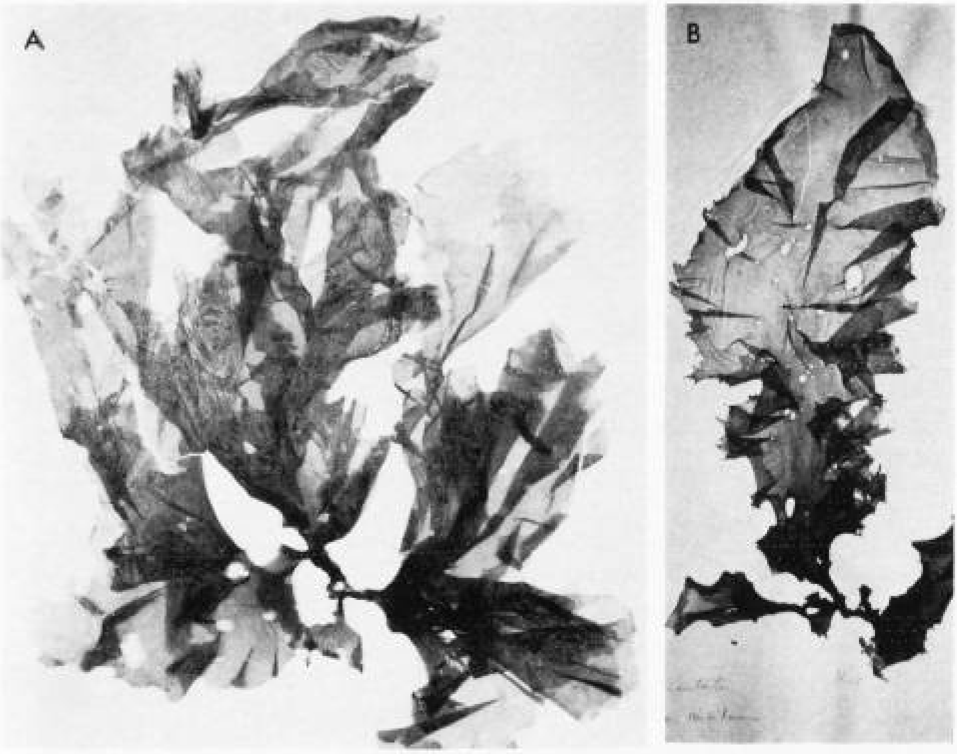


Fig. 6. *Ulva rigida*. A: Roscoff ×0.5. B: Banyuls ×0.46. C: Etang de Salces ×0.67. D: Brest ×330. E: Banyuls ×260.

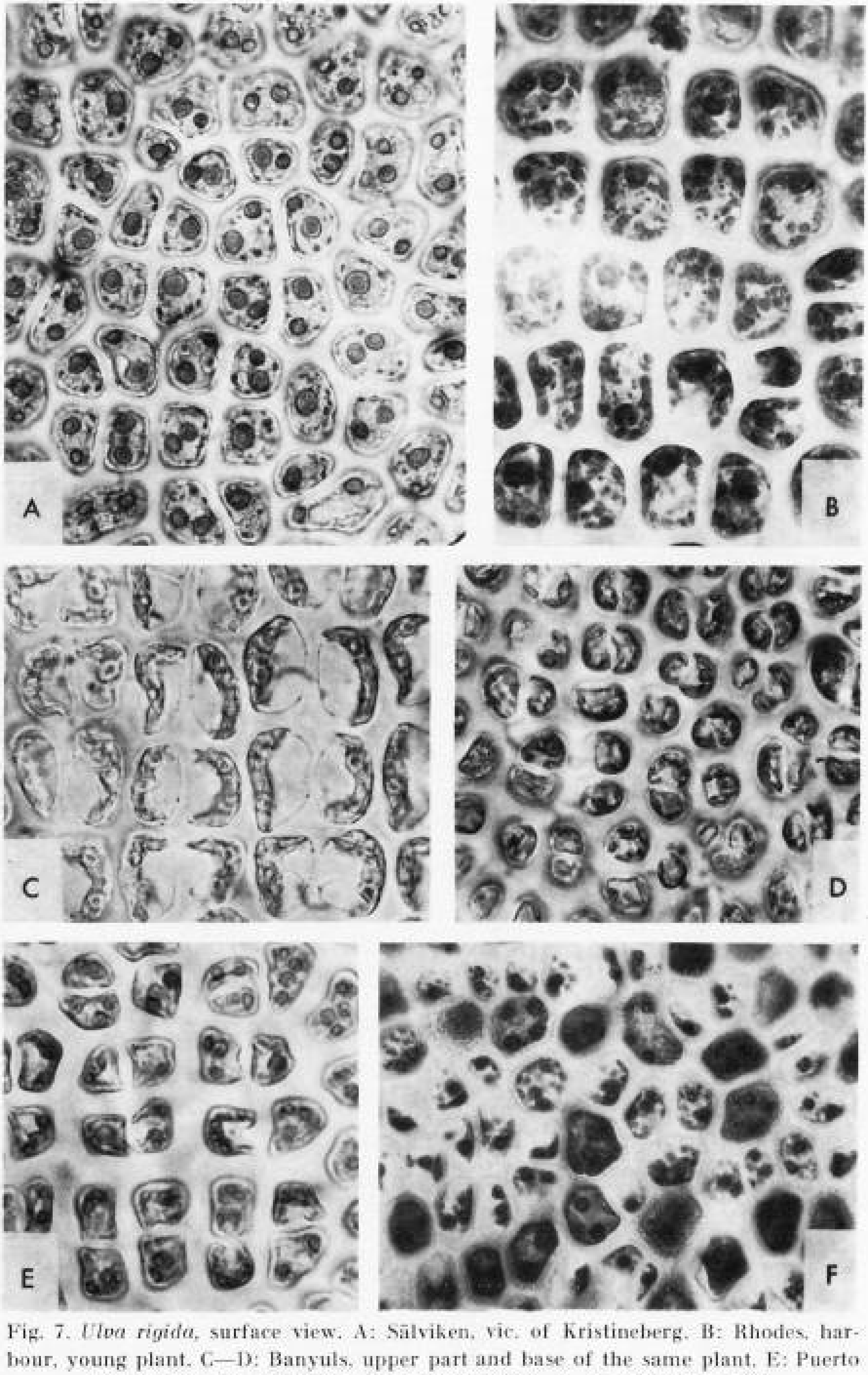


Fig. 7. *Ulva rigida*, surface view. A: Sälviken, vic. of Kristineberg. B: Rhodes, harbour, young plant. C—D: Banyuls, upper part and base of the same plant. E: Puerto de la Cruz. F: rhizoidal zone, Concarneau. A—E ×660, F ×330.

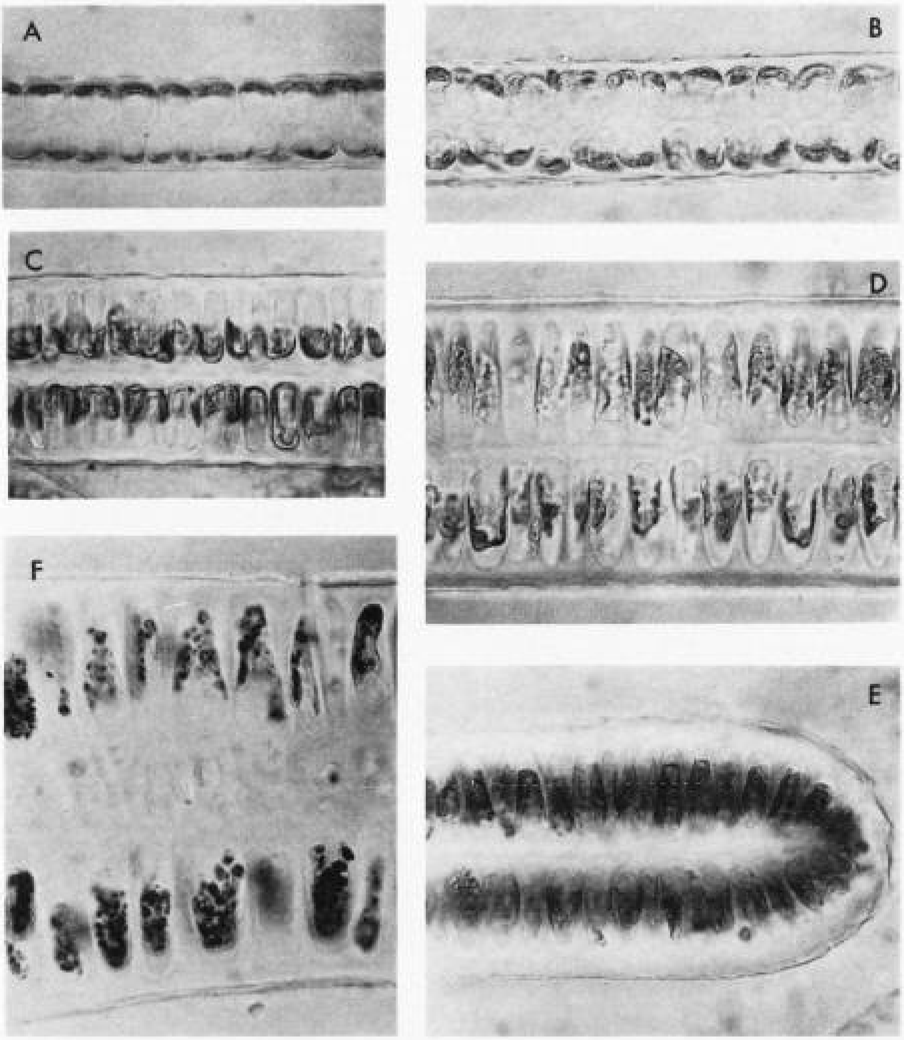


Fig. 8. *Ulva rigida*. A: Palavas; upper part, margin. B: Palavas; upper part. C: Roscoff; middle part. D—E: Roscoff; lower part. F: Roscoff; rhizoidal zone. A—F ×330.

Consequently, the cells at the base, seen from the surface, seem smaller than the cells in the other parts of the plant (cf. Fig. 7 D and 7 C from the same specimen).

The parietal chromatophore has the chlorophyll chiefly concentrated to the outer walls of the cells but sometimes to the side walls or even to the inner walls (Fig. 8 C).

The full-grown cell usually has 1—3 pyrenoids; cells with 2 pyrenoids being much more common than cells with 1 pyrenoid. Especially in southern forms it is not unusual for cells to have 2—8 pyrenoids (Fig. 7 E).

REPRODUCTION AND DEVELOPMENT. *Ulva rigida* has the alternation — common in *Ulva* species — of a haploid generation of anisogametic ♂- and ♀-plants and a diploid generation of zoospore plants. The female gametes are 6.2—7.4×3.1—4.5 μ, averaging 6.8×3.8 μ, the male gametes 5.3—6.3×2.7—3.1 μ, averaging 5.9×2.9 μ (Fig. 9 A—B). Zoospores (Fig. 9 C) are 9.1—10.6×4.6—6.0 μ, averaging 10.2×5.2 μ. Gametes of both kinds, zygotes and zoospores, bring forth a germling which is at first threadlike but later tubular (Fig. 9 F, cross-section of a plant 2—3 mm high). The cylindrical germinating plant soon becomes compressed and the walls grow together. At the base rhizoidal cells are formed which attach the alga to the substratum.

In the great majority of the forms of *rigida* the macroscopic germlings are symmetrical, lanceolate, at first narrowing upwards (Fig. 9 H) and quite easily distinguished from other European *Ulva* species, e.g. *rotundata* and *gigantea*. There are, however, forms of *rigida* which at an early stage become unsymmetrical (Fig. 9 G), with irregularly arranged protuberances from the margin of the disc. During their continued growth these protuberances form the deeply divided lobes in the final disc. A *rigida*-type with particularly characteristic germlings is KÜTZING's *lacinulata*, the disc margin of which is well provided with teeth, simple and branched (Fig. 9 I). These three forms of *rigida* with germlings of varying appearance, after cross-breeding, can bring forth developable zygotes.

LIVING MATERIAL from: Sweden, Bohuslän, Kristineberg, Sälviken and Strömmarna. England, Devonshire, Plymouth. France, Brittany, Roscoff, Brest, Concarneau; Roussillon, Banyuls, Étang de Salces; Languedoc, Palavas; Provence, Villefranche. Italy, Naples, Positano, Ischia. Yugoslavia, Rovinj, Split. Greece, Rhodes, Lindos; Symi. The Canary Islands, Tenerife, Puerto de la Cruz S:t Andrés, Candelaria.

TAXONOMY. It is to expected that this *Ulva* species which is the most common in great parts of Europe must have been named earlier than by C. AGARDH (1822). As a matter of fact ROTH's *Ulva plicata* in Catalecta I p. 208 is, according to a specimen in WULFEN's herbarium,

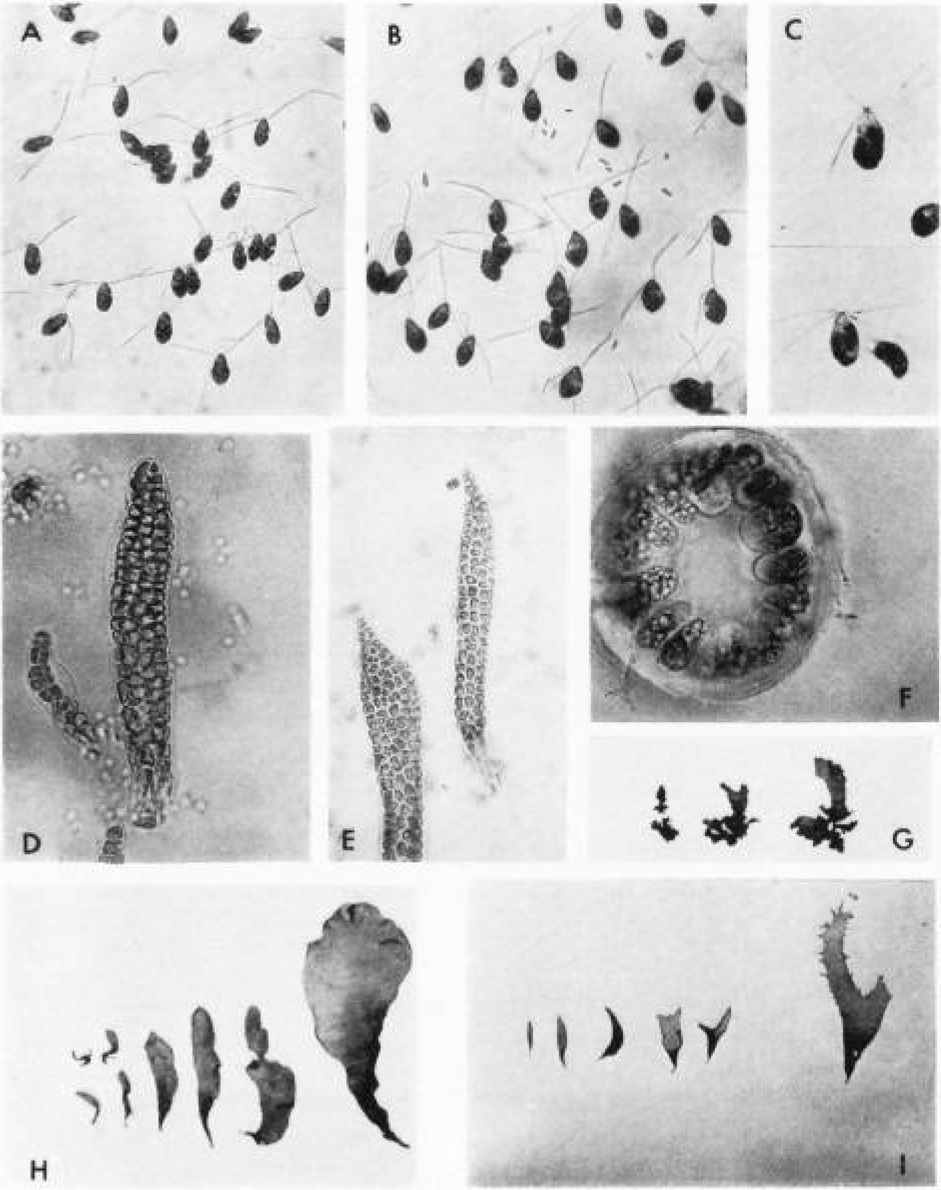


Fig. 9. *Ulva rigida.* A—B: Roscoff, ♂- and ♀-gametes from the same population. C: Roscoff, zoospores. D: germlings. E: Candelaria, germlings. F: Candelaria, section, plant 2—3 mm high. G: young unsymmetrical plants, Roscoff ×0.7. H: common type of young plants ×0.7. I: young plants, type of "*lacinulata*", Banyuls ×0.7. A—C ×660, D ×260, E ×130, F ×330.

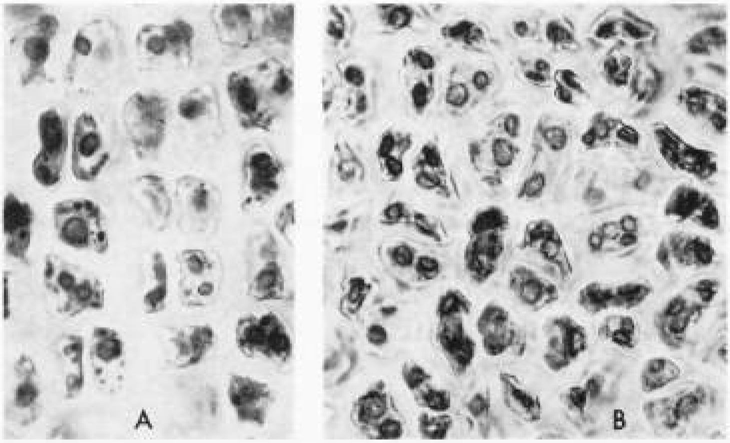
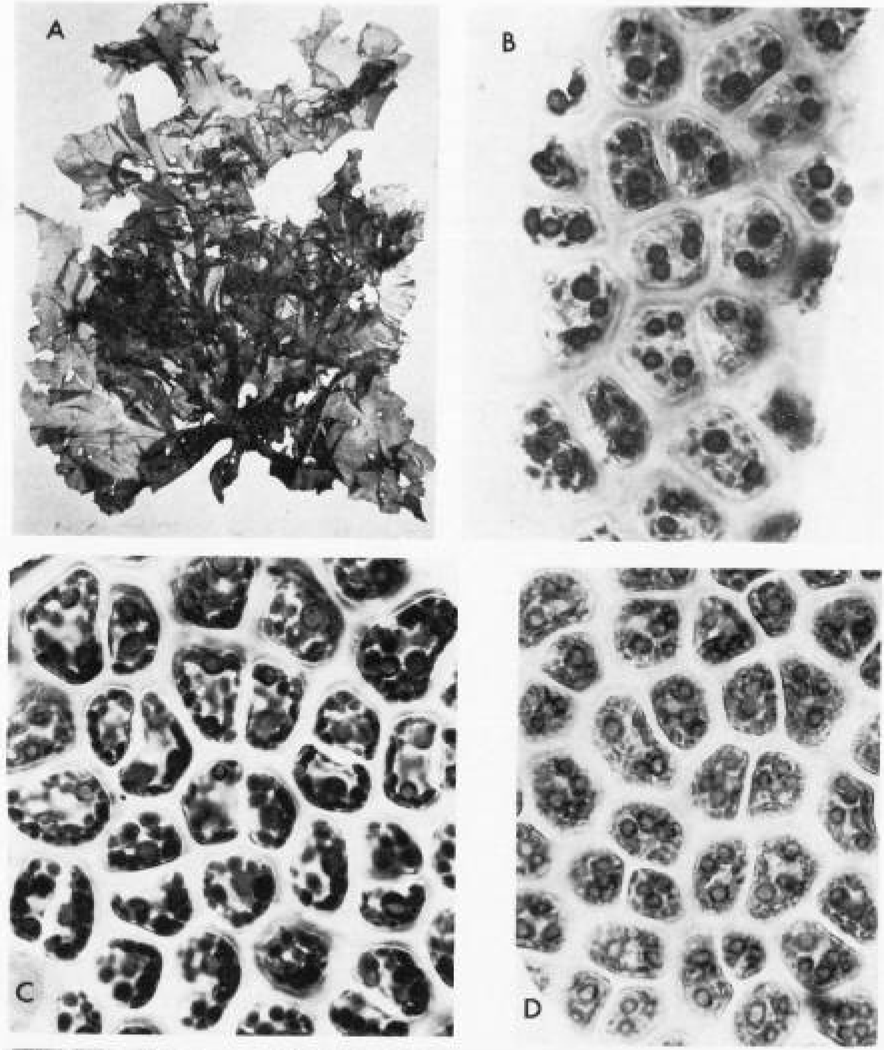


Fig. 10. *Ulva rigida.* A: *Ulva plicata* sensu ROTH in WULFEN's herb. No. 6. Wien. B: *Phycoseris gigantea* β *perforata* KÜTZING, type specimen. A, B ×660.

Bot. Inst., Vienna, labelled "*Ulva plicata* Rothii, a Rothio", an unmistakable *rigida* (Fig. 10 A). However, C. AGARDH (1822 p. 411) interprets as different species *Ulva plicata* MÜLLER in Flora Danica Tab. 829 and *Ulva plicata* in Catalecta I (by ROTH considered synonymous species). Since the type specimen of the first-mentioned, older name has not been preserved, it can not be settled whether ROTH's name of the species is applicable.

In Tab. phyc. VI, 21 a KÜTZING has a good illustration of the habitus of *Ulva rigida* under the name of *Phycoseris lacinulata* with a type specimen in Herb. Lugd. Bat. No. 938.91. .537. This form of *rigida* is common in the Mediterranean in sheltered localities. KÜTZING's *Phycoseris gigantea* β *perforata* 1849 p. 476, Herb. Lugd. 938.91. .491. is *Ulva rigida* (Fig. 10 B). Although J. AGARDH (1883 p. 168) pointed out one of the most important characteristics of *Ulva rigida*, the high cells in the lower part of the thallus, the species was later classified as a form or variety of *Ulva lactuca* (HAUCK 1885, COLLINS 1909, HAMEL 1931, NEWTON 1931) but was again given its status as a species by SETCHELL and GARDNER 1920 p. 269, FELDMANN 1937, DANGEARD 1958 a p. 22.

Fig. 11. *Ulva scandinavica.* A: Kristineberg, type specimen ×0.3. B—C: Kristineberg, upper and lower part of plant. D: Espegrend, lower part. E: Strömme, young plant, base. F: Kristineberg; margin, upper part. B—F ×660.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The type specimen of *Ulva thuretii* FÖYN is not preserved (Prof. FÖYN in letter) but the pl. 17 fig. 2, lower row, and fig. 4 (FÖYN 1955) prove the species to be *Ulva rigida*.

As lectotype of *rigida* PAPENFUSS (1960 p. 305) chose a specimen, No. 14294, in Herb. Agardhiorum, Bot. Museum, Lund.

3. Ulva scandinavica BLIDING spec. nov.

Ulva adulta 2—5 dm alta, 1.5—3 dm lata; cellulae majores, multiangulatae, fere omnino sine ordine distincto instructae, circiter 24×17 μ. Margo laminae transverse sectus in superiore parte circ. 50 μ, altitudo luminis cellulae minor quam latitudo; cellulae quae ad basin sunt non productae. Pyrenoides (1—2—) 3—6. — Generationes alternantes desunt; corpuscula propagationis neutrius generis, 2-flagellata, circ. 10×5 μ. Plantae germinantes stipite minore instructae.

Holotypus in Bot. Mus. Univ. Lund.

Type locality: Sweden, West Coast, Kristineberg; Oct. 1959.

This species seems to have a mainly northerly distribution and to prefer a salinity of 20—30 ⁰/₀₀. The material was collected on the Swedish West Coast, the Biological Station at Kristineberg (the first time in Oct. 1959) and in southwestern Norway, near the Marine Biological Station at Espegrend. The alga grows littorally on stones or is an epiphyte on algae (e.g. *Ascophyllum*). Fertile plants were 2—5 dm high and 1.5—3 dm broad, the frond often laciniated from the base upwards with slight indentations.

ANATOMY. The disc often has sparse microscopic, toothlike protuberances (Fig. 11 F), always unramified and smaller than in *U. rigida*. Cells are mainly unordered, but it is characteristic of the species that areas with unarranged cells alternate with areas where a small number of cells are arranged in rows (Fig. 11 B—D). In surface view the adult cells are polygonal to rounded, fairly big, 21—27×15—19 μ, averaging 24×17 μ. At the base of young plants the maximum dimension is often more than 30 μ (Fig. 11 E).

At the margin of the upper part the disc has a thickness of 50 μ and there the height of lumen is less than the breadth of the cell (Fig. 12 A). At the centre of the plant the thickness of thallus is about 75 μ and at

Fig. 12. *Ulva scandinavica*. A: section of margin, upper part. B: middle part. C: rhizoidal zone. D: zoosporoids. E: germlings with primary attaching cells. F: section of plant 5 mm high. G: development of rhizoidal cells, part of a section, plant 7 mm high. H: young plants ×0.7. A—C ×330, D ×660, E, G ×260, F ×130.

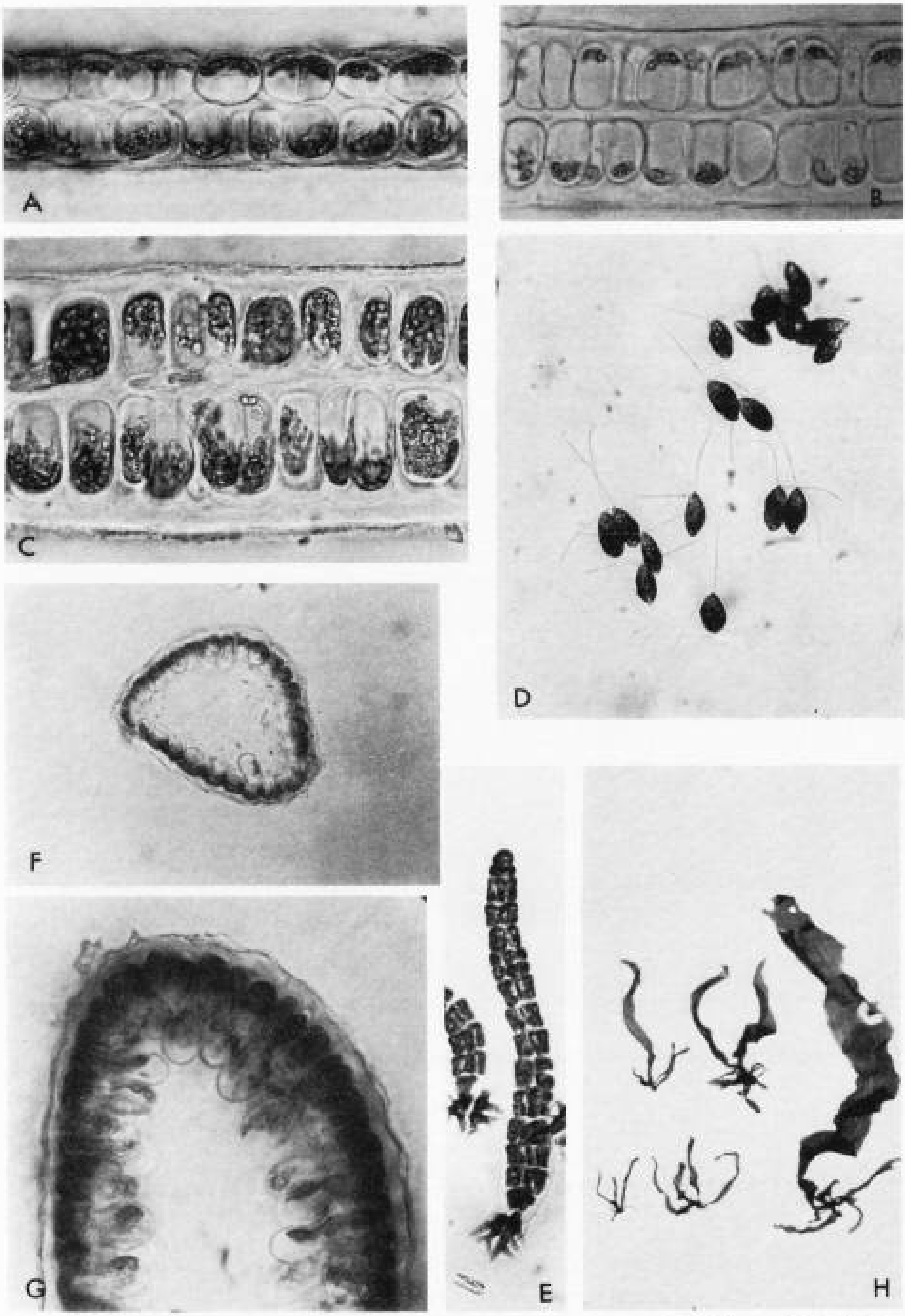
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Fig. 13. *Ulva gigantea*. ×0.5.

the upper border of the rhizoidal zone (Fig. 12 C) about 100 μ. The height of lumen is about 21 μ in the upper part of the disc and about 40 μ at the base, where cells are not tapering as in *U. rigida*.

REPRODUCTION. *U. scandinavica* has no alternation of generations and has only one kind of swarmers, 2-flagellate zoosporoids, whose

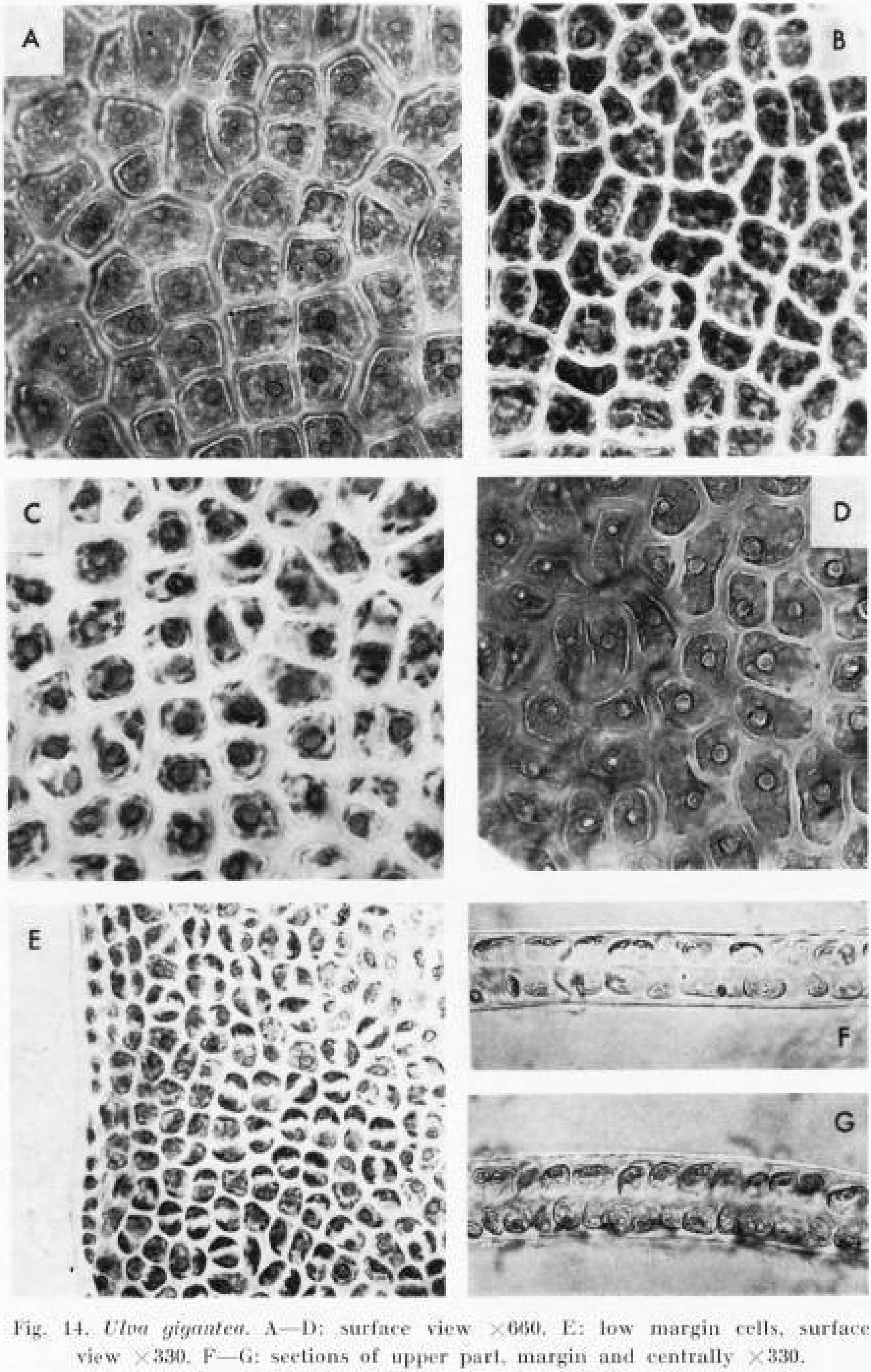

Fig. 14. *Ulva gigantea.* A—D: surface view ×660. E: low margin cells, surface view ×330. F—G: sections of upper part, margin and centrally ×330.

dimensions average 10.0×5.0 μ. At the swarming-out of the same plant some swarmers have negative, others positive phototaxis. Later the latter also become negatively phototactic. When the zoosporoids and the two kinds of gametes of *Ulva lactuca* and *rigida* were brought together, it was found out that the swarmers totally lacked sexual tendency. They germinate at once into plants which remain for a long time at the *Enteromorpha*-stage (in that respect they are only surpassed by *U. curvata*). Fig. 12 F—G shows cross-sections of plants, 5 mm and 7 mm high, respectively. The young macroscopic plants (Fig. 12 H) habitually resemble specimens of *Ulva lactuca* of the same age. They long retain a top cell, and their stipes are not very marked. Plants about 5 cm high are only 0.8 cm broad and are still tapering towards the tip.

LIVING MATERIAL from: Sweden, Bohuslän, Kristineberg and Stockevik (Oct. 1959). Norway, Hordaland, Kviturdvikspollen and Nordåsvatnet, Strömme bro (Oct. 1962).

4. **Ulva gigantea** (KÜTZING) BLIDING **comb. nov.**

Phycoseris gigantea KÜTZING 1843 p. 298, 1856 p. 9, Tab. 22.
"*Ulva lactuca* LINNAEUS" sensu THURET 1854 a p. 23.
"*Ulva latissima* LIN.?" sensu J. AGARDH 1883 p. 164.
Type locality: France, Normandy, Granville.

The material of this species was collected near the Biological Station at Roscoff (April and May 1959 and May 1964). It grew in the *Himanthalia*-region on stones and as epiphyte on large algae (e.g. *Rhodymenia*) together with *Ulva rigida, Monostroma grevillei* and others.

The fertile alga has a height of 2—4 dm with a breadth of 1.5—3 dm. The remarkably thin disc has, in its upper part, slight, in its lower part, deeper indentations and the perforations are few and inconspicuous. The margin of the disc totally lacks microscopic toothlike protuberances.

ANATOMY. The cells are as a rule distinctly ordered, especially near the margin of the disc. In the more central part of the disc areas of cells in rows alternate with regions with unordered cells. In surface view (Fig. 14 A—D) the cells are medium-sized, quadrangular with

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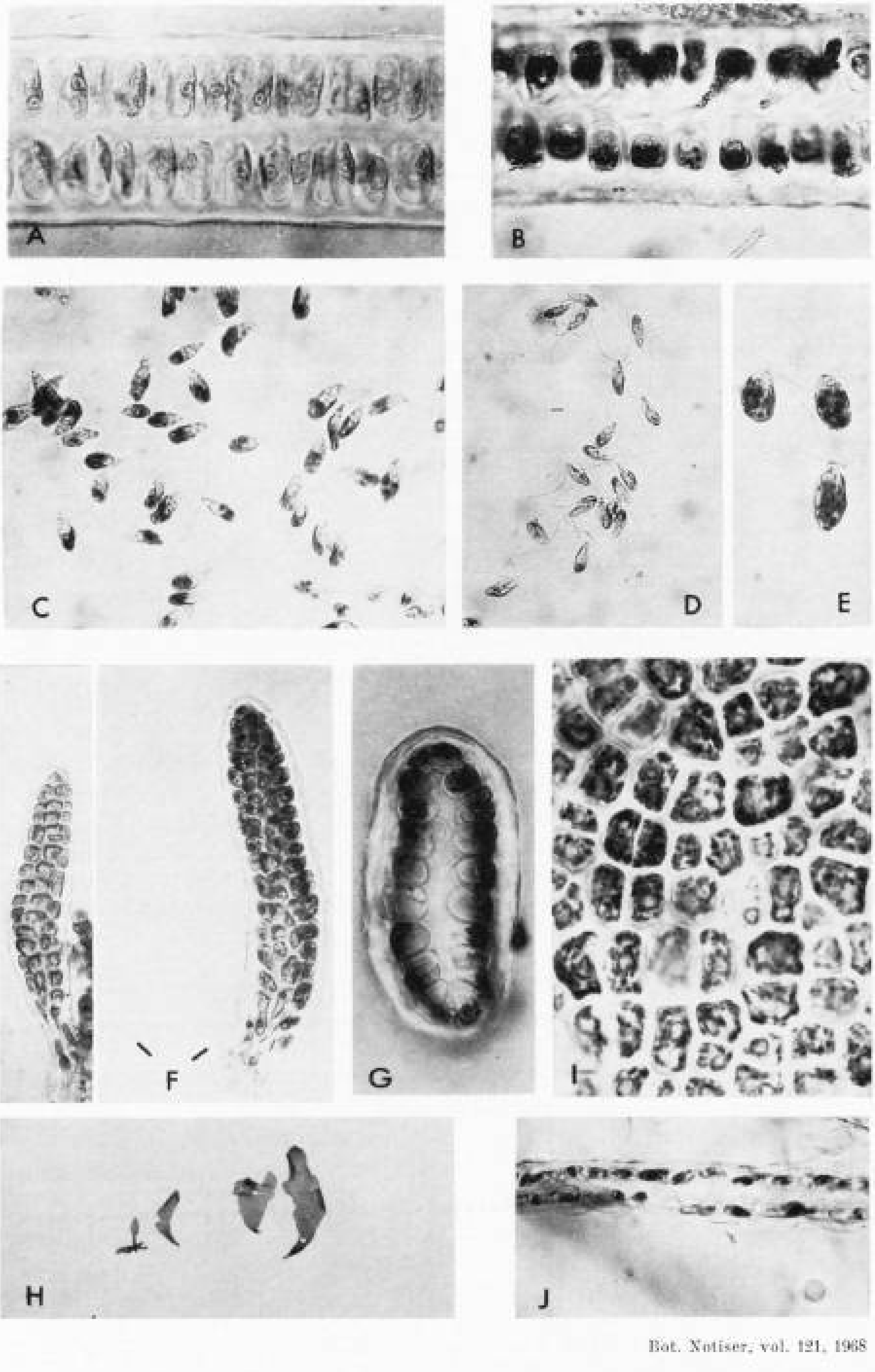
Fig. 15. *Ulva gigantea*. A—B: section of lower part and of rhizoidal zone, ×330. C—E: female and male gametes, zoospores, ×660. F: germlings ×260. G: section, plant 4 mm high, ×260. H: young plants ×0.7. I—J: *Phycoseris gigantea* KÜTZING, type specimen. I ×660, J ×330.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rounded corners about 15×15 μ, rectangular about 19×12 μ, or round with a diameter of about 14 μ. A row of such symmetrical cells is often broken by a bigger, irregular polygonal cell about 22×14 μ (Fig. 14 A). The most marked characteristic of the species is the fact that, almost throughout its extent, the disc is very thin (Fig. 14 F—G). At the margin of the upper part its cross-section is only 28 μ, centrally about 35 μ, but at the base and in the perennial rhizoidal zone with its strong thickened outer walls it comes up to about 80 μ in some specimens (Fig. 15 A—B). The height of the cell lumen is in the upper part of the plant about 12 μ and lowest down, near the base, 22—30 μ. In the upper part the chromatophore only takes up a small part of the volume of the cell at the outer wall or its parietal walls but increases in size in the lower part of the frond and there it may also cover the inner wall of the cell. It generally has 1 pyrenoid (2 pyrenoids in 2—8 % of the cells, and by way of exception 3 small pyrenoids).

REPRODUCTION. *Ulva gigantea* has alternation of generations. The sexual generation is distinctly anisogamous (Fig. 15) with big ♀-gametes, averaging 8.6×3.7 μ, ♂-gametes averaging 7.1×2.7 μ. Zoospores, about 10.5×5.5 μ, are usually 4 in each sporangium.

The young germlings (Fig. 15 F) are easily distinguished from corresponding stages of *Ulva lactuca* (Fig. 5 F—G), which grow for a long time with 1 top cell and are tapering towards the apex. When the cylindrical tubular germling has reached a diameter of about 1/2 mm, the development into the distromatic final stage begins (Fig. 15 G).

TAXONOMY. KÜTZING's herbarium in Herb. Lugd. Bat. has 9 sheets of *Phycoseris gigantea* and the labels of three of them are written by KÜTZING. One of the last-mentioned sheets contains about 30 specimens from Venice, which have been investigated and identified as *Ulva rigida*. Another sheet, No. 938,91. .527, has two specimens, one of which can be regarded as the lectotype specimen of the species in Tab. phyc. VI, 22. It is from Granville (Normandy) and was originally called "*Ulva lactuca* LIN." (written in BRÉBISSON's handwriting). The type specimen well agrees with the Roscoff *Ulva*, described above: thallus is in the upper part very thin (24—27 μ) and the breadth of the cells is considerably greater than their height (Fig. 15 J), the cells are medium-sized, in rows, with one pyrenoid (Fig. 15 I).

The name *Phycoseris gigantea* has almost completely disappeared from algal literature since THURET (1854) placed the alga as a synonym for his *Ulva lactuca* LINNAEUS.

Fig. 16. *Ulva olivascens*, Banyuls, harbour, ×0.67.

J. G. AGARDH (1883) cites — with a question mark — *gigantea* as a synonym for *Ulva latissima* LINNAEUS, the type of which is preserved in the Linnean herb. and has appeared to be representative of *Laminaria sacharina* (see PAPENFUSS 1960 p. 303). HAUCK (1885) accepts only one *Ulva* species, called *Ulva lactuca* (L.) LE JOLIS, and illustrates his *Ulva lactuca* forma *genuina* by KÜTZING's Tab. 22 of *Phycoseris* *gigantea.* DE-TONI (1889), HAMEL (1931), NEWTON (1931) do not mention KÜTZING's *gigantea.*

Regarding *Phycoseris gigantea* β *perforata* KÜTZING, see *Ulva rigida*, p. 546 and Fig. 10 B.

5. Ulva olivascens DANGEARD 1961

Ulva olivacea DANGEARD 1951 (non *Ulva olivacea* HORNEMANN in Flora Danica, Fasc. 24, 1810).

This alga, first found by DANGEARD on the French coast at Roscoff and Guéthary (Basses-Pyrénées), seems to be less variable with regard to habitus and anatomy than the majority of other *Ulva* species. Most of my material is from the Mediterranean (the harbour of Banyuls), where it grew together with *Ulva rigida.* Already by its colour the living alga could easily be distinguished from *rigida.*

Fertile plants were 2—3 dm high, the disc markedly laciniate with oval perforations (Fig. 16).

ANATOMY. The cells are mostly unordered, only here and there in the disc does one find areas with ordered cells (Fig. 17 A—C). The adult cells have great dimensions: in surface view they are about 24×18 μ, occasionally up to 35×24 μ (Fig. 17 C). In old parts of the thallus the grown-up cells are rounded in a characteristic way (Fig. 17 A).

The cross-section of the margin of thallus in the upper part of the plant is about 60 μ and the height of cell lumen is about 26 μ (Fig. 17 D). At the base, immediately above the rhizoidal zone, thallus is 100—115 μ thick, the cell lumen height is 33—47 μ (Fig. 18 A).

The chromatophore has its chlorophyll chiefly concentrated to the outer wall of the cell or the upper part of a side wall. The alga belongs to that group of *Ulva* species which has one pyrenoid, and in which 2 (—3) pyrenoids are seldom to be found.

REPRODUCTION AND DEVELOPMENT. As is usually the case in *Ulva,* fertility begins at the margin of the upper part of the disc, but in this species often inside a sterile marginal region with the breadth of a few cells, which after fertility are soon detached in threadlike masses.

In his first material of *olivascens*, described in 1951 and 1959, DANGEARD found 4-flagellate swarmers, "zoospores", and, in the material of 1963, 4-flagellate swarmers in six specimens, but in three specimens "quelques zoïdes à deux cils accompagnant les zoospores". My fertile material from two localities on the Mediterranean, about 20 specimens,

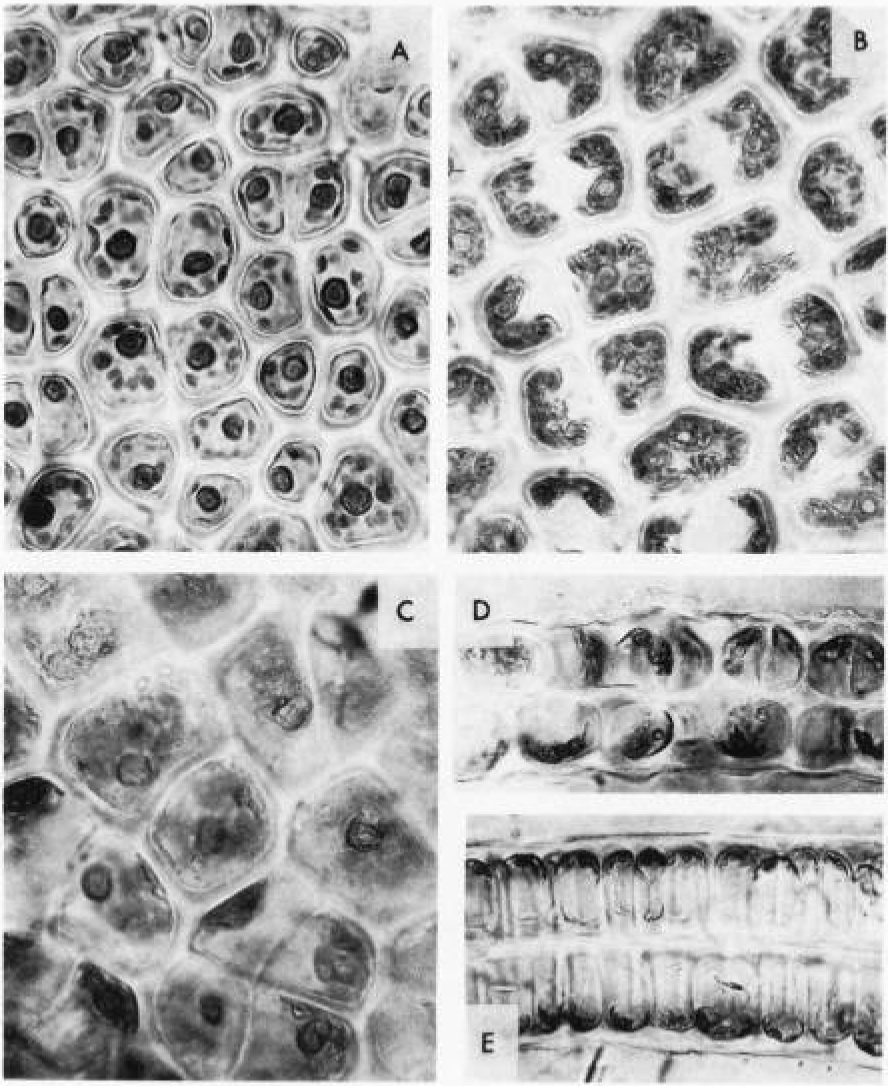


Fig. 17. *Ulva olivascens*. A: Port Bou. B: Banyuls; upper part. C: Banyuls; base. D: section, upper part, the margin. E: middle part. A—C ×660, D—E ×330.

had as sole reproductive bodies 2-flagellate, neutral swarmers. From the very beginning the greater part of them reacted as negatively phototactic, and after only 6 hours they stuck to the culture glass. The swarmers (Fig. 18 D) were 5.8—9.2×2.3—3.4 μ, consequently of very

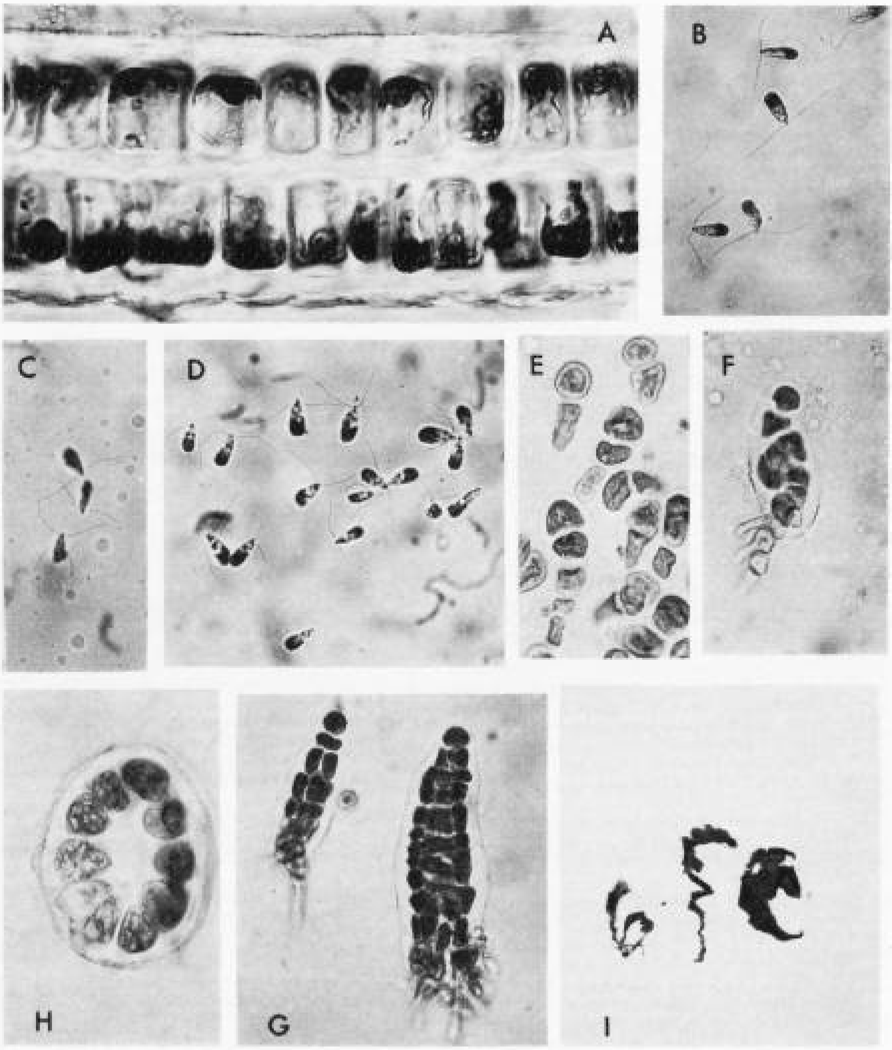


Fig. 18. *Ulva olivascens.* A: section just above the rhizoidal zone. B: Aber Benoit, 2-flagellate swarmers. C: Aber Benoit, 2-flagellate and 4-flagellate swarmers. D: Banyuls. E—G: germlings. H: section, plant 2.5 mm high. I: young plants ×0.7. A ×330. B—D ×660. E ×330. F—H ×260.

variable size, which is usually the case in neutrospores as distinguished from zoospores.

In my material from Brittany a dozen specimens had exclusively 2-flagellate swarmers (Fig. 18 B), but one specimen produced both

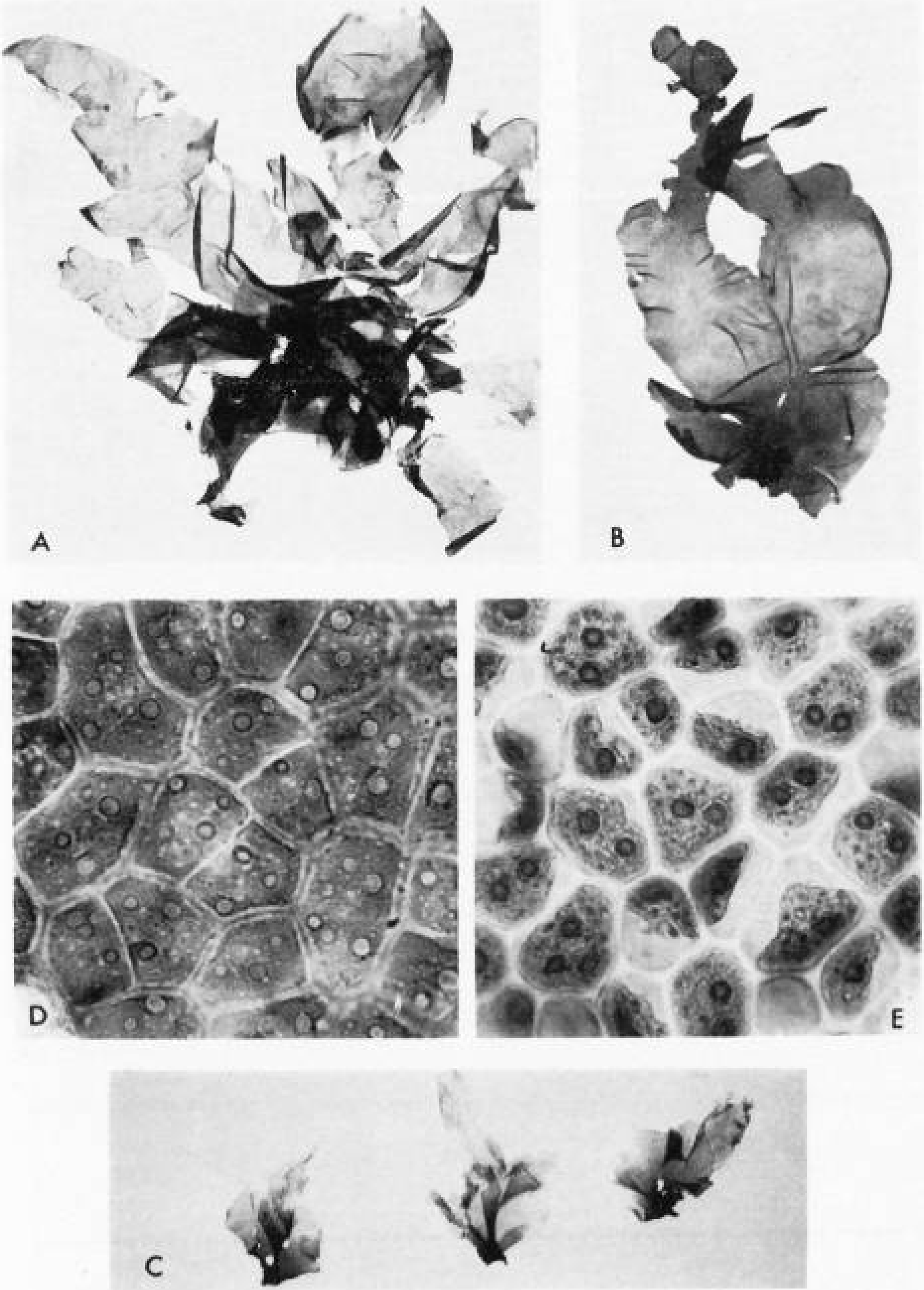


Fig. 19. *Ulva rotundata.* A: Naples ×0.7. B: Tromsö ×0.7. C: Puerto de la Cruz, fertile plants ×0.7. D: Naples, young plant. E: Split. D—E ×660.

2-flagellate and a small number of 4-flagellate swarmers (Fig. 18 C). Similar cases, implying that the same alga has two kinds of neutral swarmers, is known in *Enteromorpha intestinalis* var. *asexualis* and *Enteromorpha linza* (BLIDING 1963 pp. 144 and 130), where swarmers are normally 4-flagellate. GAYRAL (1962 a) reports the finding on the Moroccan Coast of male gametes 6—6.5×1.5 μ, female gametes 6—7×3 μ, and zoospores of the same size as that of the female gametes.

The development of the young germling is shown in Fig. 18 E—I.

LIVING MATERIAL from: France, Brittany, Aber Benoit, May 1959; Pyr. orient., Banyuls, April 1966. Spain, Port Bou, May 1958.

6. Ulva rotundata BLIDING spec. nov.

Ulva lamina rotundata, saepissime 1—2 dm alta, laciniata aut profunde lobata; cellulae juvenales a superficie visae angulares, cellulae adultae rotundatae, inordinatae, maximae; altitudo luminis cellulae in sectione laminae transversa circ. 25 μ in parte superiore plantae, circ. 33 μ in parte inferiore. Pyrenoides 1—3 (—5). — Generatio sexualis anisogama; ♂-gameta circ. 5×2.5 μ, ♀-gameta circ. 6.5×3.5 μ, zoosporae circ. 10×5.5 μ. Superior pars plantae germinantis rotundata, planta germinans magno stipite praedita.

Holotypus in Bot. Mus. Univ. Lund.

Type locality: Italy, Naples, Mergellina harbour, coll. C. BLIDING April 1958.

This species first found in some Mediterranean localities turned out to be quite common on the coasts of Tenerife and was later found in a locality in Northern Norway (about 70° N. Lat.). Plants growing littorally had a height of 1—2 dm, but specimens living supralittorally in the splash zone at very exposed localities (e.g. on the west coast of Tenerife) were only a few centimetres high (Fig. 19 C). The disc is mostly more or less lobate. Toothlike, microscopic protuberances at the margin of the disc are rare, only observed in specimens from the Adriatic Sea.

ANATOMY. In the young plants the cells are polygonal in surface view, angular, very big, 30—38 μ in their longest dimension (Fig. 19 D) and exceptionally up to 45 μ (in specimens from Tenerife, Fig. 20 C). Cells in adult plants (Fig. 19 E, 20 A) are more rounded, averaging about 26×20 μ. They are unordered in the whole of thallus.

Cross-section of the disc margin (Fig. 21 A) in the upper part of the plant is about 56 μ, and the cell height (excluding the cell walls) about 25 μ. In the lower part of the alga the corresponding values are

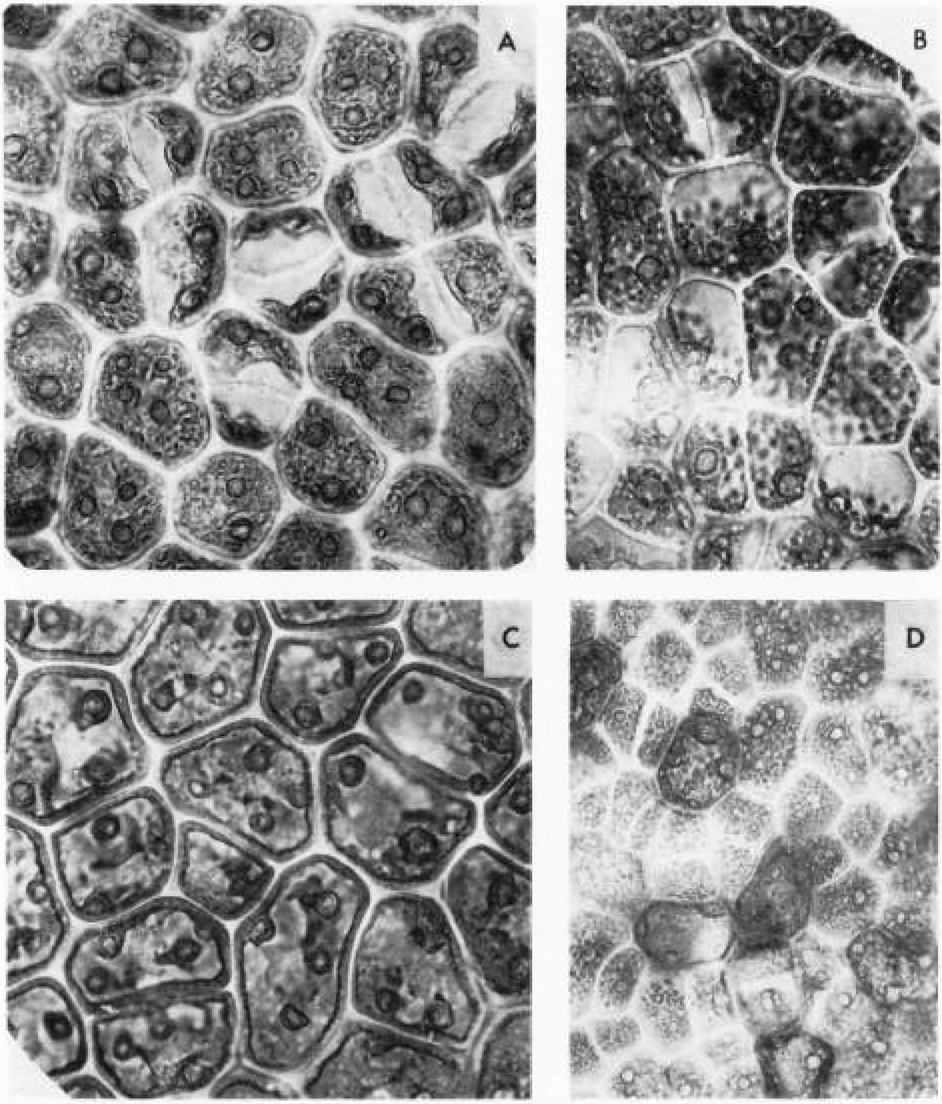


Fig. 20. *Ulva rotundata*. A: Puerto de la Cruz. B: Tromsö. C: Puerto de la Cruz, young plant. D: Tromsö; rhizoidal zone. A—C ×660, D ×330.

about 75 and 30 µ respectively, and cross-sections of the rhizoidal zone a few mm from the point of attachment of the plant give about 95 µ and 33 µ respectively (Fig. 21 C). The small difference in height between the cells in the upper part of the frond and the cells at the base

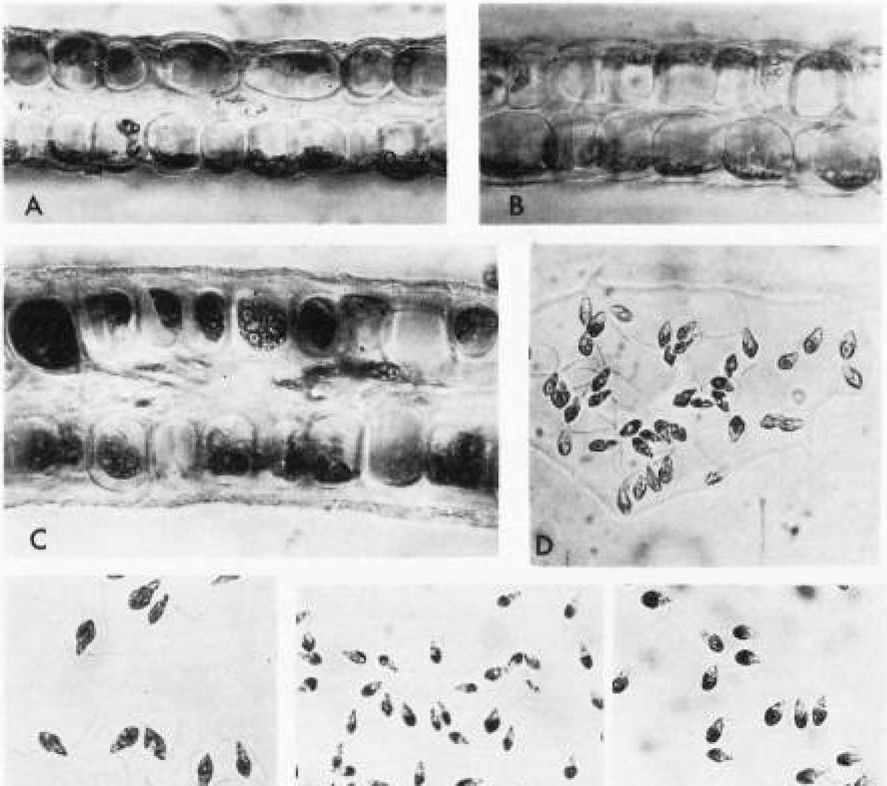


Fig. 21. *Ulva rotundata*. A: Tromsö, section, upper part, margin. B: Naples, middle part. C: Tromsö, rhizoidal zone. D: ♂-gametes, Naples. E: ♀-gametes, Naples. F: ♂-gametes, Tromsö. G: ♀-gametes, Tromsö. H: zoospores. I—J: germlings. K: section, plant 2.5 mm high. A—C ×330, D—H ×660, I—K ×260.

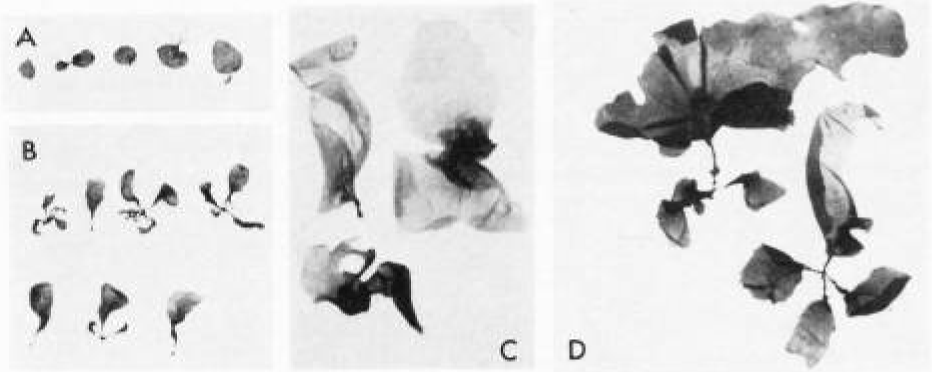


Fig. 22. *Ulva rotundata*, young plants in culture. A: Makarska ×0.74. B: Split ×0.7. C: Naples ×0.7. D: Tromsö ×0.7.

is particularly notable (cf. *rigida*). The chromatophore lies at the outer wall or the side walls and has as a rule 1—2—3 pyrenoids.

REPRODUCTION AND DEVELOPMENT. *Ulva rotundata* has the alternation of generations common in *Ulva* with a gametophyte of ♂- and ♀-plants and a sporophyte of zoospore plants. Male as well as female gametes can easily germinate without fertilization and develop into ♂- and ♀-plants respectively. The species is very distinctly anisogamous and both kinds of gametes are relatively small (Fig. 21 D—G). The female gametes average 6.7×3.6 μ, the male gametes 5.1×2.5 μ. In the sporangia of the zoospore plants mostly 8 zoospores are formed averaging 10.1×5.7 μ (Fig. 21 H).

Gametes of the material from Norway as well as from Tenerife copulated with gametes of plants from the Mediterranean and gave birth to developable zygotes.

The young plant is easily distinguishable from closely related *Ulva* species by the very form of its disc. The microscopic germling which is at first of uniform breadth (Fig. 21 I—J) soon loses its hollowness (at the height of 1—3 mm, Fig. 21 K) and in its upper part it becomes much broader and grows into a rounded disc with unordered cells (Fig. 22). In its lower part it gets a well-developed stipe, and at this stage the whole plant becomes more or less spoonlike (Fig. 22 B). The stipe often has longitudinal ridges from which new discs develop, which can unite with the original disc (Fig. 22 D).

LIVING MATERIAL from: Norway, Tromsö, Ryströmmen July 1966. Italy, Naples, Mergellina March—April 1958. Yugoslavia, Makarska and Split harbour Aug.—Oct. 1957. Greece, Rhodes, Lindos April 1965. Canary Islands, Tenerife, Puerto de la Cruz and other localities, March 1964.

7. **Ulva curvata** (Kützing) De-Toni

Phycoseris curvata Kützing 1845 p. 245, 1856 p. 8. — *Ulva curvata* (Kützing) De-Toni 1889 p. 116; van den Hoek 1963 p. 184. — "*Ulva curvata* Kützing" in Schiller 1928 p. 115; Feldmann et Magne 1964 p. 7.

Phycoseris cornucopiae Kützing 1856 vol. VI p. 11 tab. 30,1. — *Ulva cornucopiae* (Kützing) J. Agardh 1883 p. 163.

Ulva dangeardii Gayral et de Mazancourt 1958 p. 131.

Ulva incurvata Parriaud 1958 p. 141.

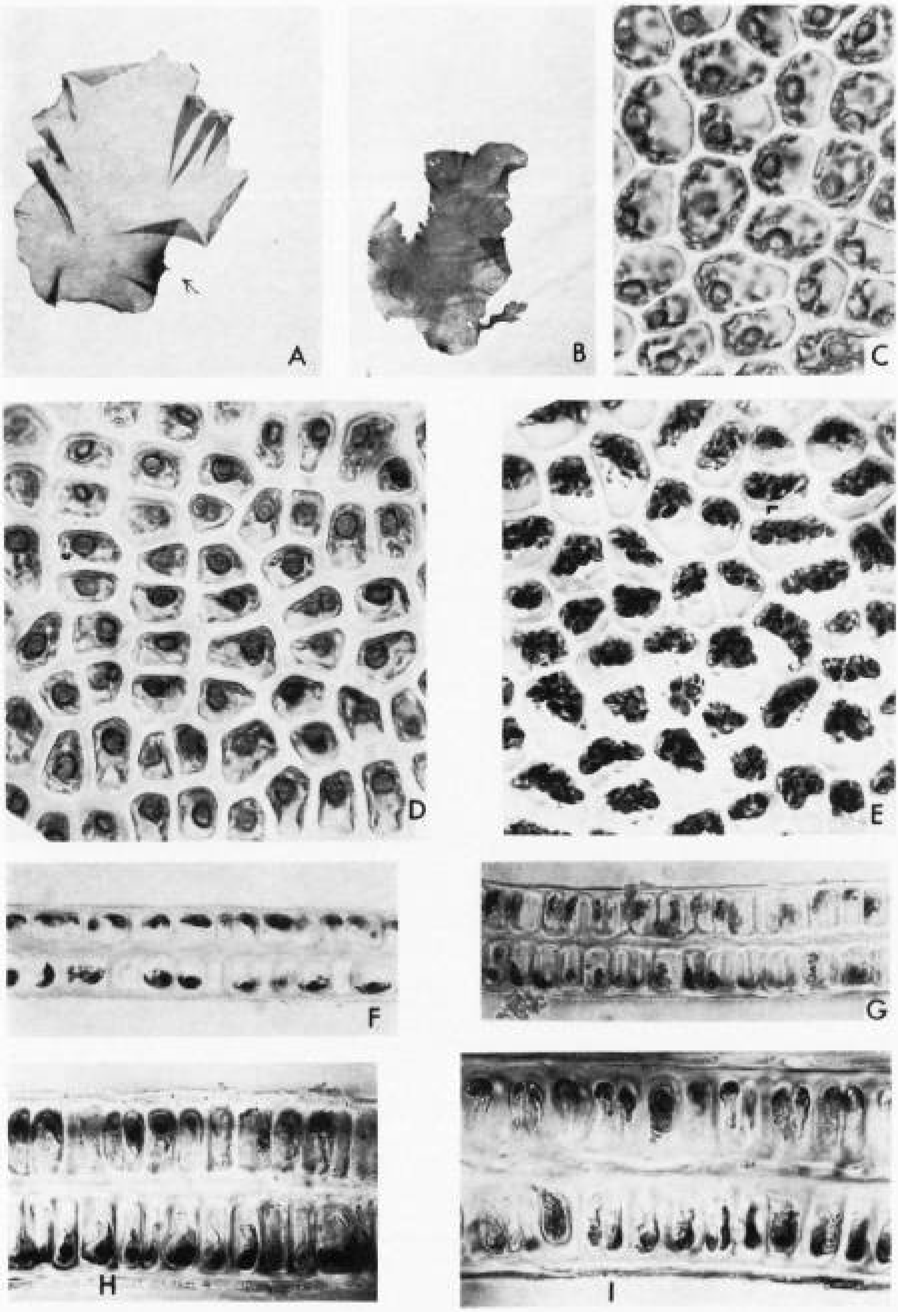
Type locality: The Island of Rügen in the Baltic Sea.

The material investigated is from Brittany growing in shallow bays with brackish water, and also from many brackish waters connected with the Mediterranean Sea (étangs) in southern France, and finally from the Swedish coast, where the species had not been found previously. By means of the holdfast of the small stipe, placed unsymmetrically (Fig. 23 A—B), the plant is attached to stones and shells of molluscs. Especially in calm waters of low salinity it often floats freely forming large floats of indefinite form. The disc is mostly venous and wrinkled, its margin lacks microscopic teeth but it often has protuberances which may grow into macroscopic lobes.

ANATOMY. In the disc, regions with rectangular cells, well arranged in rows, alternate with areas of more or less polygonal, unordered cells. In surface view adult cells in the central part of specimens from 5 different localities, widely apart, were 11.5—17.0×11.5 μ (Fig. 23 D, E). The corresponding cells in a young plant (grown up in culture 20/2—25/9) had a size of about 20×15 μ (Fig. 23 C).

The thickness of thallus (Fig. 23 F—I) in the upper part of the margin is 34—39 μ and the height of the cell lumen 12—15 μ, centrally in the upper part of the disc about 44 and 18 μ; near the base about 75 and 27 μ, and in the rhizoidal zone about 85 and 28 μ respectively.

Fig. 23. *Ulva curvata*. A: Landskrona ×0.7. B: Plounéour-Três ×0.65. C: Sète, young plant, 20/2—25/9. D: Landskrona; lower part of plant. E: Sète, older plant. F: Etang de Salces; section of upper part, margin. G: Plounéour-Trèz; upper part. H: Landskrona; lower part. I: rhizoidal zone. C—E ×660. F—I ×330.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In most cases the chomatophore only takes up a relatively small part of the volume of the cells (cf. *lactuca*) and has 1 pyrenoid (the number of cells with more than 1 pyrenoid is less than 2 %).

REPRODUCTION AND DEVELOPMENT. *Ulva curvata* has alternation of generations. In the haploid generation the ♂-gametes just swarmed out are 6.2×2.0 μ (average value in populations from several localities) and the ♀-gametes 7.3×3.3 μ; the zoospores of the diploid generation are about 11.2×5.4 μ (Fig. 24 A—C).

The young germlings have one top cell for a long time (Fig. 24 D—E), and the young macroscopic plant is easily distinguished by its pointed apex. In culture they remain unusually long at a tubular stage (Fig. 24 F), often till the plant is about 8 mm high. The young thallus, curved at the base, is a good characteristic of the species (Fig. 24 H).

LIVING MATERIAL from: Sweden, the West Coast, Landskrona and Saltholmen, vic. of Gothenburg. France, Brittany, Plounéour-Trèz; Pyr. Orient, Ètang de Sigean (near the laboratory), Ètang de Canet; Languedoc, vicinity of Sète.

TAXONOMY. After KÜTZING the species was long overlooked or included in the complex "*lactuca*". SCHILLER (1928 p. 115) was the first who, with material from Heligoland, described it more thoroughly and regarded it as a good species. HAMEL (1931) did not mention it. The presence of the species in Morocco and south Europe became known through papers by GAYRAL et MAZANCOURT (as *Ulva dangeardii*) and PARRIAUD (as *Ulva incurvata*). VAN DEN HOEK established (1963 p. 184) that the last-mentioned two taxa are synonyms for KÜTZING's *Phycoseris curvata*.

An investigation of KÜTZING's type specimen (in Herb. Lugd. Bat. No. 938.174. .392) of *Phycoseris cornucopiae* (Tab. phyc. Vol. VI, Tab. 30) has shown that the species agrees well with *Ulva curvata* with regard to the cross-section of thallus and the size, form, arrangement and pyrenoid-number of cells (Fig. 24 I—J), which is the reason why it has been regarded here as a synonym.

8. Ulva neapolitana BLIDING

Ulva neapolitana BLIDING 1960 pp. 182—184.
Holotypus in Bot. Mus. Univ. Lund.
Type locality: Italy, Naples, coll. C. BLIDING.

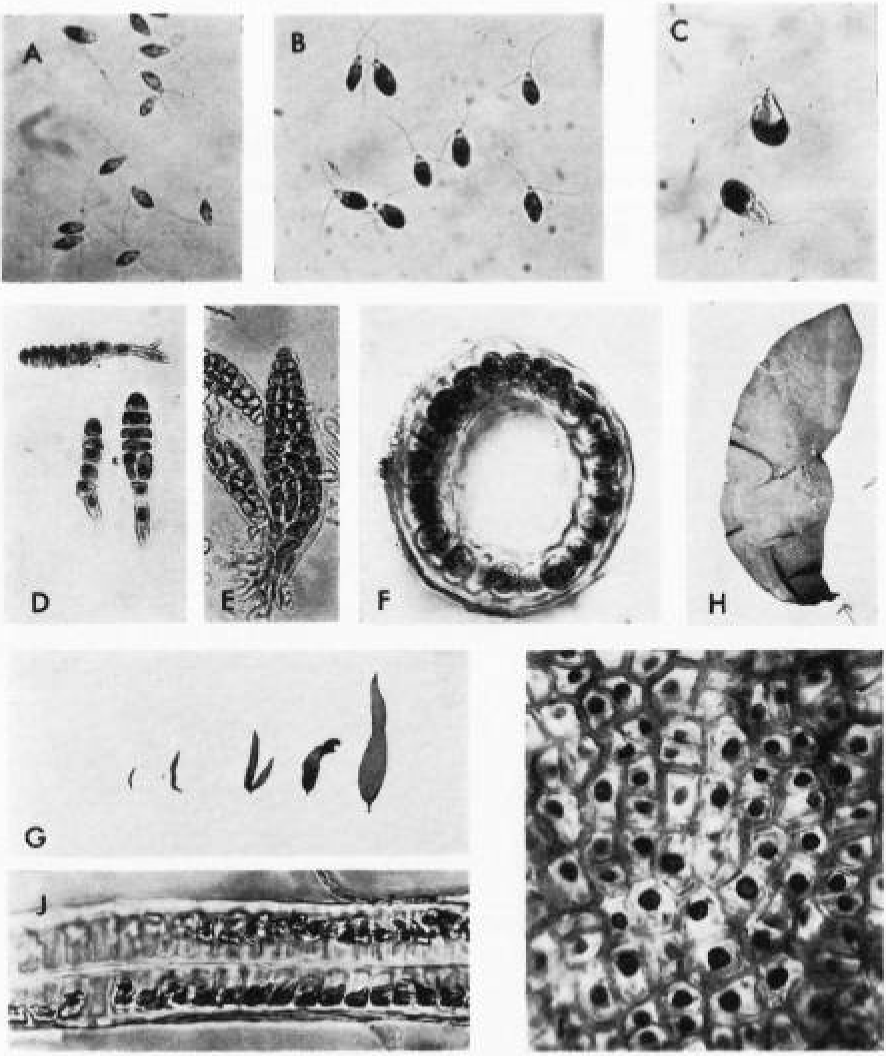


Fig. 24. *Ulva curvata.* A: ♂-gametes. B: ♀-gametes. C: zoospores. D—E: germlings, Plounéour-Trez. F: section, plant 2—3 mm high. G—H: plants from zoospores ×0.7. I—J: *Phycoseris cornucopiae* KÜTZING, type specimen, surface view and section. A—C ×660, D—E ×330, F ×260, I ×660, J ×330.

The investigation material was collected in March and April, 1958, in Porta S:a Lucia, Naples, where it grew in the upper littoral zone in thick masses on stones. The specimens which habitually reminded most of *Enteromorpha linza* and *E. stipitata* var. *linzoides,* were 7—15 cm high and at the most 4 cm broad (BLIDING 1960 Fig. 10 A), tapering towards the base into a distinct stipe. Some plants, however, were narrow, ribbonlike (Fig. 25 B), and up to 0.5 m in length.

ANATOMY. The cells are arranged in longitudinal rows (Fig. 25 C—D), although less distinctly in the rhizoidal zone. As fully grown they are 16—25×8—17 µ, in the ribbonlike specimens up to 35×11 µ in the central part of the plant. The parietal chromatophore with 1(—2) pyrenoids is well developed and often covers the inner wall, too (Fig. 26 A—B).

The cross-section of the disc shows that the difference in thickness between the upper part of the plant, 43—46 µ, and the lower part, 48—52 µ, is remarkably small.

REPRODUCTION AND DEVELOPMENT. All specimens investigated had 2-flagellate, asexual, negatively phototactic swarmers, 8.4×4.2 µ in size (Fig. 26 C).

The swarmer grows into a threadlike germling with a primary attaching cell, the lower cells of the germling forming secondary attaching cells and cells developing into branches (Fig. 26 D—H). The young plant goes through a tubular stage (Fig. 26 I) before the final distromatic stage with rhizoidal cells is reached.

TAXONOMY. *Ulva neapolitana* is a primitive species, undoubtedly closely related to the Moroccan *Ulva linearis* DANGEARD, but it differs from the latter particularly by its cell dimensions, which are about twice as great. *Ulva linearis* is 4—5 cm high, 2—3 mm broad, in surface view the cells are unordered, 10—12×5—6 µ, and the thallus 25—30 µ thick (DANGEARD 1957 p. 1591, 1963 p. 195, GAYRAL 1959 p. 87, CAURO 1958 p. 91).

Genus Ulvaria Ruprecht 1851 p. 410

Species typica: *Ulvaria obscura* (KÜTZING) GAYRAL.

1. Ulvaria obscura (KÜTZING) GAYRAL var. blyttii (ARESCHOUG) BLIDING comb. nov.

Ulva blyttii ARESCHOUG 1850 p. 186 tab. I fig. B (1846 p. 129 pro nom. nud.) — *Monostroma blyttii* (ARESCHOUG) WITTROCK 1866 p. 49; J. AGARDH 1883 p. 113. — *Ulvaria blyttii* (ARESCHOUG) VINOGRADOVA 1967 p. 117, vide p. 582. — *Monostroma fuscum* (POSTELS et RUPRECHT) WITTROCK forma *blyttii*

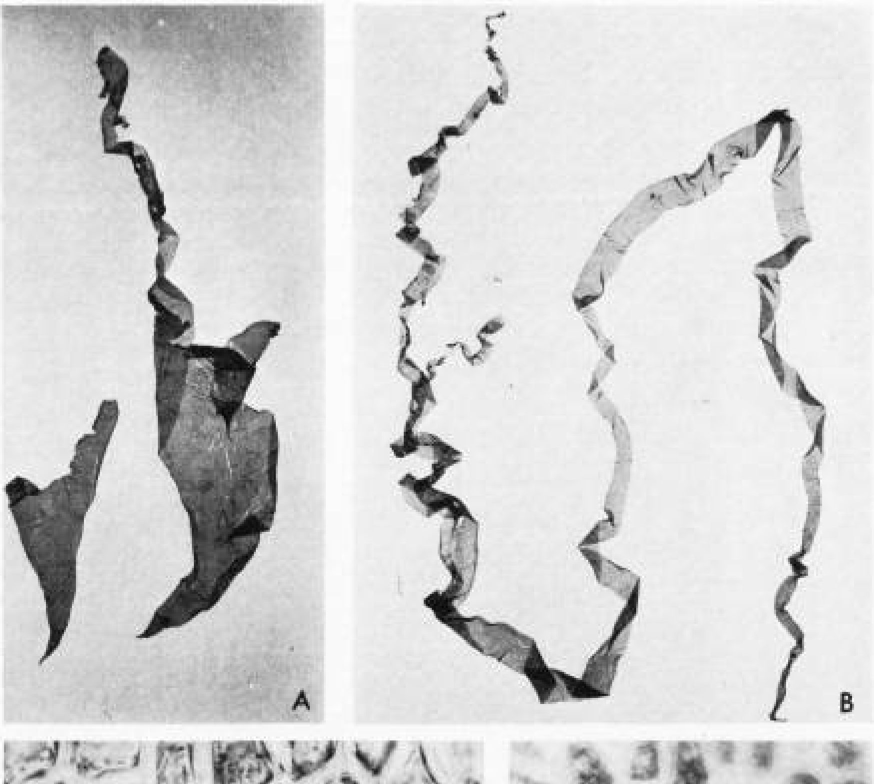


Fig. 25. *Ulva neapolitana*. A: ×0.65. B: ×0.7. C: middle part ×660. D: lower part ×660.

(Areschoug) Collins 1903 p. 12. — *Monostroma fuscum* (Postels et Ruprecht) Wittrock var. *blyttii* (Areschoug) Setchell et Gardner 1920 p. 243.

Ulva fusca Postels et Ruprecht 1840 p. 21 (nom. illeg.). — *Ulvaria fusca* (Postels et Ruprecht) Ruprecht 1851 p. 218; Vinogradova 1967 p. 115. — *Monostroma fuscum* (Postels et Ruprecht) Wittrock 1866 p. 53 (=*Monostroma fuscum* Wittrock, vide p. 584); J. Agardh 1883 p. 113; Papenfuss 1960 p. 315; Bliding 1963 p. 8.

Ulva sordida Areschoug 1850 p. 187 tab. I fig. H.

Ulvaria splendens Ruprecht 1851 p. 218. — *Monostroma splendens* (Ruprecht) Wittrock 1866 p. 50; J. Agardh 1883 p. 112. — *Monostroma fuscum* (Postels et Ruprecht) Wittrock var. *splendens* (Ruprecht) Rosenvinge 1893 p. 942; Setchell et Gardner 1920 p. 242.

Monostroma crispatum Kjellman 1883 p. 300 Pl. 28 figs. 11—13, according to specimen in Bot. Mus., Uppsala, collected by Kjellman at Maasö in the Norwegian Polar Sea 14/8 1876.

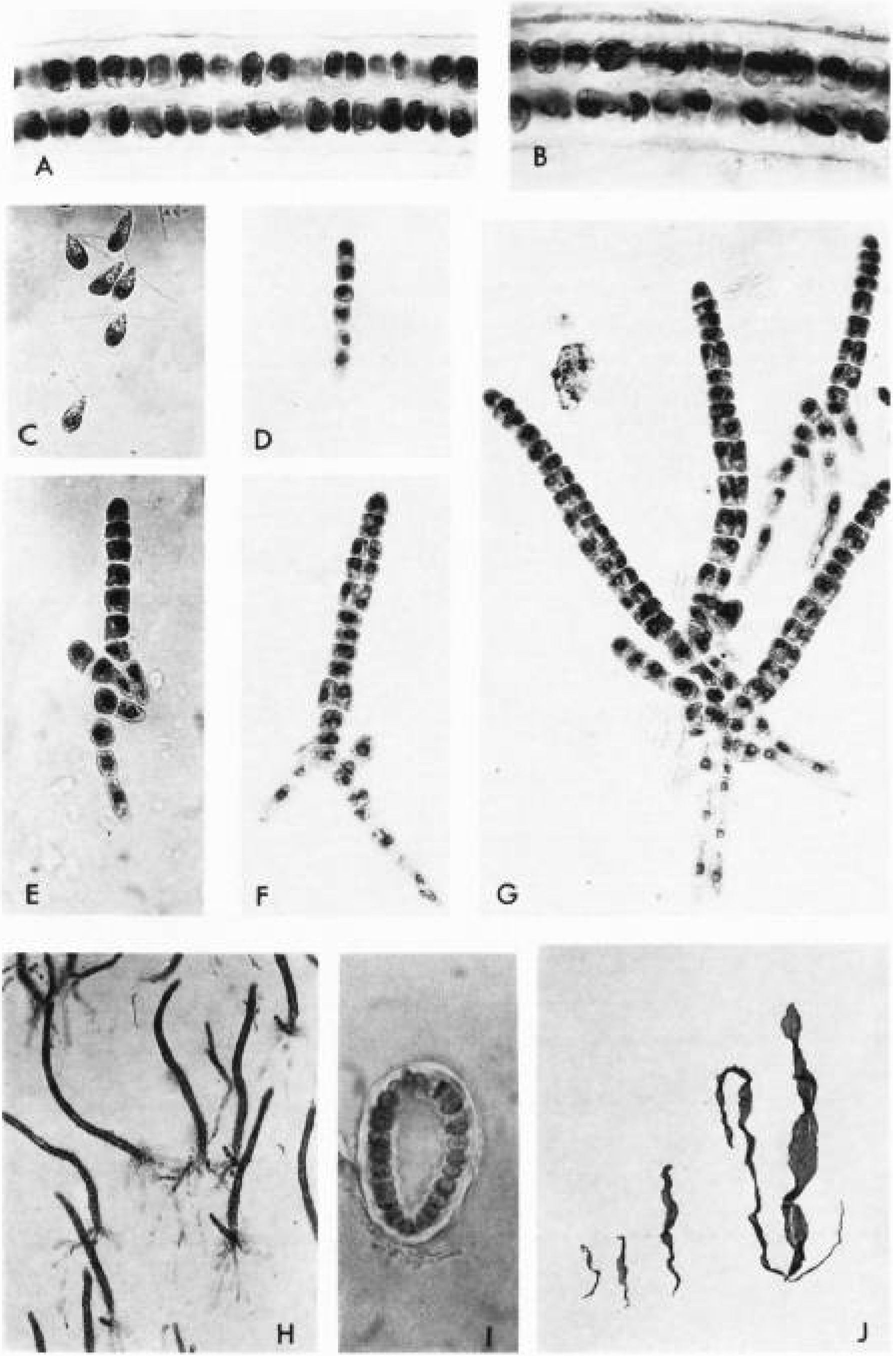
Type locality: Norway, Finnmarken, Renö.

Ulvaria obscura var. *blyttii*, as it is circumscribed here, is a circumpolar alga widely distributed in northern parts of the coasts of the Atlantic and the Pacific, in Europe, Asia, and the western and eastern parts of North America. On the coasts of Southern Europe and Northern Africa the place of var. *blyttii* is taken by var. *obscura*, which is very closely related to it.

My material was collected on the Swedish West Coast, in southwestern Norway, Hordaland, and the north of Norway (Tromsö). As a rule the alga is 10—30 cm high (Fig. 27 A) and grows in the sublittoral and the littoral zone on algae, stones, and shells but often floats freely and assembles at the bottom of harbours and calm bays, where, in nutritious waters it may form large sterile floats. Dried specimens usually become entirely or partially dark in colour and give the paper a brown colour.

ANATOMY. The cells are mostly unordered but with an indication of rows in smaller or larger areas. In surface view they are rectangular or slightly polygonal, seldom rounded. When fully grown they are the size of 18—28×10—20 μ, averaging 23×15 μ (Fig. 27 B). In plants growing in slightly brackish water cells are somewhat smaller than the average value (Fig. 27 C).

Fig. 26. *Ulva neapolitana*. A: section, upper part, margin. B: section just above the rhizoidal zone. C: swarmers. D—G: germlings with primary and secondary attaching cells and cells developing into branches. H: germlings with young rhizoidal cells and branches. I: section, plant 2—3 mm high. J: young plants ×0.73. A—B ×330, C ×660, D—G, I ×260, H ×130.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In the rhizoidal zone the thallus may be 100 μ thick (Fig. 28 C), in the other parts of the disc very variable, chiefly between 60 and 28 μ (Fig. 28 D—H), but in the thinnest part (marginal zone) of the upper part of the plant the cross-section of many specimens only amounts to 16—25 μ (Fig. 28 I).

ROSENVINGE (1893 p. 942) reports that the cells of *Monostroma fuscum* (also including WITTROCK's *M. splendens* and *blyttii*) have 2 chromatophores, one at each outer wall. Fig. 30 D shows part of a cross-section of a young tubular germling (Fig. 30 E), where young cells have a chromatophore with, as a rule, 1 pyrenoid at the outer wall of the cell. Later the chromatophore increases inwards so that, in the grown-up cell, it generally gets an unbroken parietal extent from the outer wall to the inner wall with a maximum accumulation of chlorophyll and pyrenoids inside the two free walls (Fig. 28 D—F).

Even in grown-up plants the material of the chromatophore is accumulated at the outer wall of the cell in the thinner part of thallus (Fig. 28 G, 29 A). Earlier DUBE (1963, in *M. fuscum* from Oregon and Washington) and SCAGEL (1966 p. 37, in *M. fuscum* var. *blyttii* from Alaska) have reported the presence of one choloroplast. *Ulvaria obscura* var. *obscura* also has a single chromatophore (GAYRAL 1965 p. 629).

The number of pyrenoids is very variable in different parts of the thallus, mostly 2—6.

REPRODUCTION. On the Swedish coast and in southern Norway the alga is fertile in September and October, in northern Norway in July and August. Fertility starts inside the big marginal cells (Fig. 28 B), and the swarmers leave the fertile cell by a round opening in the outer wall (Fig. 29 F).

The life-history of the alga was preliminarily outlined (BLIDING 1963 p. 8) under the specific name of *fusca*. Gametophyte plants are isogamous and have small swarmers. In two intercopulating individuals the size of the +-gametes averaged 5.3×3.1 μ and the −-gametes 5.4×3.2 (Fig. 29 C—D). Both kinds of gametes showed a positively phototactic reaction, but in one form in streaming, slightly brackish water (Nordåsvatnet at Strömme bridge), the gametes, on swarming out, at once swam to the bottom of the culture vessel. They were also somewhat smaller than the average and almost ball-shaped (Fig. 29 B) but copulated, forming groups, with positively phototactic gametes of a plant from a marine, strongly exposed locality (the skerry of Nordre Oddane).

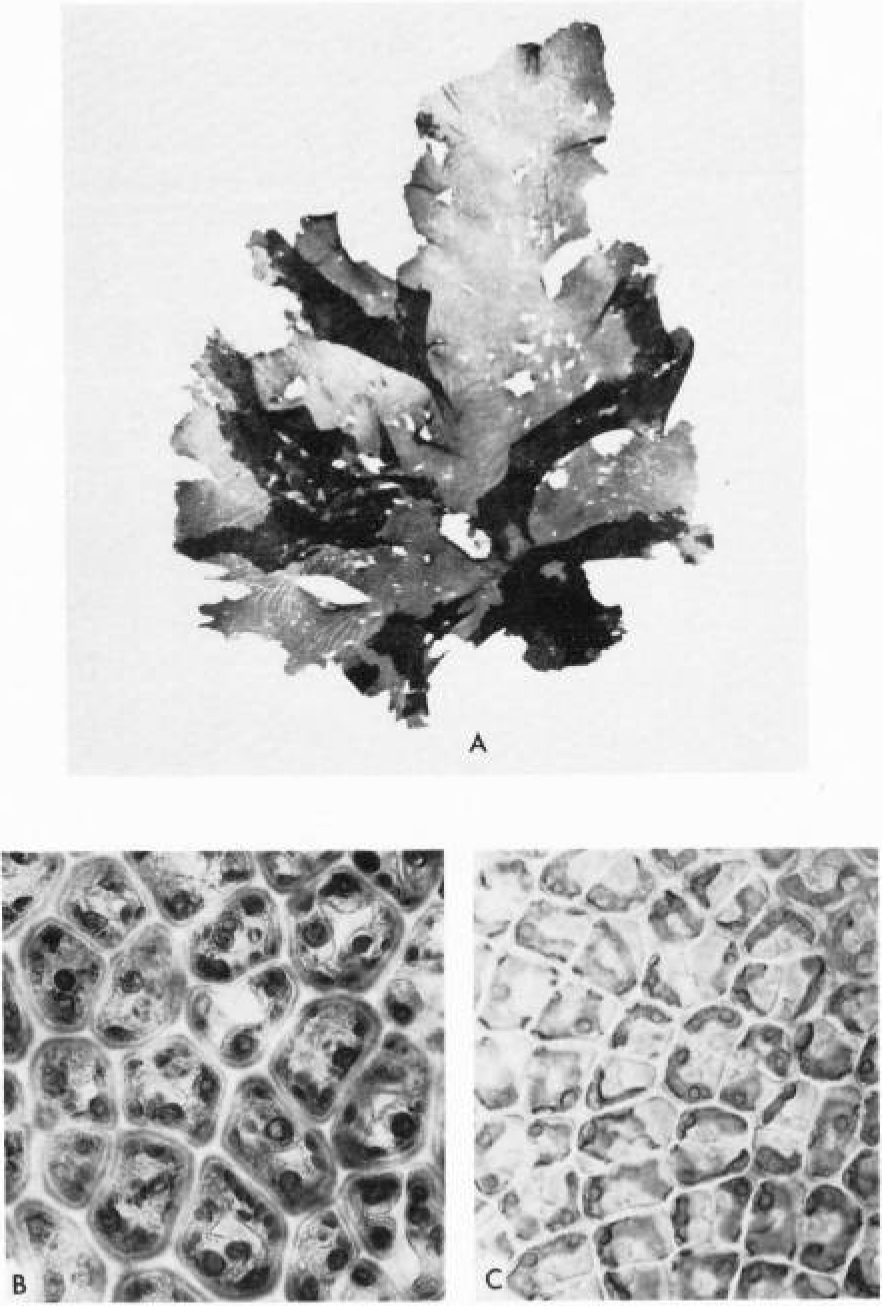


Fig. 27. *Ulvaria obscura* var. *blyttii*. A: Nordre Oddane, on *Corallina* in a deep rocky pool ×0.85. B: Nordåsvatnet ×660. C: Saltholmen ×660.

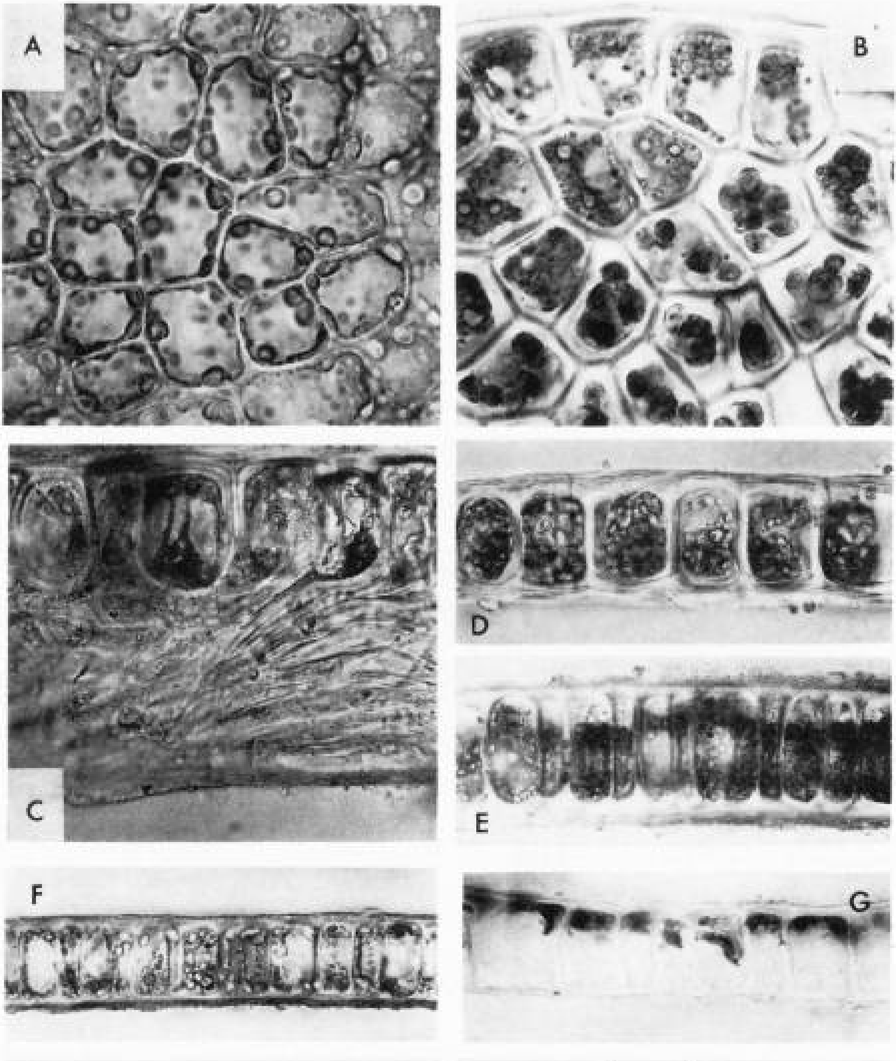


Fig. 28. *Ulvaria obscura* var. *blyttii*. A—B: Nordåsvatnet, Strömme bridge. C: Nordåsvatnet, section, rhizoidal zone. D: Strömme. E—F: Saltholmen. G: Nordre Oddane, chromatophore unipolar. H: Saltholmen. I: Nordre Oddane, two sections, upper part. A—B ×660. C—I ×330.

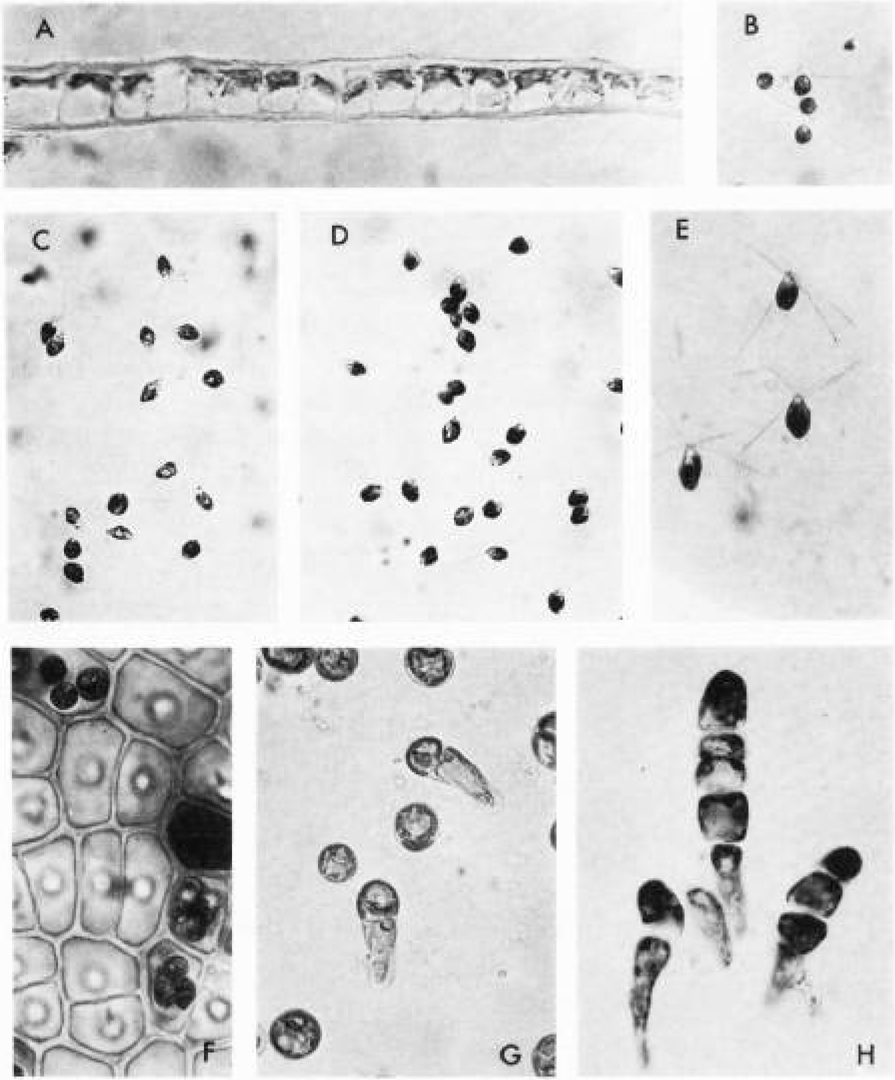


Fig. 29. *Ulvaria obscura* var. *blyttii*. A: section, c:a 0.28 mm long, lamina varies in thickness between 27 and 17 μ. B: negatively phototactic gametes. C—D: +- and —-gametes. E: zoospores. F: fertile region. G—H: germination of the zoospores and their first divisions. B—F: ×660, A, G, H ×330.

Both kinds of gametes germinate without fertilization into new gametophyte plants. The zygotes developed in culture at 12—15° C. into sporophyte plants which generated small zoospores averaging 9.1×4.6 μ (Fig. 29 E).

Gametes, zygotes and zoospores first form a monosiphonous, threadlike germling with a well-developed primary attaching cell (Fig. 29 G—H). Then the germling goes through a hollow, *Enteromorpha*-like stage. In its upper part (Fig. 30 A—B) it finally becomes more or less widened into a sack-shaped, macroscopic plant. When the plant is about 5 mm high (at the age of 2—3 months) the sack is partitioned in its upper part (Fig. 30 F), so that a funnel-shaped lower part remains as part of the stipe of the fully developed plant, while the outspread lobes of the upper part develop into the leaflike, monostromatic disc (Fig. 30 G).

At the base of the plant the rhizoidal cells develop with a clublike upper part (Fig. 30 C).

LIVING MATERIAL from: Sweden, West Coast, Saltholmen, Uddevalla, Rågårdsvik (vic. of Kristineberg). Norway, Hordaland, Nordre Oddane, Nordåsvatnet, Strömme bridge; Troms, Tromsö.

TAXONOMY. In its ontogeny the present alga obviously has a very great resemblance to *Ulva* and has been proposed to be transferred from *Monostroma* to a resurrected genus *Ulvaria* Ruprecht (Bliding 1963 p. 8, Dube 1963, Gayral 1964 p. 2149, Vinogradova 1967 a p. 110).

The oldest legitimate specific name in *Ulvaria* is *obscura* (*Ulva obscura* Kützing 1843 p. 296, type specimen from the Bay of Biscay in Herb. Lugd. Bat. No. 938.53. .77), which has the same anatomy as var. *blyttii* and is distinguished from the latter only by its anisogamy (Gayral 1961 Figs. 2—8) and the more rounded form of the young sack-shaped germling (J. Agardh 1883 p. 91, Rosenvinge 1932 Fig. 2, Gayral 1962 pl. I—II).

Hamel (1931 p. 50) and Vinogradova (1967 a p. 117) considered *obscura* a synonym of *fusca* and *blyttii* respectively. Consequently, the taxon *Ulvaria blyttii* (Areschoug) Vinogradova 1967 p. 117 should have been listed as a synonym of *Ulvaria obscura* (Kützing) Gayral var. *obscura*.

The combination *Ulva fusca* Postels et Ruprecht 1840, the first *Ulvaria* species to be described, is made illegitimate by the older name *Ulva fusca* Hudson. About Hudson's species C. Agardh wrote (1822 p. 428): "*Ulva fusca* (Huds.) est *Laminaria Sacharina*".

In 1851 Ruprecht described a new species belonging to this category, *splendens*, and on the latter and on *Ulva fusca* Postels et Ruprecht, he established the new genus *Ulvaria* introducing the combination *Ulvaria fusca* (Postels et Ruprecht) Ruprecht and *Ulvaria splendens* Ruprecht.

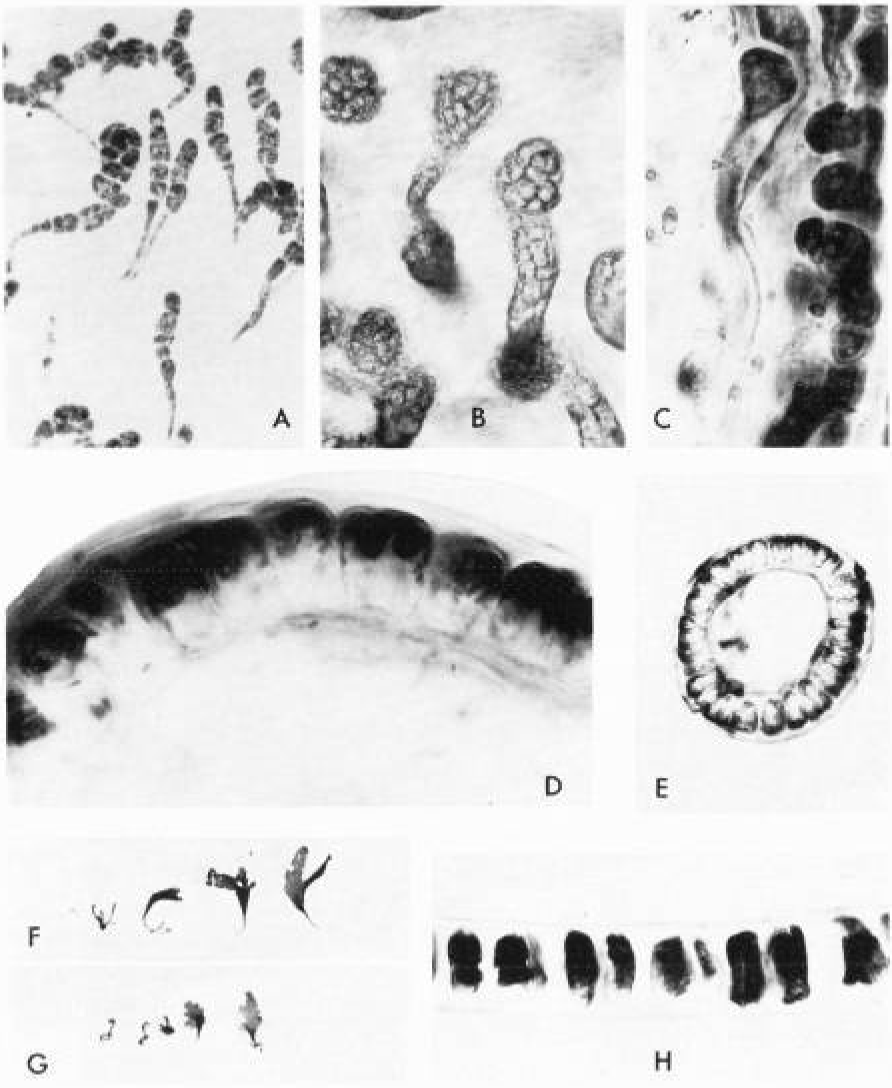


Fig. 30. *Ulvaria obscura* var. *blyttii*. A: Nordre Oddane, germlings. B: Strömme, germlings hollow, upper part sack-shaped. C: Nordre Oddane, rhizoidal cells from a plant 5 weeks old. D: Tromsö, part of section through a hollow germling, one chromatophore at the outer cell wall. E: Tromsö, section through a plant, ca. 4 mm high. F—G: young plants ×0.75 and ×0.72. H: section through one of RUPRECHT's orig. specimens of *Ulvaria splendens*. A, B, C, E × 130, D ×660, H ×330.

It is to be noted that *Ulvaria fusca* (POSTELS et RUPRECHT) RUPRECHT (as well as *Ulvaria splendens* RUPRECHT) is based on material from the Pacific, whereas the name *Monostroma fuscum* was used by WITTROCK (1866 p. 53) for material from the Swedish and Norwegian coasts, e.g. from Udsire, southwestern Norway (op. cit. Tab. IV Fig. 13 a—f). The last-mentioned taxon has been proposed as species lectotypica of *Ulvaria* (PAPENFUSS 1960 p. 315) and agrees completely with var. *blyttii*.

As early as 1846 and 1850 ARESCHOUG published two taxa belonging to *Ulvaria*: *Ulva blyttii* (1846 p. 129, 1850 p. 186, Tab. I G) and *Ulva sordida* (1850 p. 187, Tab. I H), the former from northernmost Norway with the disc 80 μ in cross-section (certainly from the lower part of the thallus), and *sordida* from the Scandinavian coasts with the cross-section of thallus 20—30 μ (ARESCHOUG 1850 p. 187 and ARESCHOUG 1854 p. 371). That the measures of *sordida* only apply to the upper part of the plant is evident from the specimen No. 120 in ARESCHOUG's Exsicc.

Ulva sordida was rightly considered a synonym for *Monostroma fuscum* WITTROCK by WITTROCK 1866 and J. AGARDH 1883, and since then it has not been published as an autonomous taxon.

I have been given the opportunity to study RUPRECHT's original specimens of *Ulvaria splendens* from the Sea of Okhotsk, deposited in the Bot. Museum in Leningrad. The specimens are only 2—5 cm high with a strongly laciniated frond. In surface view the cells in the middle of the plant are about 21×18 μ with 2—5 pyrenoids and the cross-section of thallus 35—40 μ (Fig. 30 H). WITTROCK 1866 p. 51 gives the thickness of thallus in *splendens* as 49—53 μ.

In *Monostroma* literature, *fuscum, blyttii* and *splendens* occur as names of species, varieties, or forms in many combinations. Nearly everywhere WITTROCK's measurements of the thickness of thallus are cited as the sole distinguishing feature.

Recently VINOGRADOVA (1967) dealt with the morphology of some *Ulvaria* taxa and considered as different species *Ulvaria fusca* (P. et R.) RUPR. from northern Pacific and *Ulvaria blyttii* (ARESCH.) VINOGRADOVA from Atlantic coasts, the latter species with *Monostroma obscurum* (KÜTZING) J. AGARDH as a synonym (see above, p. 582). VINOGRADOVA distinguishes the two species chiefly by the thickness of thallus in the upper part which is, in *Ulvaria fusca*, 24—60 μ, averaging 41 μ in *Ulvaria blyttii* 16—40 μ, averaging 30.3 μ (VINOGRADOVA 1967 a p. 116 and p. 119).

Finally, with regard to the ontogeny and the alternation of generations in the taxa dealt with here, there is an investigation by Tatewaki (1963), who had cultivated *Monostroma fuscum* var. *splendens* Rosenvinge from the Pacific (Hokkaido, Japan). Tatewaki's results agree in most respects — even in regard to the size of gametes and zoospores — with what is stated above about var. *blyttii* from the Swedish and the Norwegian coasts.

A paper by Dube (1963) which deals with *Monostroma fuscum* from the northwestern region of North America (Oregon and Washington) also corroborates a development with alternation of isomorphic generations.

Consequently, with our present knowledge of these taxa, the preservation of more than one taxon (besides *Ulvaria obscura* var. *obscura*) must be based for the main part on the slight difference in the thickness of thallus, which is in my opinion an insufficiently distinguishing characteristic, especially bearing in mind the great variation in thickness in quite contiguous parts of the thallus (Fig. 29 A), and the fact that all the thallus measurements given for *fusca* and *splendens* are to be found in var. *blyttii* in different parts of the same plant.

2. **Ulvaria oxysperma** (Kützing) Bliding **comb. nov.** var. **oxysperma**

Basionym: *Ulva oxysperma* Kützing 1843 p. 296. — *Monostroma oxyspermum* (Kützing) Doty 1947 p. 12; Kornmann 1964 p. 17. — *Monostroma oxyspermum* (Kützing) Doty forma *oxyspermum*; see Feldmann et Magne 1964 p. 6.

"*Ulva oxycocca*" Kützing 1845 p. 244 (sphalm.). — *Monostroma oxycoccum* (Kützing) Thuret 1854 a p. 29; Wittrock 1866 p. 32.

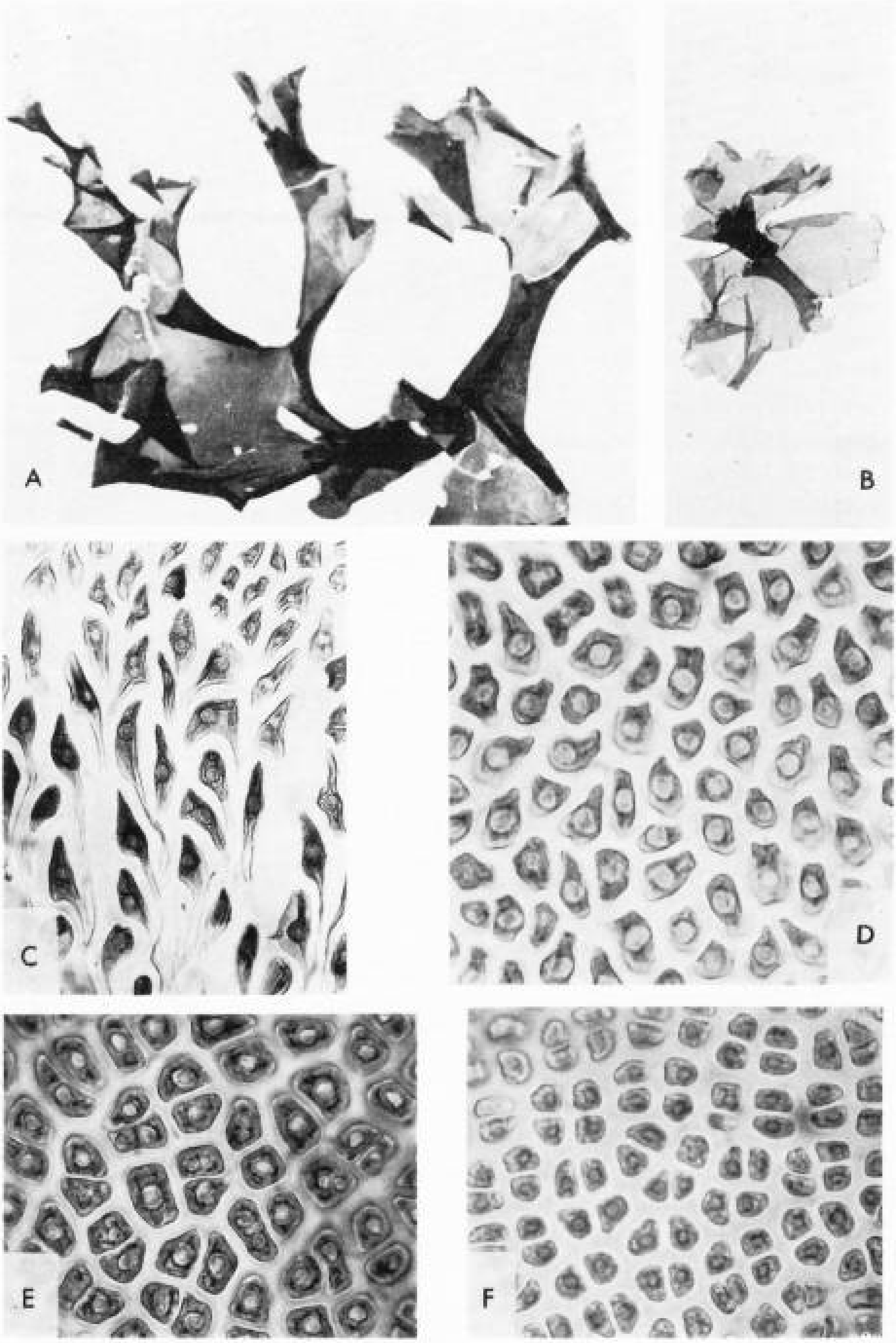
Monostroma laceratum Thuret 1854 a p. 32.

Monostroma latissimum Wittrock 1866 p. 33, non *Ulva latissima* Linnaeus, nec "*Ulva latissima* Lin." sensu Kützing 1843 p. 296. — "*Monostroma latissimum* (Kützing) Wittrock" sensu Wittrock 1866 p. 33; Levring 1940 p. 3; Kylin 1949 p. 14.

Ulva quaternaria Kützing 1856 p. 6, Tab. 13, 2; vide p. 594 et Fig. 33.

"*Monostroma wittrockii* Bornet" sensu Bliding 1935 p. 60 et Kylin 1949 p. 14.

The principal variety of this species, which was first described on material from the Baltic, is of frequent occurrence within large regions of Europe. It grows in waters of very variable salinity: in brooks near their outfall into the sea, in the brackish water of the Baltic and in the pools (étangs) in the south of France but also in water with a salinity of c:a 30 ‰ in sheltered bays on the Atlantic coast. The alga is usually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only 4—10 cm in height and breadth (Fig. 31 A—B), but freely floating forms may reach large dimensions. On the Swedish West Coast the alga is fertile from April to November.

ANATOMY. The base of the leaflike, one-layered plant is attached to the substrate in a zone of rhizoidal cells which have a dark-green upper part, 25—40×10—15 µ, and a threadlike lower part, several hundred µ long (Fig. 31 C). Outside the rhizoidal zone is a region with large, unequal, polygonal cells (Fig. 31 D).

Cells in the upper outer part of the thallus vary very much. In localities with fairly great salinity (e.g. Rhosneigr and Saltholmen) the adult cells were 15—20 µ long in surface view (Fig. 32 B; cf. *obscura* var. *blyttii* from the same locality Fig. 27 C), and their walls were not gelatinous, while specimens from localities with low salinity (e.g. the Baltic and the étangs in the south of France) had cells with considerably smaller lumen and markedly gelatinous walls (Fig. 31 F).

The circumstance that the gelatinosity of the walls is a modifiable quality in this species is of interest, because THURET (1854 a) gives as one of the principal characteristics of the genus *Monostroma* the fact that the cells lie embedded in a homogeneous substance. In consequence of an exaggeration of the taxonomic value of this feature the genus *Monostroma* came to include heterogeneous elements from the very beginning (see p. 600).

Cells are often arranged in distinct rows in large areas — but not in the rhizoidal zone and the adjacent region —; in other forms the arrangement in rows is limited to a zone at the periphery of the disc. The chromatophore with 1 (—2—3) pyrenoid(s) is mostly best developed at the outer wall of the cell lumen but often also reaches the inner wall (Fig. 32 D—E). The thickness of thallus varies between the different zones of the same specimen, in the outer and larger part 17—27 µ with cell-height 10—15 µ, in the rhizoidal region up to 45 µ (Fig. 32 C), with cell-height about 24 µ.

REPRODUCTION AND DEVELOPMENT. The alga lacks alternation of generations, and its only kind of reproductive bodies are 2-flagellate, neutral swarmers, which are formed in the marginal cells of the disc and are liberated by the decomposition of the walls of the mother

Fig. 31. *Ulvaria oxysperma* var. *oxysperma*, Lago di Patria, April 1958, ×0.92. B: Saltholmen ×0.92. C: Rhosneigr, rhizoidal cells, young plant. D: Lago di Patria; near the rhizoidal zone. E: Kviturdvikspollen; middle part of plant. F: Plouescat, in brackish water, upper part. D, E, F ×660. C ×260.

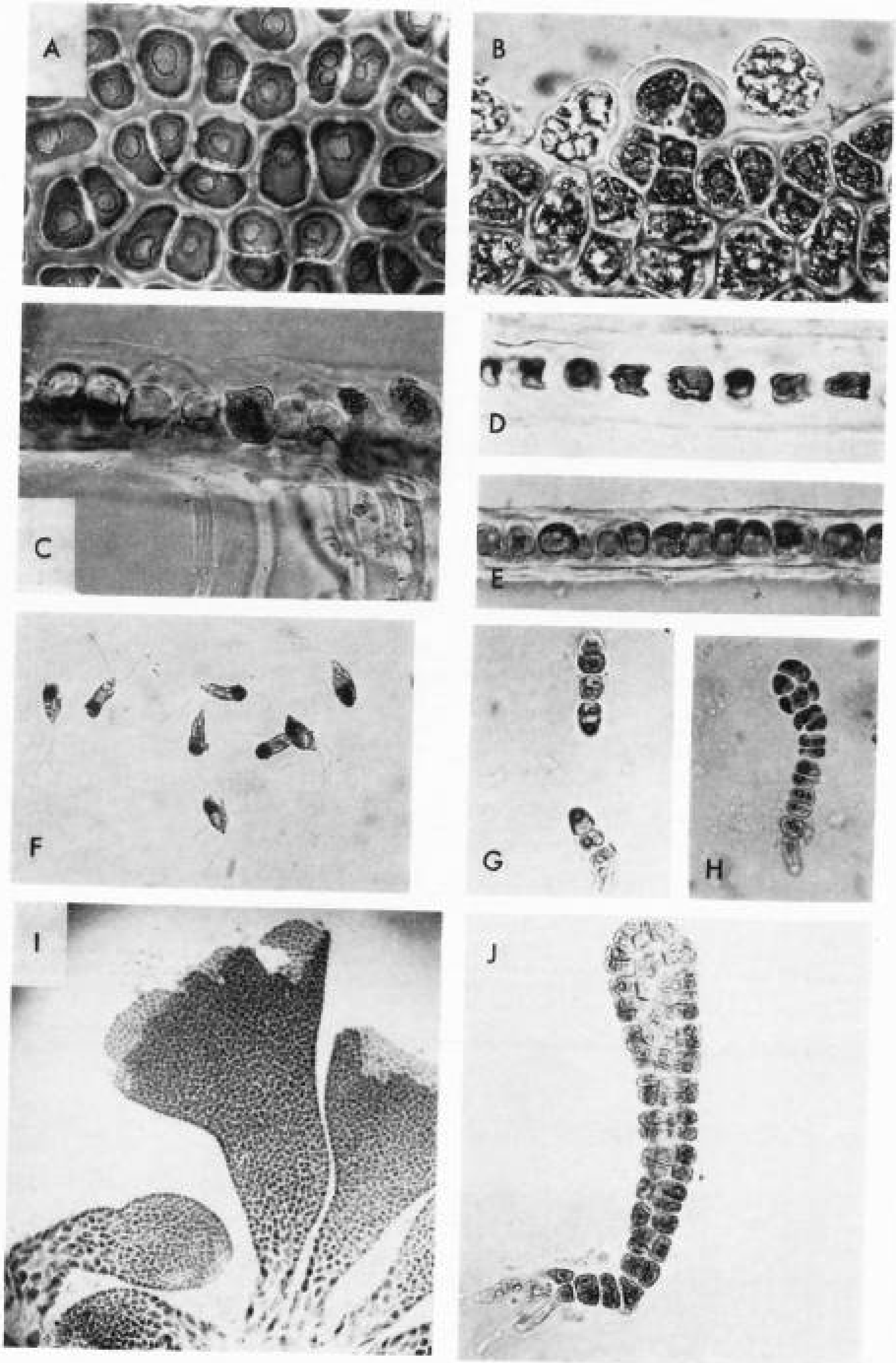
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Fig. 33. *Ulvaria oxysperma* var. *oxysperma*. Surface view of *Ulva oxysperma* KÜTZING β *quaternaria*, in KÜTZING's herb. ×660.

cell. They are from the beginning, or at an early stage, negatively phototactic. Their mean size has varied between different localities from 8.4×3.4 μ to 9.0×4.2 μ (Fig. 32 F). On the germination of the swarmer a multicellular simple thread is formed, which, in the same way as in *Ulvaria obscura* var. *blyttii*, grows into a tubular germling (cf. Fig. 32 and Fig. 30). In its upper distal part, the germling thickens so as to form a one-layered sack, which opens by the decomposition of the walls of the upper cells. The lobes of the sack expand horizontally and grow into the leaflike, one-layered thallus (Fig. 32 I).

LIVING MATERIAL from: Norway, Hordaland, Kviturdvikspollen and Lönningshamn (vic. of Espegrend). Sweden, West Coast, Kristineberg, Uddevalla, Saltholmen, Varberg; Baltic Sea, Karlshamn, Ronneby, Öland (Källa). Great Britain, Wales, Anglesey, Rhosneigr. France, Brittany, Plouescat, Goulven, Brest; Pyr. Orient., Étang de Canet, Étang de Sigean, La Nouvelle. Italy, Lago di Patria (vic. of Naples).

Fig. 32. *Ulvaria oxysperma* var. *oxysperma*. A: Uddevalla. B: Saltholmen; upper part of plant. C: Saltholmen; section, rhizoidal zone. D: Baltic Sea, Öland, Källa; base. E: Saltholmen, upper part. F: 2-flagellate neutral swarmers. G—H: Saltholmen, germlings. J: Saltholmen, germling, hollow in the upper part 15/11—27/11. I: Rhosneigr, sack-shaped germlings, two opened. A, B, F ×660, C, D, E, G, H, J ×330, I ×65.

2 a. **Ulvaria oxysperma** var. **oxysperma** forma **wittrockii** (BORNET) BLIDING **comb. nov.**

Basionym: *Monostroma wittrockii* BORNET in BORNET et THURET 1880 p. 176 pl. 45 (non sensu BLIDING 1935 p. 60, nec KYLIN 1949 p. 14). — *Monostroma oxyspermum* (KÜTZING) DOTY forma *wittrockii* (BORNET) FELDMANN et MAGNE 1964 p. 6.

Monostroma oxycoccum (KÜTZING) THURET forma *quaternarium* (KÜTZING) HAMEL 1931 p. 53.

This alga lives under such ecological conditions that it is exposed to a long stay in the air and consequently varying salinity. It grows high up in the littoral region on stones, walls and quays, and has been found on the French coast of the Channel. Habitually (Fig. 34 A) it is most like the common type of var. *oxysperma*.

ANATOMY. Fig. 34 B—E shows a surface view of cells from the rhizoidal zone (note the broad rhizoidal cells), further the angular cells of different sizes in the main part of the disc, and finally the cells of the margin region, more or less distinctly arranged in rows and sometimes in pairs. In the greater part of the thallus the cross-section is about 30 μ (Fig. 34 F).

REPRODUCTION AND DEVELOPMENT take place in the same way as in var. *oxysperma* forma *oxysperma*. The neutral, 2-flagellate swarmers (Fig. 34 G) have an average size of 7.7×3.9 μ. Fig. 34 H shows the opened tubular plant with rhizoidal cells at the base.

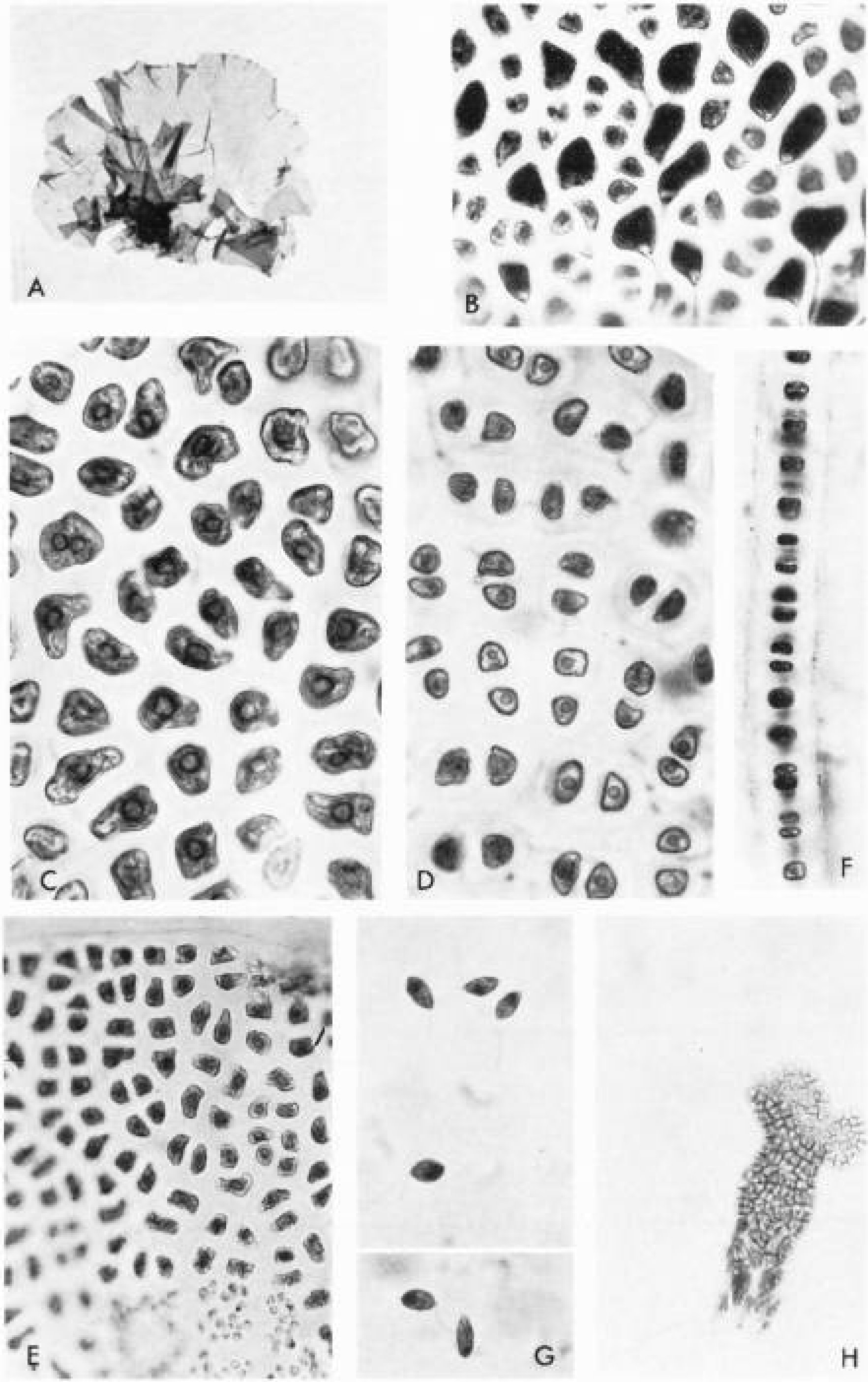
LIVING MATERIAL from: France, Brittany, Roscoff, harbour and Biological Laboratory, April and May 1959 and 1964; Rade de Brest, April 1959.

3. **Ulvaria oxysperma** var. **orbiculata** (THURET) BLIDING **comb. nov.**

Basionym: *Monostroma orbiculatum* THURET 1854 b p. 388; WITTROCK 1866 p. 39; SETCHELL et GARDNER 1920 p. 242. — *Monostroma oxycoccum* (KÜTZING) THURET var. *orbiculatum* (THURET) HAMEL 1931 p. 53. — *Monostroma oxyspermum* (KÜTZING) DOTY forma *orbiculatum* (THURET) FELDMANN et MAGNE 1964 p. 6.

Monostroma oxyspermum (KÜTZING) DOTY 1947 p. 12.

Fig. 34. *Ulvaria oxysperma* var. *oxysperma* forma *wittrockii*. A: Roscoff ×0.96. B: rhizoidal zone. C: middle part. D—E: upper part. F: section, middle part. G: zoosporoids. H: tubulous germling, opened in upper part, at the base rhizoidal cells. B, E, F ×330. C, D, G ×660. H ×260.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Living material was collected in Brittany, Kernéléhen (vicinity of Morlaix), where it grew in a bay with brackish water at the base of *Juncus maritimus* and other phanerogams. Thallus mostly has a round circumference (Fig. 35 A), it is folded in a characteristic radiate way, at the margin flounce-formed and wrinkled. Loose-lying specimens usually have a longish thallus, with deeper indentations at the margin.

ANATOMY. The rhizoidal cells are generally somewhat narrower than in var. *oxysperma*. At the periphery of the rhizoidal zone in young lobes of the thallus (Fig. 35 A, at the bottom) there are big rounded, symmetrical cells, about 30×15 μ, to be seen (Fig. 35 C). On splitting they give rise to irregular, angular cells, which are smaller in the direction of the periphery of the disc (Fig. 35 D and 36 A). In this variety the marginal region is made up of unordered, angular cells (Fig. 36 B), and also the fertile cells are in surface view of irregular form. In cross-section thallus is at the base 48—60 μ, in its thinnest part about 32 μ (Fig. 36 C—E).

REPRODUCTION. The neutral 2-flagellate swarmers are on an average 6.8×3.3 μ (Fig. 36 F). Their development is essentially in agreement with the development of var. *oxyspermum* but with small differences in detail (Fig. 36 H compared with Figs. 32 I and 34 H).

TAXONOMY of *Ulvaria oxysperma*. *U. oxysperma* var. *oxysperma* was cultivated by Bliding (1935, under the name of *Monostroma wittrockii*) and by Kornmann (1964 a); Bornet (1880 pl. 45) described the first stages of the development of forma *wittrockii*, and Gayral (1965 pl. 2) illustrated later stages. The concordant results of these investigations — coupled with the investigation of var. *orbiculata* described above — show that the species *oxysperma* with regard to its ontogeny completely follows the *Ulvaceae*-pattern: the germling is at first an unbranched thread, which, by the longitudinal splitting of the cells and their arrangement round a central cavity forms a tubular germling. In the same way as in *Ulvaria obscura* var. *blyttii* the germling later becomes more or less sack-shaped in the upper part, opens at the top and grows into a monostromatic thallus.

On account of these facts *oxyspermum* is transferred here to fam. *Ulvaceae* and the genus *Ulvaria* Ruprecht, preliminarily proposed earlier by Bliding (1960 p. 172). The circumstance that *oxysperma* lacks alternation of generations is no objection to placing the species in the same genus as *Ulvaria obscura*. The other genera of *Ulvaceae* (*Entero-*

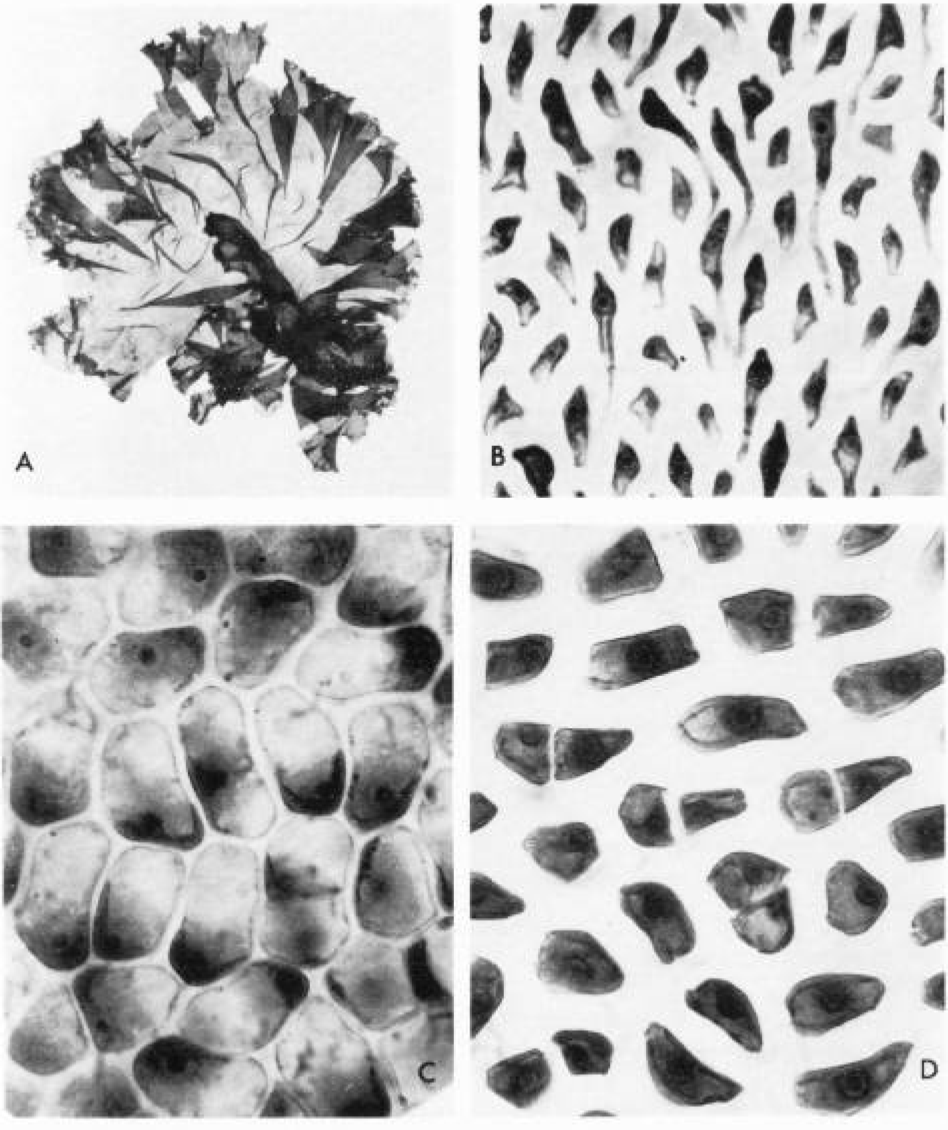


Fig. 35. *Ulvaria oxysperma* var. *orbiculata*. A: ×0.7. B: rhizoidal zone ×330. C—D: explanation in text ×660.

morpha and *Ulva*) include sexual species with alternation of generations as well as asexual ones without such alternation. *Ulvaria obscura* and *oxysperma* differ in other respects, too, e.g. in colour and number of pyrenoids, but it does not seem necessary to introduce a new genus for the forms of *oxysperma*, which have the same characteristic development from swarmer into fully-grown plant as *Ulvaria obscura* var. *blyttii*, described above.

The type specimen of *Ulva oxysperma* KÜTZING from the Baltic Sea, Schlei bei Winning (KÜTZING 1843 p. 296), is preserved in Herb. Lugd. Bat. as No. 938.53. .82 a.

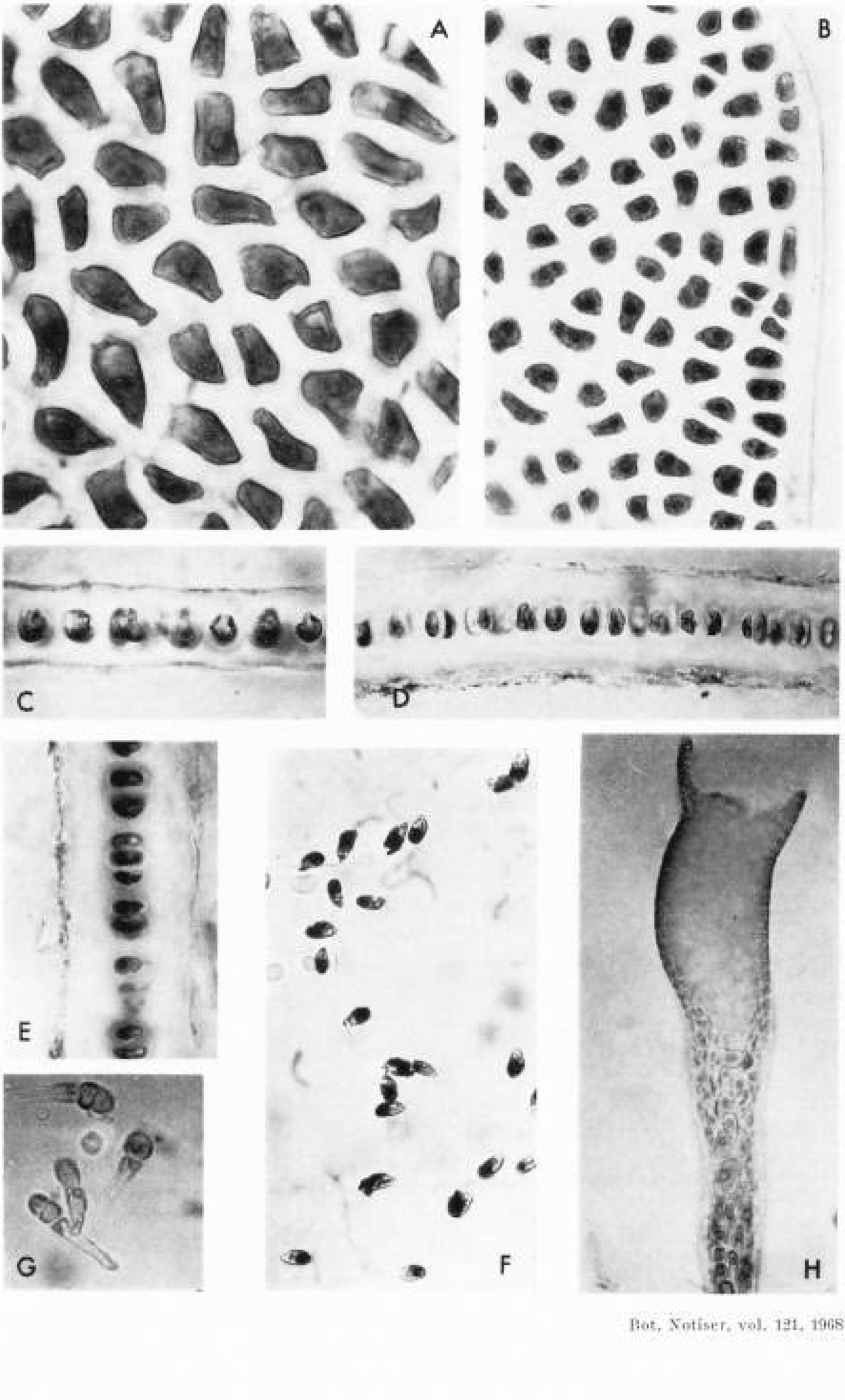
KÜTZING (1843 p. 296) incorrectly used the name *Ulva latissima* LINNAEUS (=*Laminaria saccharina*; SILVA 1952 p. 296; PAPENFUSS 1960 p. 303) for an alga from the Baltic Sea, Flensburg, collected by FRÖHLICH (in Herb. Lugd. Bat. No. 938.53. .109). This has appeared to be *Ulva curvata* (KÜTZING) DE-TONI. However, another specimen in KÜTZING's herbarium (No. 938.53. .63), from another locality, labelled "4. *Ulva latissima*" in KÜTZING's hand, is clearly *Ulvaria oxysperma*.

Monostroma latissimum (KÜTZING) WITTROCK 1866 p. 33 is based upon tab. 20, fig. 4 in KÜTZING 1843, upon KÜTZING 1849 p. 474, and tab. 14 fig. a—e in KÜTZING 1856, but with the addition (WITTROCK 1866 p. 34): non Linné nec alii auctores (translated from the Swedish text). Therefore this species ought to be listed *Monostroma latissimum* WITTROCK, and from the diagnose (WITTROCK op. cit. p. 33), the fig. 4 a—f and No. 145 in Exsicc. WITTR. and NORDST. it is evident that the species is a synonym for *Ulva oxysperma* KÜTZING=*Ulvaria oxysperma* var. *oxysperma*.

"*Monostroma latissimum* (KG) WITTR." sensu CARTER 1926 is a misapplication (disclosed by its development), certainly of *M. grevillei*. Also "*Monostroma latissimum* WITTROCK?" sensu SEGI and GOTO 1956 and *M. latissimum* (KÜTZING) WITTROCK sensu HIROSE et YOSHIDA 1964 seem to have nothing to do with *Ulvaria oxysperma*.

The type of *Ulva quaternaria* KÜTZING 1856 Tab. phyc. VI, pl. 13, 2, preserved in Herb. Lugd. Bat. as No. 938.53. .82 b has the annotation "Eau douce près de la mer, Calvados", and the label: "*3. Ulva (oxysperma) oxycocca β quaternaria*, Calvados" in KÜTZING's hand. It has angular cells in groups and rows (Fig. 33) and conforms to *Ulvaria oxysperma* var. *oxysperma*.

Fig. 36. *Ulvaria oxysperma* var. *orbiculata*. A: explanation in text. B: upper part, margin. C—E: sections. F: zoosporoids. G: young germlings. H: tubulous germling. A, B, F ×660, C, D, E, G ×330, H ×130.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FAM. MONOSTROMATACEAE Kunieda ex Suneson

Genus Monostroma Thuret 1854

Species lectotypica: *Monostroma bullosum* (Roth) Thuret.

1. Monostroma bullosum (Roth) Thuret

Ulva bullosa Roth 1806 p. 329. — *Monostroma bullosum* (Roth) Thuret 1854 a p. 29; Kornmann 1964 p. 13.

The investigated material of this fresh-water alga was collected in the river Saxån, Scania, during the months of March—May. It grows on grass and other phanerogams in small specimens, about 2—3 cm in length and breadth.

ANATOMY. The cells in the monostromatic thallus often lie 2—3—4 together, the cell-groups being more or less widely separated by a gelatinous wall-substance. The adult cells are, in surface view, round—semicircular with the larger dimension about 12 μ (Fig. 37 A), and, at least in the upper part, arranged in rows. The cell lumen has a height of 12 μ and the thickness of thallus is at most 18 μ (Fig. 37 B). The cells have one pyrenoid, rarely two, centrally at the outer wall.

REPRODUCTION. The plant described is the gametophyte generation of the species forming 2-flagellate swarmers (Fig. 37 C, D) with isogamous fertilization. Measurements of +- and —-gametes in two copulating plants averaged 5.2×3.8 μ in +-gametes and 5.7×3.5 μ in —-gametes. Isogamy is also evident from the fact that the germinating copulating pairs (Fig. 37 E) have two pyrenoids of the same size (in anisogamy ♂-gametes have a smaller pyrenoid than ♀-gametes). The copulating pairs do not become negatively phototactic at once but can move about for many hours before settling down to germinate. Both +-gametes and —-gametes can germinate without fertilization. During the subsequent development of zygotes and gametes (Fig. 37) they remain one-celled and are enclosed by a thick cell-wall. The main part of the cell becomes ball-shaped and grows very rapidly. The young zygotes in Fig. 37 H (21/5—30/5 1961) already have a diameter of about 25 μ and have 7—8 pyrenoids; after 6 weeks the cell contents have begun to be divided, resulting in the formation of zoospores, 4-flagellate, about 10.5×6.0 μ (Fig. 37 I—J). The fully-developed zoosporangia vary in size between 30 and 60 μ.

The zoospore germinates at once and its development into a gametophyte plant can be followed in Figs. 37 K—38 G. The young 3—4-celled

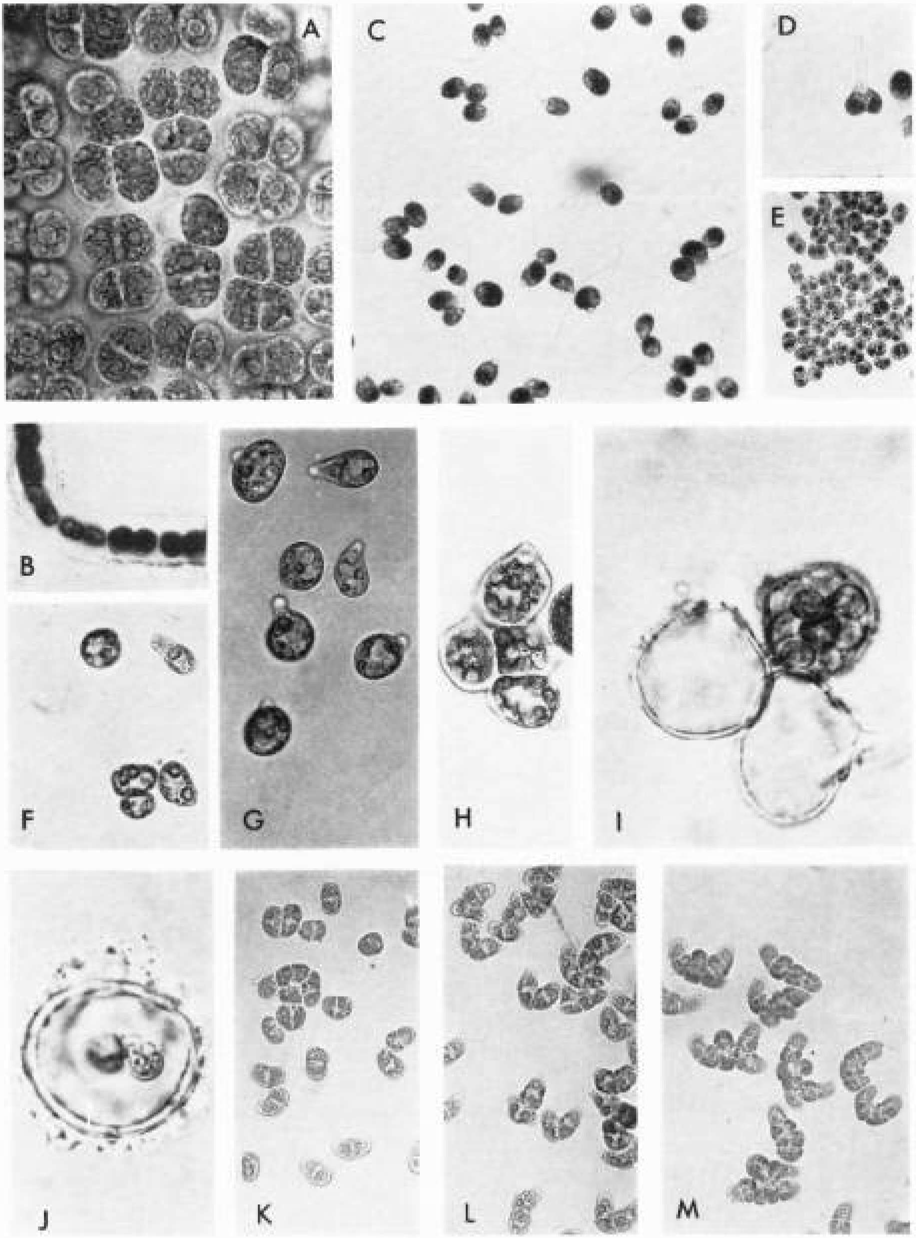


Fig. 37. *Monostroma bullosum.* A: upper part, near the margin. B: section through the thallus. C: gametes. D: copulation pair. E: germinating zygotes. F—H: zygotes, 4, 6 and 9 days old. I: one sporangium with mature zoospores, two emptied. J: sporangium with two zoospores left. K—M: germlings, derived from zoospores, the oldest 4 days. A, C, D, I, J ×660, B, E—H, K—M ×330.

germling (Fig. 37 M) forms side-branches and grows into a horizontal disc (Fig. 38 A—D, cf. *Blidingia minima*; BLIDING 1963 Fig. 7).

In the middle of the disc, during horizontal cell-divisions, a region of cells rich in nourishment is formed (Fig. 38 C—D), which by continued divisions form the sack-shaped gametophyte (Fig. 38 E—G). The latter opens completely so as to form a monostromatic gametophyte plant, anchored to its prostrate disc and without rhizoidal cells.

Horizontal cell-divisions quite often take place in a prostrate disc consisting of very few cells (Fig. 38 B). In extreme cases (Fig. 38 H) the new gametophyte has a great resemblance to the first stages of the development of *Blidingia marginata* (BLIDING 1963 Fig. 13 c—d).

Young, few-celled gametophytes often form accessory swarmers, two in each cell, which are liberated simultaneously (Fig. 38 I—J). They are 4-flagellate with stigma and pyrenoid, negatively phototactic and germinate into new gametophyte-discs.

KORNMANN (1964 p. 17) considers that the gametophyte plant in *bullosum* is monoecious. I can confirm that cultures (particularly when standing a long time), can have plants giving both +- and −-gametes. The following observations, however, seem to make it probable that *M. bullosum*, like its close relative *M. grevillei*, is dioecious with determination of sex at the formation of zoospores:

1. Fig. 38 K is a photo from a culture of zoospores, only three days old (12/11—15/11 1961). The small 2—3-celled discs are division products of one zoospore each. The large disc consisting of some forty well-developed cells is the result of many zoospores germinating near each other and growing together into one tissue. In cultures the accessory swarmers from different, young discs form similar mixed gametophytes in the same way.

2. Fig. 38 L shows one instance when the zoospores have remained in their sporangium and germinated into one gametophyte which has advanced far in its development (cf. Fig. 38 B).

Even in nature it must be possible for swarms of negatively phototactic reproductive bodies — zoospores and accessory swarmers — from thickly growing individuals of *Monostroma* to give birth to androgynous gametophytes. In this way we can also explain KORNMANN's observation (1962 b p. 305) that out of the investigated plants of *Monostroma grevillei* 2 % were monoecious. Then KORNMANN's statement does not really contradict the earlier conception, e.g. SUNESON's (1947 p. 245), that *M. grevillei* is "strictly dioecious".

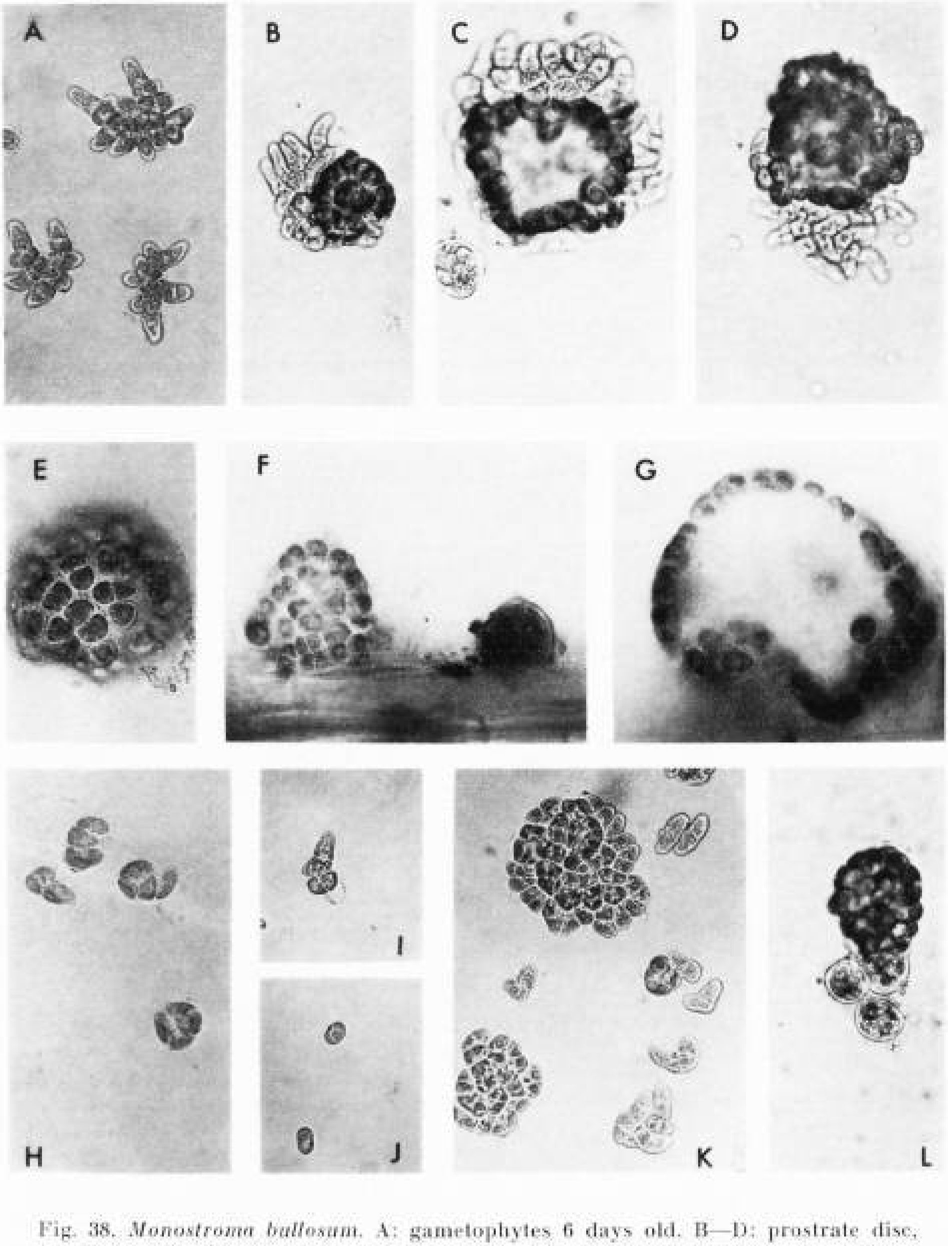


Fig. 38. *Monostroma bullosum*. A: gametophytes 6 days old. B—D: prostrate disc, developing the gametophyte sack. E: young sack-shaped gametophyte. F: gametophyte sack and sporangium in situ. G: sack with great cavity. H: explan. in text. I: two accessory swarmers leaving their mother cell. J: accessory swarmers, just settled. K—L: explan. in text. A, D, L ×260, B, C, E—K ×330.

LIVING MATERIAL from: Sweden: Scania, the River Saxån, Västra Strö and Reslöv Church, found by Dr. ÅKE BLIDING in May 1961.

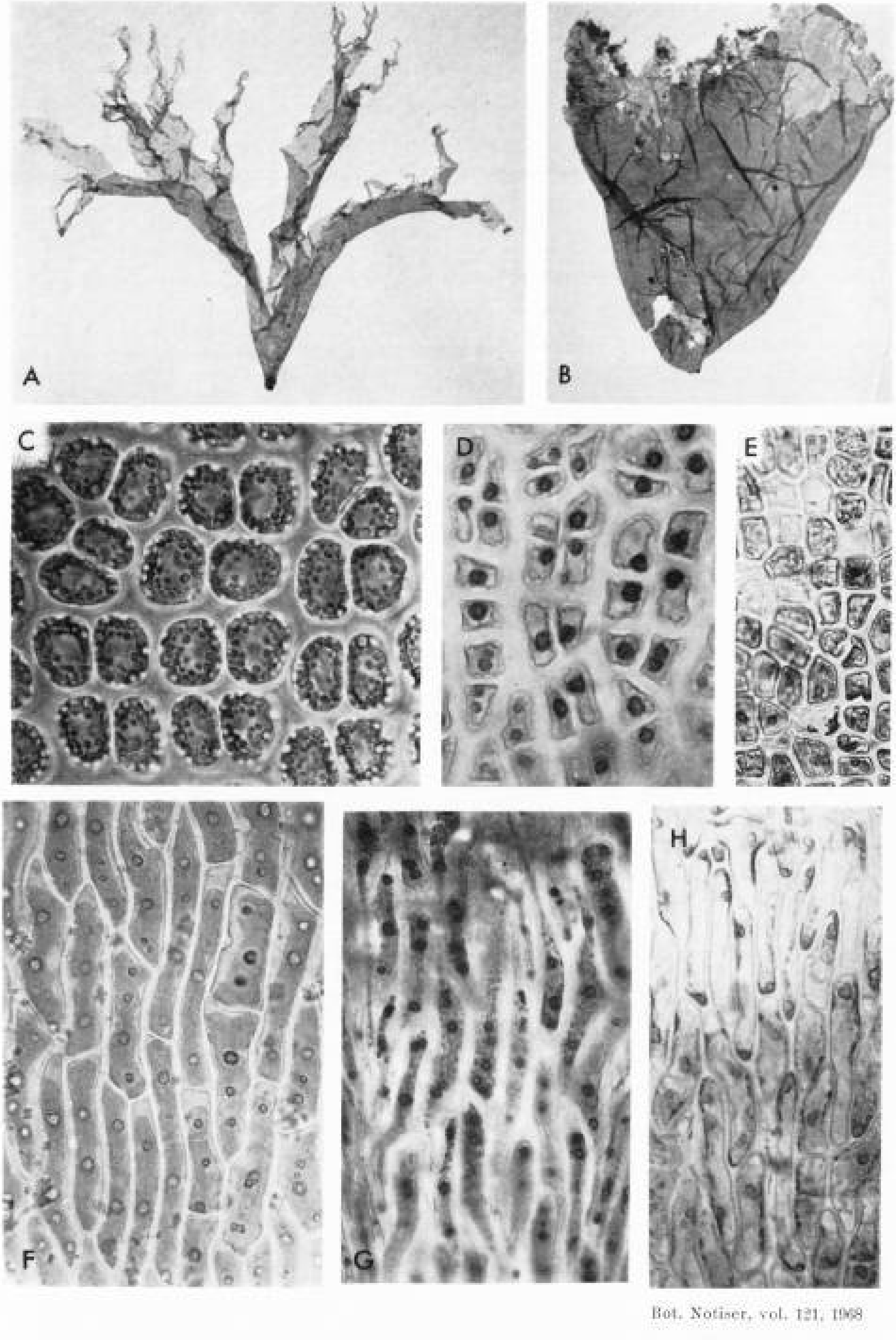
TAXONOMY. *Monostroma* THURET is based upon *Ulva bullosa* ROTH and *Ulva oxycocca* KÜTZING (=*oxysperma* KÜTZING). When the genus was lectotypified with the latter species as type (PAPENFUSS 1960 p. 315), the life history of *bullosum* was not known. MOEWUS had described (1938) under the wrong name *Monostroma wittrockii* an alga with the same life history as *M. grevillei*.

KORNMANN (1964) stated that THURET's both species of *Monostroma* must be considered members of different genera and proposed *M. bullosum* as lectotype. My investigations (1935 and above) give reasons for complete agreement to KORNMANN's proposal. Already THURET's diagnose of the genus (1854 p. 29) indicates that *M. bullosum* is the principal species of the new genus: "Frons plana aut saccata . . . Cellulae subrotundae (saepius quaternatae) in membrana homogenea nidulantes . . .". All of this is well applicable to *bullosum* (Fig. 37 A) but not to *oxyspermum* with its polygonal, angular cells (Figs. 31—36).

The lectotypification of *Monostroma* THURET with *oxyspermum* as type species would mean that the valid name *Monostromataceae* KUNIEDA ex SUNESON 1947 (PAPENFUSS 1960 p. 315) would be out of use and had to be replaced by a new family name, further that the taxa *bullosum*, *grevillei*, *arcticum* and others would have to be transferred to a new genus (*Ulvopsis* is proposed by GAYRAL 1964 and 1965) with many subsequent re-combinations, not yet (1967) made. More important is, however, the fact that *oxyspermum* on basis of its morphology and ontogeny must be transferred to the family *Ulvaceae* and to genus *Ulvaria* — an older name than *Monostroma* —, while *bullosum* has the same ontogeny and life history as *Monostroma grevillei* under *Monostromataceae*.

The family *Monostromataceae* GAYRAL 1965 is a later homonym to *Monostromataceae* KUNIEDA ex SUNESON and illegitimate.

Fig. 39. *Monostroma grevillei*. A: Kristineberg ×0.96. B: Varberg ×0.95. C: Tromsö, upper part. D: Varberg, middle part. E: Kullaberg, emptied gametangia. F: Saltholmen, the base. G: Roscoff, the base; cells tapering upwards or downwards. H: Tromsö, base. C—D ×660, E—G ×330, H ×260.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2. Monostroma grevillei (Thuret) Wittrock

Enteromorpha grevillei Thuret 1854 a p. 25. — *Monostroma grevillei* (Thuret) Wittrock 1866 p. 57; Suneson 1947 p. 235; Kornmann 1962 p. 195. — *Ulvopsis grevillei* (Thuret) Gayral 1964 p. 2151.
"*Ulva lactuca* Linn." sensu C. Agardh 1817 p. 41 et Kützing 1843 p. 296.
"*Monostroma latissimum* (Kützing) Wittrock" sensu Carter 1926 p. 616.

Like the previous species, *Monostroma grevillei* begins its macroscopic stage as a sack-shaped plant, but it remains at this *Enteromorpha*-like stage much longer than *M. bullosum*, and by way of exception the sack does not open until fertility begins, when the plant can be over 10 cm high.

The outer shape of the species varies within wide limits. When living as an epiphyte on other algae in a moderately exposed position, it often only becomes 1—2 cm high, but in water rich in nourishment, e.g. in harbours and quiet bays, the thin thallus may grow into enormous loose-lying floats. On the Swedish West Coast the species is fertile from the end of February to the beginning of June.

ANATOMY. In the very young plant (in Fig. 41 F—G about 0.5 mm high) the cells of the sack have a uniform appearance (about 17×11 μ long, in surface view), with the cells at the base only slightly longer. Later, however, a differentiation of the cells in different parts of thallus takes place. In the upper part of the plant the cells lie fairly well arranged in groups and rows, separated by gelatinous substance whose broad courses come out in the microscope as a network (Fig. 39 C—D). The adult cells are almost round in surface view, 16—18 μ in diameter. The parietal chromatophore usually reaches even the lower cell wall and mostly has 1 pyrenoid, nearest the upper cell wall.

In the central and lower parts of the plant (Fig. 39 D, F—H) the cells are mostly four-sided (quadrangular 16×16 μ, rectangular 20×16 μ) or slightly polygonal, 24×16 μ. Near the base the cells often have several pyrenoids and become much longer (up to 100 μ, Fig. 39 F—H), with their ends, tapering upwards or downwards, or in both directions, wedged in between each other. *Monostroma* lacks the typical zone of poly-nuclear club-shaped rhizoidal cells with solely downwards point-

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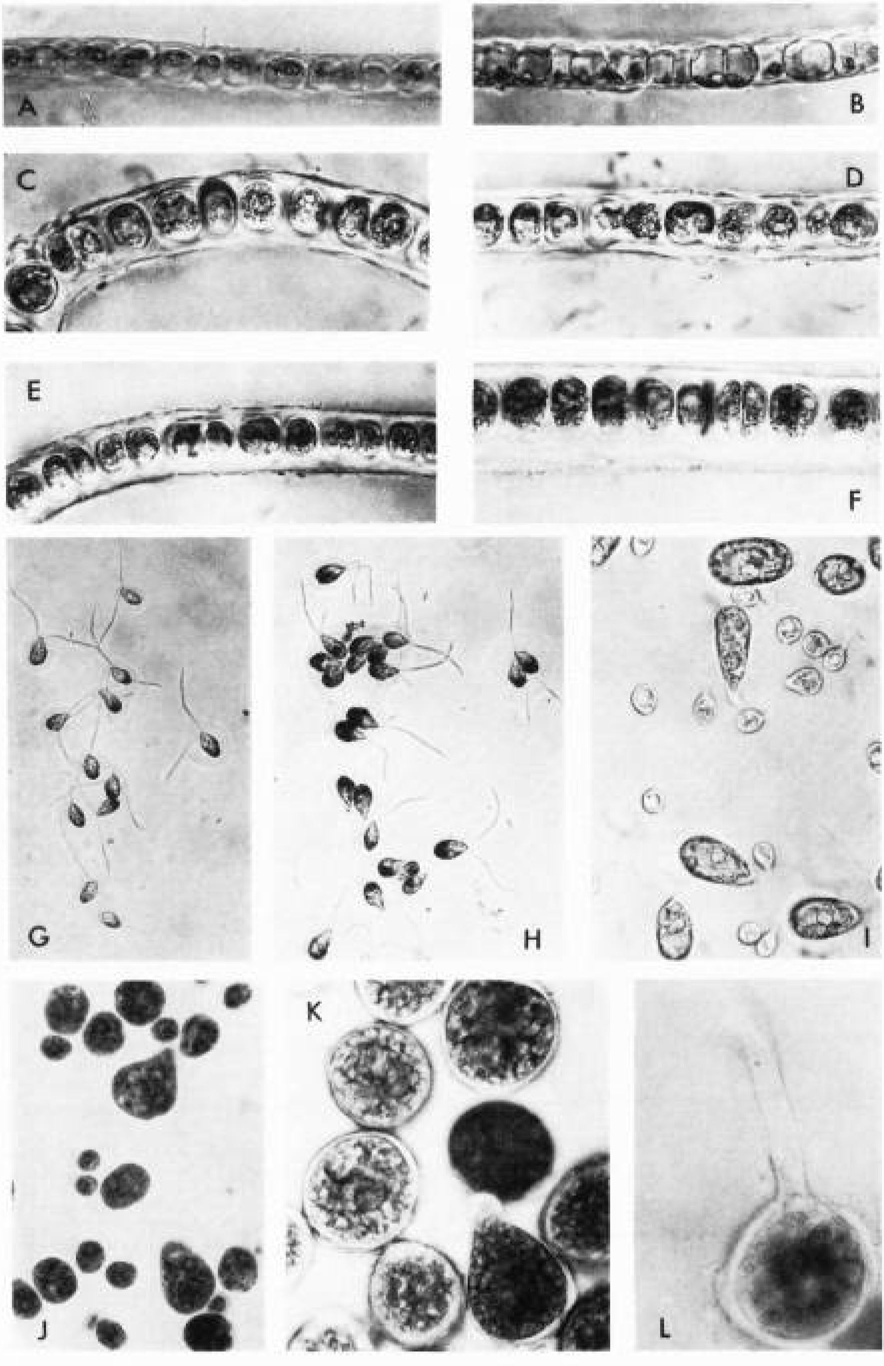
Fig. 40. *Monostroma grevillei*. A—B: Saltholmen, section through the base. C—D: Kristineberg; base and upper part. E—F: Tromsö; plant base. G—H: Tromsö, ♂- and ♀-gametes. I—K: Tromsö, zygotes and surplus gametes, 9, 11 and 30 days. L: Varberg, mature sporangium with zoospores. A—F, I—L ×330, G—H ×660.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ing, thread-like elongations that are found in *Enteromorpha*, *Ulva* and *Ulvaria* (Figs. 4 F and 28 C).

The thickness of thallus varies considerably. In the material from a harbour (Saltholmen) on the Swedish West Coast the thallus was about 18 μ at the base, out of which the height of cell lumen was 12 μ (Fig. 40 A—B), but in an exposed locality near the Biological Station at Kristineberg the corresponding measurements were 28 and 19 μ respectively at the base, and 25 and 17 μ respectively in the upper part (Fig. 40 C—D).

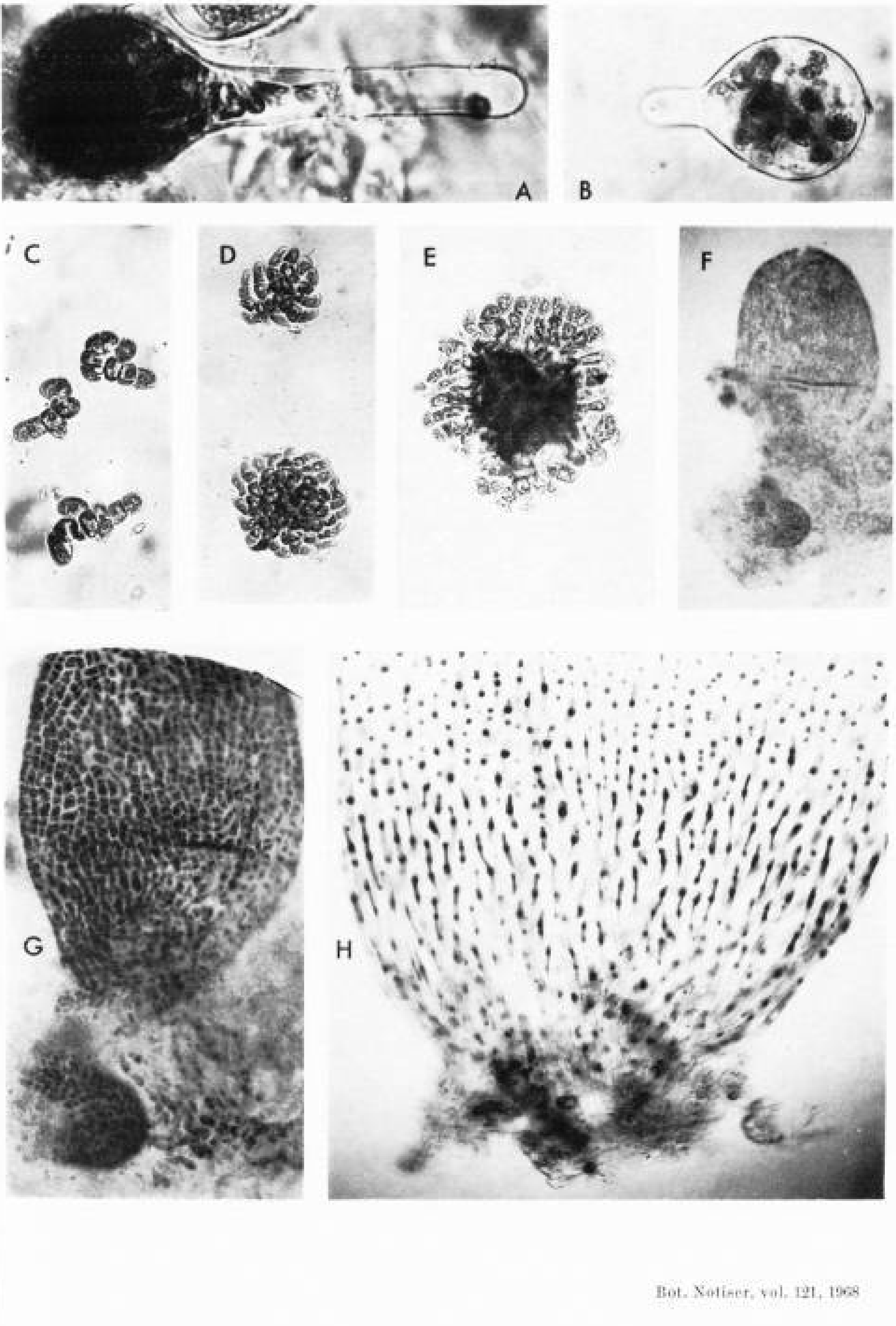
The material from northern Norway showed still greater variation and, in general, higher values. While a population from Tromsö Biological Station had a thickness at the base of about 25 μ (Fig. 40 E), material from more exposed localities had a thallus 33—40 μ thick and the cell lumen was 21—25 μ high (Fig. 40 F). It is notable that the two above-mentioned populations from the Swedish West Coast copulated with each other, forming groups, and gave rise to developable zygotes, and that this also applies to the material from northernmost Norway.

REPRODUCTION AND DEVELOPMENT. *Monostroma grevillei* is, like *bullosum*, a diplohaplont with heteromorphic generations. The gametophyte plants are dioecious and anisogamous. The size of gametes in the populations from northern Norway was slightly smaller than in populations from the south of Sweden. Male gametes (Fig. 40 G) are 5.1—6.0×2.1—3.0 μ, averaging 5.6×2.7 μ; female gametes 6.1—7.3×2.4—4.5 μ, averaging 6.7×3.8 μ. The majority of the newly-swarmed gametes are distinctly positively phototactic, copulating pairs are negatively phototactic.

Kornmann (1962 b p. 198) showed by experiments in culture that the zygotes are facultatively lime-boring and can pass their sporophyte-stage in shells in the same way as the genus *Gomontia* (Kornmann 1962 a p. 38).

The development of the sporophyte in culture on a microscope slide (Fig. 40 I—L, 41 A—B) is the same as in *M. bullosum*. Sporangia,

Fig. 41. *Monostroma grevillei*. A: Tromsö, zoospores, ready to leave the sporangium. B: Tromsö, sporangium derived from a male gamete. C—D: young gametophytes derived from zoospores. E: prostrate disc, developing the gametophyte sack. F: prostrate disc with two sack-shaped plants. G: enlargement of F, cells of the sack undifferentiated. H: Varberg, base of an older plant, cells tapering upwards and downwards. A—B ×660, C, E ×330, D ×260, G—H ×130, F ×65.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deriving from zygotes were mature after about 2 months and had the size of 40—60 μ in diameter with a tube about 65 μ long. Its numerous 4-flagellate zoospores average 10,3×4,6 μ (Fig. 41 A).

Sporangia developing from ♂- or ♀-gametes (Fig. 41 B) matured earlier (in about 7 weeks) and were a little smaller but had spores of about the same size. KORNMANN (1962 b p. 200) found that all such spores from a parthenogenetical sporangium gives gametophytes of the same sex, that of the mother-gamete. KORNMANN interprets it is a case parallel to FÖYN's observation (1934 b), verified cytologically, that in *Cladophora suhriana* a gamete can germinate parthenogenetically, become diploid and develop into a zoospore-plant whose spores give gametophytes of the same sex.

At low temperature, about 4—9° C, the zoospore in *M. grevillei* goes through the same stages in its development into a gametophyte-plant (Fig. 41 C—H) as in *M. bullosum*: the zoospore forms a horizontal, one-layered prostrate disc; when the disc is 30—50-celled, horizontal divisions start in its centre, and from there one or several erect, sack-shaped gametophyte plants upheave (Fig. 41 F).

In cultures of young gametophytes at higher temperatures (12—18° C) big elevations were formed on the basal disc, which were up to 1 mm in cross-section, and the disc could live for years without forming normal gametophyte plants.

LIVING MATERIAL from: Sweden, the West Coast in many places, e.g. Kullaberg, Varberg, Saltholmen, Kristineberg. Norway, Tromsö, July—August 1966. France, Roscoff, April and May 1964.

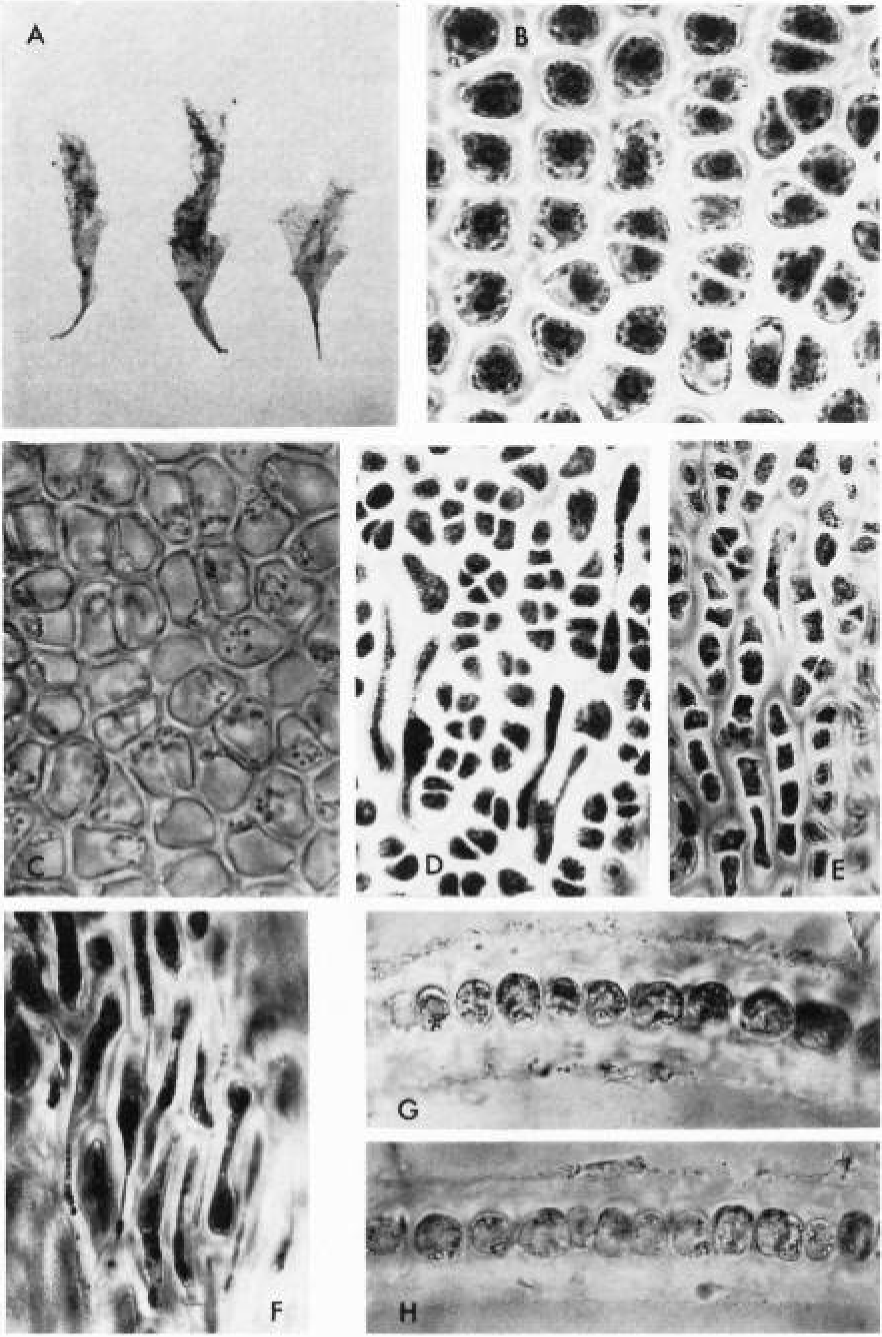
3. Monostroma arcticum WITTROCK

Monostroma arcticum WITTROCK 1866 p. 44; KJELLMAN 1883 p. 299; KORNMANN et SAHLING 1962 p. 305; JAASUND 1965 p. 20. — *Monostroma grevillei* var. *arcticum* (WITTROCK) ROSENVINGE 1893 p. 949.

Monostroma grevillei (THURET) WITTROCK sensu VINOGRADOVA 1967 b p. 129.

The material of *Monostroma arcticum* was collected on the skerry of Musvaer, north-west of Tromsö, in July 1966 and on the Swedish West Coast, Saltholmen, vicinity of Gothenburg, in March and April 1966 and 1967. At the first-mentioned, strongly exposed locality it grew on

Fig. 42. *Monostroma arcticum*, Musvaer. A: ×0,94. B: upper part. C: middle part. D—F: the base, explanation in text. G—H: sections, base and middle part. B—C ×660, D—H ×330.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rocks, supralittorally in the splash-zone, but in the Swedish habitat littorally and sublittorally in well-sheltered positions together with *M. grevillei* and *Ulvaria obscura* var. *blyttii*.

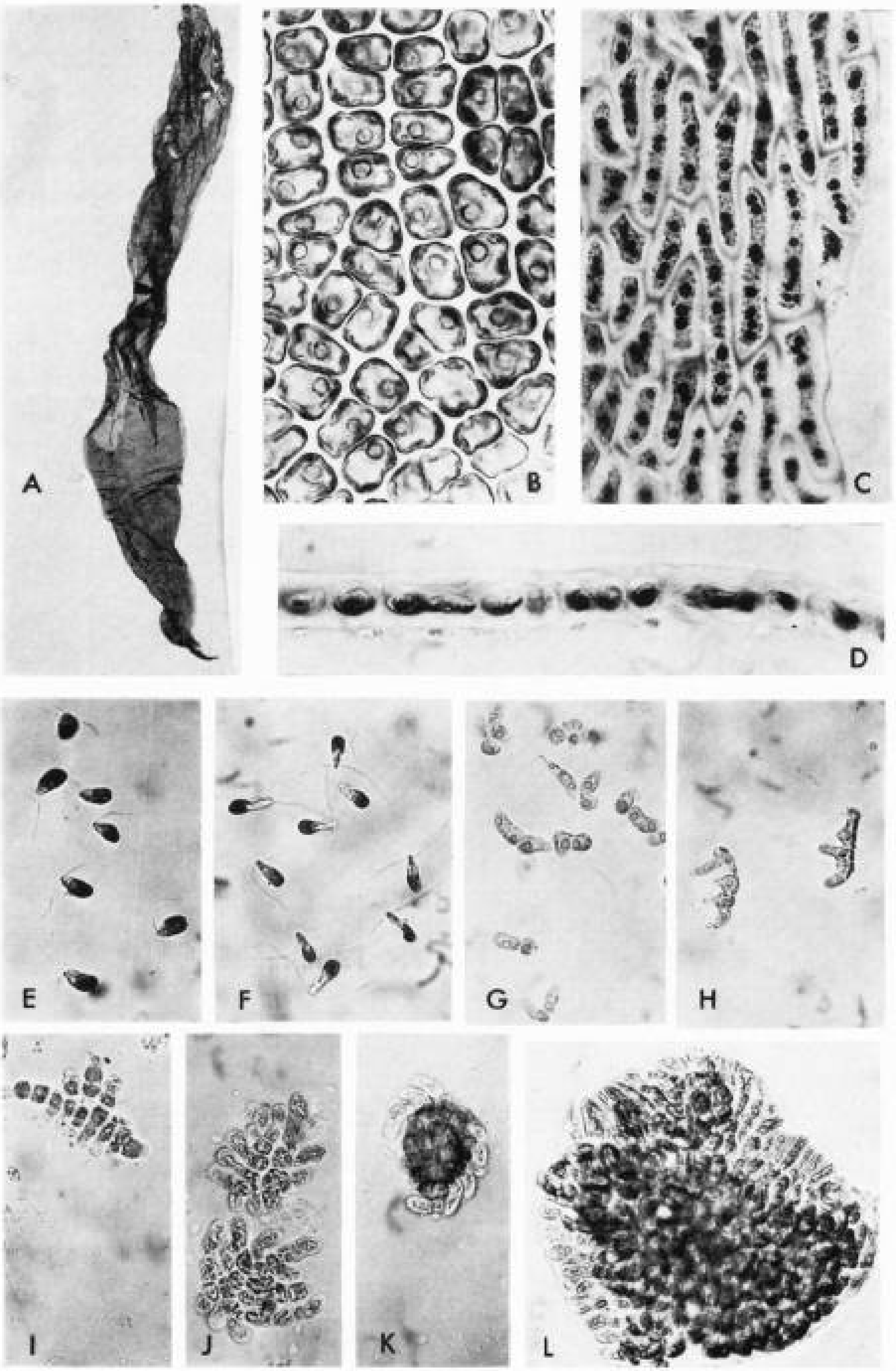
ANATOMY. Lowest down at the base (Fig. 42 F) the material from Northern Norway has a zone, only 2—5 mm high, of narrow cells, often more than 100 μ long, with, generally, one pyrenoid and thick walls, wedged in between each other. Only the elongations of the lowest cells reach down to substratum (cf. rhizoidal cells). Immediately above there is a small region (Fig. 42 D—E), where most of the long cells have been divided into a number of small cells, enclosed by the common mother-wall. The shape of the cells in the two basal zones mentioned above seems to constitute a distinctive anatomic feature separating the arctic type of *M. arcticum* from *M. grevillei*.

In the middle of the plant the cells mostly lie unordered (Fig. 42 C), they are about 16 × 11 μ and 4—6-angular. In the topmost part, especially in the fertile region, the cells are arranged in rows, rounded in shape, and 15—17 μ in diameter (Fig. 42 B).

The thickness of thallus varies between about 48 μ in the central part of the plant (Fig. 41 H) and about 60 μ at the base with the height of cell lumen about 22 μ. JAASUND (1965) investigated a comprehensive material of *Monostroma* species from northern Norway and gives the measures (40—) 50—75 μ for the thickness of thallus in *arcticum*, and points out that the cell wall is distinctly layered, which has not been observed in other species (cf. Fig. 42 G).

My material of *arcticum* from the Swedish coast only consists of 6 specimens. Habitually and morphologically it agrees almost completely with *grevillei* from the same locality. The cells in the upper part of the plant are regularly arranged, in the topmost part about 15 × 10 μ (Fig. 43 B), at the base there are longish cells, wedge-shaped at both ends, with up to 10 pyrenoids (Fig. 43 C). The thickness of thallus at the base is about 22 μ (Fig. 43 D), which is only slightly more than in *grevillei* from the same locality.

Fig. 43. *Monostroma arcticum*. A: Saltholmen × 0.7. B: Saltholmen; upper part. C: Saltholmen; the base. D: Saltholmen; section, base. E: Musvaer, neutral swarmers. F: Saltholmen. G—H Saltholmen, development of the prostrate disc. I: Musvaer. J—K: Saltholmen. L: Musvaer, prostrate disc with long terminal cells (cf. Fig. 41 E). B—C, E—F × 660, D, G—J, L × 330, K × 260.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REPRODUCTION AND DEVELOPMENT. On material from Heligoland KORNMANN and SAHLING (1962 p. 305) established that *arcticum* lacks alternation of generations and has 2-flagellate neutral swarmers as sole kind of motile reproductive bodies. As WITTROCK described *M. arcticum* on material from northern Norway (1866 p. 44), it has been of interest to investigate its development also on material from the region of the type. It has become evident that *arcticum* from northernmost Norway has the same pattern of development as *arcticum* from Heligoland and from the Swedish West Coast.

In specimens from northern Norway the swarmers had an average size of 6.9×3.6 μ (Fig. 43 E), and in specimens from the Swedish coast 8.0×2.9 μ (Fig. 43 F). They are formed to the number of about 16 in a middle-sized mother-cell and leave the sporangium by a round opening in one of the outer walls. Experiments to copulate swarmers from different *arcticum*-plants with each other had a negative result, nor did swarmers of *arcticum* copulate with male or female gametes of *grevillei*. Consequently they are neutral swarmers of the type of zoosporoids, or possibly — since they are 2-flagellate of small size — gametes which have totally lost their sexuality. In the fertile material from Musvaer all the swarmers were very strongly negatively phototactic as well as in 2 specimens from Saltholmen, but the other specimens from the latter locality had swarmers which were at first positively phototactic.

In the same way as the zoospores in *M. bullosum* and *grevillei* the neutral swarmers in *M. arcticum* develop into a horizontal prostrate disc (Fig. 43 G—L). Its peripheric end-cells are in *arcticum* longer in proportion to their breadth than in *grevillei* (compare Fig. 43 L with Fig. 41 E). From the rapidly growing basal disc sack-shaped elevations rise, which constitute the early stage of the one-layered plant, leaf-like in its upper part (Fig. 43 L, KORNMANN and SAHLING 1962, Fig. 4).

Kornmannia Bliding genus novum

Planta laminae similis, monostromatica, stipes aut nullus aut cavus; cellulae parvae, lamina pertenuis; cellulae rhizoidales desunt. Pyrenoides aut parvi aut qui demonstrari non possint.

Corpuscula propagationis asexualis minima, circ. 4.5×4.0 μ, 4-flagellata, sine stigmate et sine pyrenoide, ad laminam prostratam germinantia.

Species typica: *Kornmannia leptoderma* (KJELLMAN) BLIDING.

Type habitat: Novaya Zemlya, Matotshin Shar.

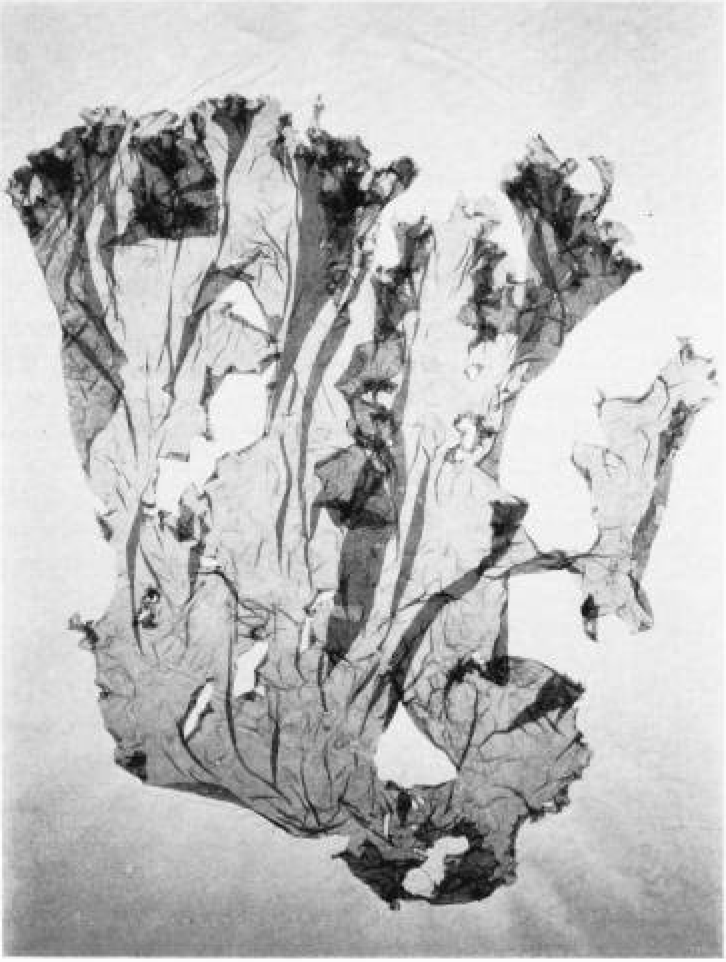


Fig. 44. *Kornmannia leptoderma*. Tromsö, Juledagsskär ×0.5.

1. Kornmannia leptoderma (KJELLMAN) BLIDING comb. nov.

Monostroma leptodermum KJELLMAN 1877 p. 52; KORNMANN et SAHLING 1962 p. 312; VINOGRADOVA 1967 b p. 125.

Monostroma tenue SIMMONS 1898 p. 119.

Living material of this species was collected in a bay at Juledagsskär in Tromsö, Northern Norway. All the specimens lay loose, laid bare at low water, growing in large floats (Fig. 44 is a part of a big specimen). The disc was light-green, very thin with large perforations, lobate and at the margin uneven and undulating.

ANATOMY. The most remarkable fact about the cell structure of the species is that (at an enlargement of ca. ×700) pyrenoids cannot be detected, either in living cells or in cells treated with iodine.

In the outer parts of the plant the cells are well arranged in rows radiating towards the margin (Fig. 45 A—B), more centrally the arrangement in rows is often less conspicuous (Fig. 45 C).

In surface view cells are relatively small, only exceptionally do maximum dimensions exceed 9 μ. Grown-up cells are 6.4—9.1×4.7—6.8 μ, averaging 7.8×5.6 μ. Cross-sections (Fig. 45 D) show that cell lumen has a height of about 8 μ. Since the cell-walls and the disc margin are very thin, the thickness of the whole thallus is about 12 μ at most.

Attached specimens have a mostly well-developed, hollow stipe with longer cells (ROSENVINGE 1893 Fig. 49; KORNMANN and SAHLING 1962 Fig. 10; VINOGRADOVA 1967 b Fig. 4).

REPRODUCTION. Loose-lying forms of marine green algae with markedly vegetative multiplication have often, partly or completely, lost their capacity for forming swarmers. My basic material of the alga had feeble fertility in culture, but a small number of swarmers could be gathered up on microscope slides, immersed in the culture vessels. The swarmer grows into a bent cell without pyrenoids (Fig. 45 F—G). The product of its division, the 2-celled germling, is curved more or less like a bow. Repeated divisions gradually give rise to a disc, consisting of small cells, densely packed in the middle, sending out radial rows of somewhat longer cells (end cells bent, about 15×3.5 μ, Fig. 45 H—I). All the cells of the horizontal disc lack demonstrable pyrenoids.

In the centre of prostrate discs, about one month old, groups of dark-green cells are detached by horizontal walls (Fig. 46 A—C). In surface view these cells may be arranged in a closed ring (Fig. 46 C) giving rise to the erect plant with a monostromatic lamina and a tubular lower part. Often, however, the cells developing into the erect plant are arranged in an open ring (like a horse shoe in Fig. 46 B at the top). In such cases the result is a monostromatic plant with a very short hollow stipe (Fig. 46 E).

The cell structure of plants grown up in culture fully agreed with that of the basic material and with KJELLMAN's type specimen.

In cultures (temp. 5—9° C) plants only one cm high were richly fertile. Fertility often started inside the margin of the disc, as in *Ulvaria obscura* var. *blyttii*, and, in conformity with this species, swarmers leave their mother-cells by a round opening, centrally in one of the

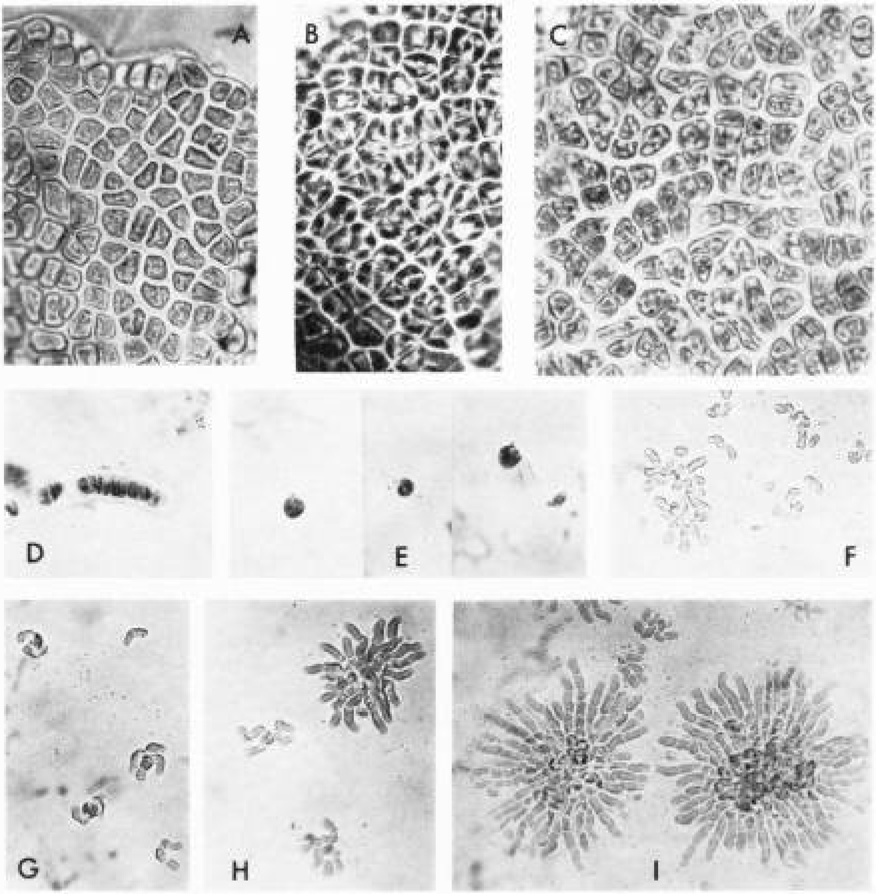


Fig. 45. *Kornmannia leptoderma*. A: upper part, margin. B: preserved by iodine. C: central part. D: cross-section. E: zoosporoids. F—I: the swarmers form the prostrate disc. A—C, E ×660, D, F—H ×330, I ×260.

outer walls, the walls of the empty cells remaining for a long time. Each mother-cell generates 4—8 small swarmers (Fig. 45 E) with protruding front, without stigma and without pyrenoids, 3.8—4.7×3.5—4.6 µ, averaging 4.4×4.1 µ. These neutral swarmers are confusingly like the neutral swarmers in the genus *Blidingia* (Bliding 1963 Fig. 7 f).

The ontogenetic development in *leptoderma* has a great resemblance to the development in the genus *Blidingia* (Addenda Fig. 47 and Bliding 1963 p. 23). They both have asexual swarmers of the same characteristic type, which germinate into a horizontal disc from which new plants

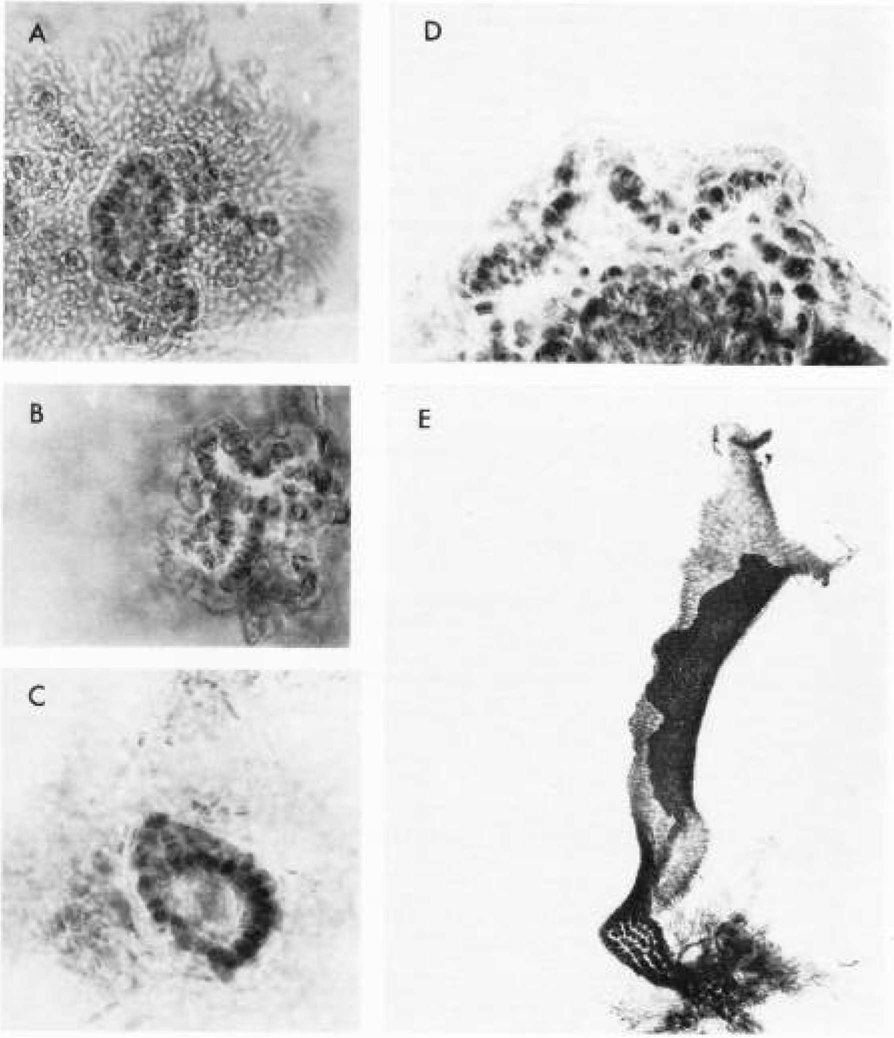


Fig. 46. *Kornmannia leptoderma*. A—C: disc from above with developing new plants, explanation in text. D: section through a prostrate disc with three plants in development. E: plant 0.6 mm high with its prostrate disc. A—D ×330, E ×130.

rise. But whereas the fully-developed *Blidingia* plant is tubular and *Enteromorpha*-like, *K. leptoderma* quite early a leaflike monostromatic thallus, which, however, has a tubular stipe. A cytological peculiarity in *leptoderma* is the absence of clearly differentiated pyrenoids in reproductive as well as in vegetative cells. On account of its anatomy and life history *leptoderma* ought to be separated from *Monostroma* and transferred to a new genus, which we propose to be named *Kornmannia* after Dr. P. KORNMANN, Heligoland, who in several works of great value described the development of many species within *Monostroma* sensu WITTROCK, including the present species.

Addenda to Part I, 1963

1. *Blidingia chadefaudii* (FELDMANN) BLIDING 1963 p. 30.

In a letter Professor J. FELDMANN has had the kindness to point out that on material from Banyuls he has found certain differences between *Blidingia chadefaudii* and *minima* even in their earliest development (at the time between the stages Fig. 11 d and e in Part I p. 33). A supplementary investigation was made at Lab. Arago Banyuls in April 1966, at Kristineberg Biological Station in September 1966 (the alga was new to Sweden) and at the Biological Station at Tromsö July—August 1966. In northern Norway the species was first found in two localities in Finnmarken by JAASUND (1965 p. 15).

Fig. 47 A illustrates the mentioned stage of *chadefaudii* from an exposed locality in Banyuls. The comparison with *minima* (BLIDING 1963 Fig. 7 i—k) shows that cells in *chadefaudii* are longer and young discs more open. The difference is particularly striking at comparison with a rare form of *minima* from the harbour of Banyuls (Fig. 47 B), where even very young discs are tigthly closed.

Fig. 47 C—F shows important stages of the ontogeny in *chadefaudii* from Tromsö, and especially the final stages will show the close relationship of the genus to *Kornmannia*.

2. *Enteromorpha linza* (LINNAEUS) J. AGARDH.

As a synonym for *Enteromorpha linza* ought to be listed *Ulva lapathifolia* (KÜTZING) ARESCHOUG in Exs. Aresch. No. 25, Ser. 2 (Fig. 47 H). As to its basionym, *Phycoseris lapathifolia* KÜTZING, a sheet No. 938.91 . .530 in Herb. Lugd. Bat. is labelled "16. *Phycoseris lapathifolia*" in KÜTZING's hand. Since "16" is the number of *lapathifolia* in KÜTZING 1849 p. 477, the sheet must contain the type specimen. However, there are two specimens on this sheet; one original, which is *E. linza* (Fig. 47 G) and pasted above it a specimen of *Ulva curvata*, which agrees with Fig. 25 in Tab. phyc. VI.

Systematical Conclusions with Reference to Families and Genera in Part I and II

Capsosiphon. In Part I (BLIDING 1963 p. 19) this genus was included, with some hesitation, in *Ulvaceae*, as it was also done by CHIHARA (1967) in a morphologic-systematic investigation on material from Japan. IWAMOTO (1959) considers that the genus stands closer to *Monostroma* than to *Enteromorpha*.

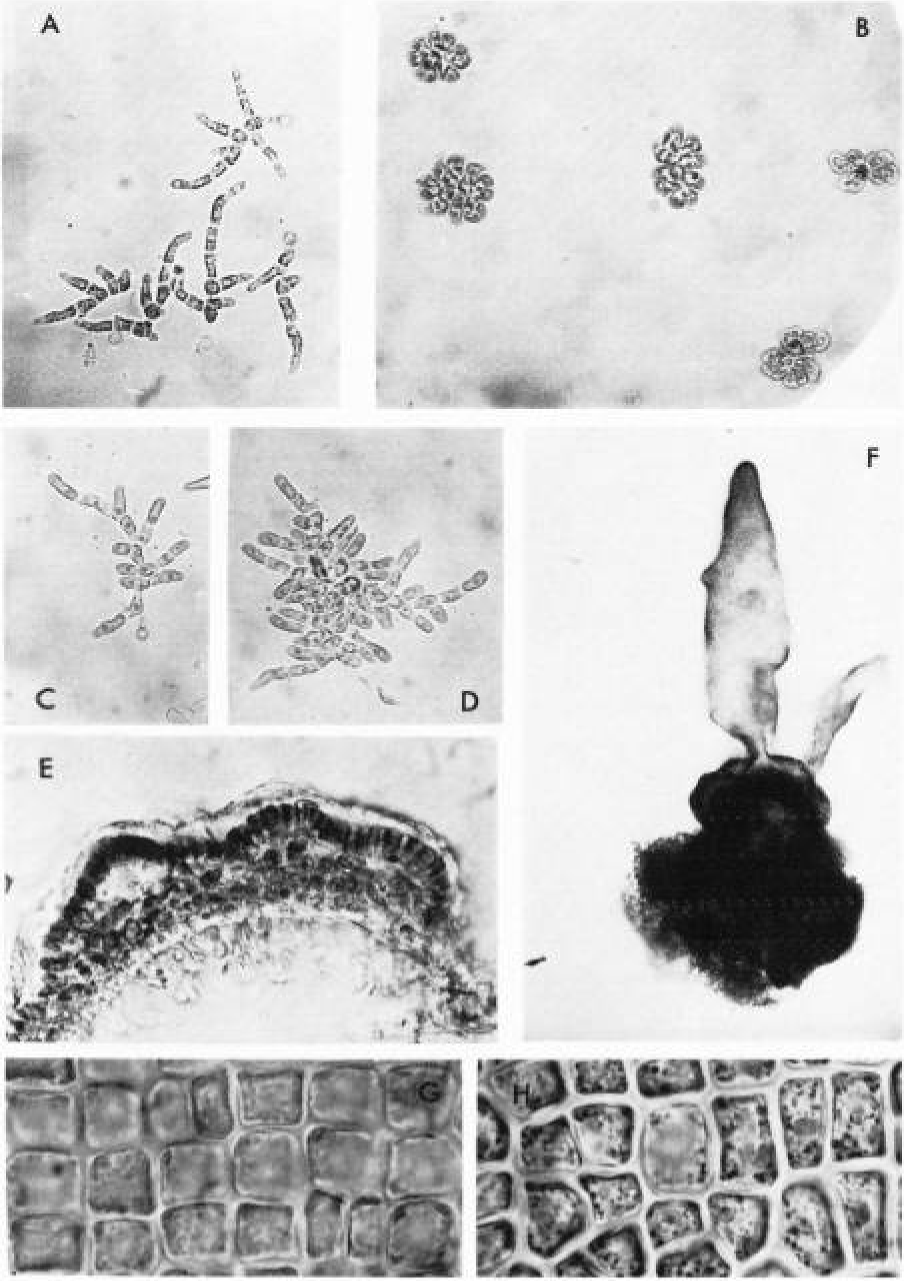
PAPENFUSS (1960 pp. 311 and 313) pointed out that *Capsosiphon* differs strikingly from other genera of *Ulvales*, but considered that at that time there was no adequate reason for transferring the genus to the family *Capsosiphonaceae* proposed by CHAPMAN in 1952.

However, experiences from cultivation of *Ulvales* algae during the last years have given reason to point out, more strongly than was earlier the case (BLIDING 1963 pp. 15 and 18), differences between *Capsosiphon* and other genera of *Ulvales* in regard to the young germling and its holdfast (cf. *Ulva* Fig. 26 D—H and *Capsosiphon*, BLIDING 1963, Fig. 4 g—i). In *Capsosiphon* the primary attaching cell of the germling remains rounded (BLIDING 1935 Fig. 4 and 1963 Fig. 4), and by longitudinal divisions it gives rise to a basal ring of round cells which with their gelatinous walls attach the plant to substratum. Rhizoidal cells are lacking. As the presence of such cells seems to be one of the most essential features by which *Ulvaceae* is distinguished from other families of Green algae, this should be yet another reason to transfer *Capsosiphon* from *Ulvaceae* to *Capsosiphonaceae* CHAPMAN.

On account of the ontogeny of *Capsosiphon* it is not possible to place the genus among *Monostromataceae*.

Percursaria differs from other genera in *Ulvales* by the fact that the alga is not hollow at any stage of its development. It has no rhizoidal cells and its reproductive bodies usually germinate into a horizontal disc (KORNMANN 1956, BLIDING 1963 Figs. 5—6), and consequently its closer relationship to *Enteromorpha* (CHAPMAN 1956 p. 429) seems excluded. The subsequent development of the disc, in the course of

Fig. 47. A: *Blidingia chadefaudii*, Banyuls, early stages, see text. B: *Blidingia minima*, Banyuls, see text. C—F: *Blidingia chadefaudii*, Tromsö. C—D: young prostrate discs. E: section through an older disc with three erect plants in development. F: prostrate disc with two erect plants. G—H: *Enteromorpha linza*. G: Type of "*Phycoseris lapathifolia*" KÜTZING, see text. H: "*Ulva lapathifolia*" (KÜTZING) ARESCHOUG in Exs. Aresch. A—D ×330, E ×260, F ×65, G, H ×660.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which its margin cells form the 1—2-seriate *Percursaria*-threads, is quite different from the development in *Monostromataceae*. Possibly *Percursaria* has its most closely related forms within *Chaetophorales* (cf. DANGEARD 1961 b Pl. I—IV). *Percursaria* is separated here from *Ulvaceae* and is proposed to be transferred to a new family, *Percursariaceae*, with the distinctive marks of the genus.

Percursariaceae Bliding fam. nov.

Planta iuvenis, lamina horizontalis microscopica, generans fila marginalia non cava neque ramosa cum cellulis in (1—) 2 series longitudinales dispositis. Generationes alternantes; anisogametae, zoosporae satis parvae; corpuscula propagationis ad laminam prostratam germinantia.

The closely related genera *Enteromorpha*, *Ulva* and *Ulvaria* form a natural family, *Ulvaceae*, with a characteristic anatomy and ontogeny: all reproduction bodies, sexual and asexual, germinate into an uniseriate germling with a lengthened attaching cell; by longitudinal and transverse cell divisions and arrangement of the cells round a central cavity the germling soon becomes a cylindrical tube with a one-celled wall. At this stage the *Enteromorpha* plant remains throughout its life. In the young *Ulva*-plant, a few mm high, the walls of the tube grow together entirely to the distromatic lamina. In *Ulvaria* the tubular germling becomes more or less sack-shaped, opens at the distal part and its lobes grow up to the monostromatic plant. — As regards the life history of *Ulvaceae* the sexual species have an alternation of isomorphic generations, gametophyte and sporophyte; asexual species have no alternation of generations, their sole reproduction bodies are 2- or 4-flagellate, negatively phototactic, neutral swarmers. — As to the anatomy they have at the base rhizoidal cells which are multinuclear contrary to the other cells of the plant.

Of the genus *Monostroma* THURET, the typical members *bullosum*, *grevillei* and *arcticum* are dealt with. The two former species are sexual with heteromorphic generations: the erect, at first hollow, later monostromatic plant with its basal, prostrate disc, derived from a zoospore, is the gametophyte; the sporophyte stage is represented by the zygote, remaining one-celled and growing to a big cyst, discharging zoospores. *M. arcticum* is asexual and has no alternation of generations. — Asexual swarmers (4-flagellate zoospores in *bullosum* and *grevillei*, 2-flagellate neutral swarmers in *arcticum*) germinate into a prostrate system from which new plants upheave. As to the anatomy of the plants; they have no rhizoidal cells, but the cells at the base become prolonged, tapering upwards, downwards, or in both directions. These cells, earlier mistaken for rhizoidal cells, are one-nuclear like the other cells of the plant (CARTER 1926). In view of these developmental and anatomical facts it seems impossible to assign a place for the genus *Monostroma* THURET under the family *Ulvaceae* as circumscribed above. The genus must be placed in *Monostromataceae* KUNIEDA ex SUNESON (PAPENFUSS 1960 p. 315). KORNMANN has stated that *Monostromataceae* shows connections with *Ulotrichales*.

Monostroma leptodermum KJELLMAN, referred to a new genus, *Kornmannia*, shows a great agreement with *Blidingia* regarding swarmers and ontogenetic data. Also morphologically the genera are approaching since *leptoderma* mostly has a long tubular stipe. As to its anatomy *leptoderma* is most similar to *Monostroma zostericola* TILDEN, and COLLINS (1909 p. 213) considered them the same taxon. The life history of *zostericola* from its type locality (the State of Washington, U.S.A.) is as yet incompletely investigated (cf. SCAGEL 1966 p. 41), but on material from Japan two developmental studies have been published. The first of them (YAMADA and KANDA 1941) states a life history in principal features agreeing with that of *Kornmannia leptoderma* (4-flagellate swarmers of *Blidingia*-type germinate into a microscopic disc, from which new macroscopic plants grow up). The second investigation (YAMADA and TATEWAKI 1965) reports an alternation of two heteromorphic generations. The leafy thallus belongs to the sporophyte generation, producing 4-flagellate zoospores; the zoospore germinates into a microscopic prostrate disc, the gametophyte generation, discharging isogametes; the zygotes give rise to a new prostrate system, from which the macroscopic plants grow up.

YAMADA and TATEWAKI expressed the opinion that *zostericola* in Japan may consist of two different strains, one of them with alternation of generations.

A comparison between *Blidingia*, *Kornmannia leptoderma* and *Monostroma zostericola* with consideration also to morphologic-anatomical characteristics brings out the following.

1. *Blidingia*: plant tubular, cells c:a 7 μ in diam.; pyrenoids distinct; germinating swarmers mostly cut off an empty cell (Addenda Fig. 47 A; 1963 Fig. 7 g).
2. *Kornmannia leptoderma:* sessile plant monostromatic, with a tubular stipe, cells c:a 8×6 μ (in the stipe up to 15 μ); pyrenoids not distinguishable (at the magnif. of ×700); germinating swarmers without an empty cell.

3. *Monostroma zostericola* TILDEN from its type locality: plant monostromatic, without tubular stipe; cells 2.5—5 µ in diam.; pyrenoids very small (according to Pl. 18 A in SCAGEL 1966).
4. *Monostroma zostericola* TILDEN sensu YAMADA-KANDA-TATEWAKI: plant monostromatic, without tubular stipe; pyrenoids distinct (according to Pl. I in YAMADA-TATEWAKI 1965); germinating zoospores and zygotes often with an empty cell.

On the basis of these characteristics it seems evident that *leptoderma* and *zostericola* should be considered two separate species of *Kornmannia* and further that *zostericola* TILDEN from its type habitat and *zostericola* TILDEN sensu YAMADA-KANDA-TATEWAKI represent two different taxa (as suggested by SCAGEL 1966 p. 41).

Kornmannia zostericola (TILDEN) BLIDING, **comb. nov.** — Basionym: *Monostroma zostericola* TILDEN, American algae 1900 no. 388.

From what is said above, it appears too, that *Blidingia* and *Kornmannia* differ from *Monostroma* THURET in some important features. In the sexual species of *Monostroma* the macroscopic plant is the haploid generation, but in *Kornmannia* and *Blidingia* a diploid generation. The zygotes in *Monostroma* grow into one-celled cysts, in *Kornmannia zostericola* TILDEN sensu YAMADA and TATEWAKI the zygotes develop into prostrate discs. However, before diagnosing a new family of *Ulvales*, comprising *Blidingia* and *Kornmannia*, we need more information about the anatomy and life history of some hitherto incompletely investigated taxa belonging to *Monostroma* sensu WITTROCK and of the species *Monostroma groenlandicum* J. AGARDH (=*Enteromorpha groenlandica* [J. AGARDH] SETCHELL and GARDNER). Preliminarily *Blidingia* and *Kornmannia* are placed as divergent genera of *Monostromataceae* KUNIEDA ex SUNESON.

SYNOPSIS OF THE FAMILIES AND GENERA IN PART I—II

Capsosiphonaceae CHAPMAN 1952

Capsosiphon GOBI 1879
Species typica: *C. fulvescens* (C. AGARDH) SETCHELL et GARDNER

Percursariaceae BLIDING fam. nov.

Percursaria BORY 1823
Species typica: *P. percursa* (C. AGARDH) BORY

Monostromataceae KUNIEDA ex SUNESON 1947

Monostroma THURET 1854
Species lectotypica: *M. bullosum* (ROTH) THURET

Divergent genera:
Kornmannia Bliding gen. nov.
Species typica: *K. leptoderma* (Kjellman) Bliding comb. nov.
Blidingia Kylin 1947
Species typica: *B. minima* (Nägeli ex Kützing) Kylin

Ulvaceae Lamouroux orth. mut. Dumortier 1822
Enteromorpha Link 1820
Species lectotypica: *Ulva intestinalis* Linnaeus (vide Papenfuss 1960)
Ulva Linnaeus 1753
Species lectotypica: *Ulva lactuca* Linnaeus
Ulvaria Ruprecht 1851
Species lectotypica: *Ulvaria obscura* (Kützing) Gayral

Index to Genera and Species in Part II

(Synonyms in *italics*)

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Studies in Galápagos Plants[1]

VII. On some New or otherwise Noteworthy Plants from the Archipelago

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ABSTRACT

Five species of various groups of vascular plants are treated, two of which are new to science, and another two new to Galápagos. *Botrychium Underwoodianum* MAXON is the first species of the genus to be known from the islands. Another species of the same family, *Ophioglossum reticulatum* L., was previously known only from Volcán Santo Tomás on the island of Isabela. Now it is reported also from Volcán Alcedo on Isabela and from another two islands. *Salicornia fruticosa* L., not previously collected in Galápagos, is reported from two islands. Two species of *Linum*, *L. cratericola* and *L. Harlingii*, are described as new to science. The plants were collected by my wife and myself during a nine month period in the archipelago in 1966—1967. The last-named plant had been found by earlier collectors but had been confused with *L. oligophyllum* WILLD., a plant of unknown origin, deposited in the Willdenowian herbarium in Berlin-Dahlem.

Unless otherwise stated, the collections studied are deposited at the Riksmuseum, Stockholm (S).

Botrychium Underwoodianum MAXON — Fig. 1.

Botrychium Underwoodianum MAXON 1905 p. 220.
Sceptridium Underwoodianum (MAXON) LYON 1905 p. 458.

Up to 32 cm high. Sterile stalk up to 8 cm long, diverging from the fertile stalk 2—3 cm from the base of the plant. Sterile leaf blade 5-angular (Fig. 1), up to 12 cm long and 16 cm wide; the ultimate segments suboval to spathulate, crenate, 5—12 mm long, 3—7 mm wide; venation flabellate. Fertile stalk up to 25 cm long. Fertile leaf blade (fruiting spike) up to 7 cm long and 5 cm wide. Sporangia yellowish brown, 0.7—1.0 mm in diameter.

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Fig. 1. *Botrychium Underwoodianum* MAXON (ELIASSON 1445) from Volcán Santo Tomás on Isabela in the Galápagos archipelago.

Known from the West Indies (Jamaica), Central America (Costa Rica) and northern South America (Colombia, Venezuela) (CLAUSEN 1938 p. 47). The Galápagos plant agrees in all important characteristics with the type specimen (JENMAN s. n., collected in Jamaica during 1874—1879. Holotypus in NY).

The genus is new to Galápagos.

COLLECTION STUDIED: Isabela. ELIASSON 1445, Volcán Santo Tomás, upper part of the southern slope, in grass area, alt. 920 m, March 2, 1967.

Ophioglossum reticulatum L.

LINNÉ 1763 p. 1518.

Perennial, 5—22 cm high. Rhizome when well developed more or less cylindrical, up to 4 mm in diameter, often stoloniferous, erect, with numerous roots about 1 mm wide. Rhizome generally with only 1 but sometimes with several leaves. Common stalk 1.5—9 cm long. Sterile blade cordate, broadly ovate, roundly triangular or suborbicular, at base cordate, truncate or broadly attenuate, at apex rounded, apiculate or acute, 1.5—6 cm long, 1.5—4.5 cm wide, with reticulate venation. Fertile stalk 4—12 cm long. Fruiting spike 1—3.5 cm long. Sporangia 1—1.2 mm in diameter.

A pantropical species of wide distribution. In Galápagos collected on the islands of Isabela, San Salvador and Santa Cruz. On Isabela it was found at elevations above 800 m on the volcanoes Alcedo and Santo Tomás. Especially on the first-named volcano the plant is common. The species is also common on the top of San Salvador at elevations between 850 and 900 m, an area where the vegetation is very strongly influenced and ruined by free-ranging pigs, goats and donkeys. On Santa Cruz the plant is found at elevations between 500 and 850 m. It grows in clearings and along trails in the *Miconia* belt and in the open grasslands around the top.

In Galápagos previously known only from Volcán Santo Tomás ("Villamil Mt.") on Isabela (CLAUSEN 1938 p. 133).

COLLECTIONS STUDIED: Isabela. ELIASSON 1248, Volcán Alcedo, the outer southern slope of the crater, alt. 820 m, Feb. 11, 1967. ELIASSON 1447, Volcán Santo Tomás, north-eastern slope, alt. 920 m, March 2, 1967. — San Salvador. ELIASSON 1135, alt. 880 m, Jan. 27, 1967. ELIASSON 1335, alt. 900 m, Feb. 21, 1967. — Santa Cruz. FAGERLIND & WIBOM 2981, 3034, 3194, on the central plateau, April—May, 1953. ELIASSON 310, 326, 330, north of Bella Vista, alt. 500—520 m, Oct. 18, 1966. ELIASSON 343, 349, north of Bella Vista, along the trail to Mt. Crocker, alt. 510 m, Oct. 19, 1966. ELIASSON 548, the highland, alt. ca. 600 m, Nov. 8, 1966.

Fig. 2. *Salicornia fruticosa* L. (dark) and *Batis maritima* L. (light) growing on the shores of a small salt lagoon on the north-eastern side of San Salvador in Galápagos. Photo: U. E. 22.2.1967.

Salicornia fruticosa L. — Figs. 2, 3.

Salicornia fruticosa Linné 1762 p. 5.
S. peruviana Humboldt, Bonpland & Kunth 1817 p. 193.

Perennial, suffrutescent, to 3 dm high, richly branched with ascending or erect branches. Stems and branches jointed, glabrous, fleshy, the joints dilated at apex into a short sheath. Sterile joints 7—12 mm long. Sheaths with very obtuse-angled lobes. Leaves rudimentary, reduced to minute scales. Flowers perfect or polygamous, sunken in groups in the joints of the stem, flower groups decussately opposite. Flowering joints 2—4 mm long. Perianth obpyramidal, the outer part rhomboid or rounded, about 2 mm in diameter, at the top with a small mouth through which the stamens and stigmas protrude. Stamens 1—2; anthers 0.8—1.0 mm long. Stigmas 2, about 0.5 mm long. Seed 1.3—1.5 mm long, 0.9—1.0 mm wide, pale brown, hispidulous.

A species of wide distribution on seashores of both hemispheres. It has not previously been collected in Galápagos, although STEWART (1911 p. 53) reported that "a plant resembling a *Salicornia* in habit and inflorescence was seen growing on the shores of salt lagoons" on the north-east side of the island of San Salvador. This locality is very probably identical with the one pictured in Fig. 2, where my collection No. 1390 was made.

ERIKSSON's (1956 p. 55) report of a *Salicornia* from a salt water lake on the bottom of a crater near James Bay, no doubt refers to *Batis maritima* L. The habit and the colour of ERIKSSON's plant (op. cit., plate opposite p. 93) point to the last-named species. Moreover, in the herbarium of the Botanical Museum, University of Göteborg (GB), there is a *Batis maritima* from exactly the same locality, collected by ERIKSSON, naval surgeon on the Swedish Deep-sea Expedition 1947—1948. On the labels attached to the sheet there is the annotation: "At the salt lake on the floor of the crater. 3/4 m high. Stem woody. Dense thickets. Abundant. Sept. 8, 1947."

COLLECTIONS STUDIED: San Cristóbal. ELIASSON 2276, between Cerro Brujo and Caleta de Sappho, sea level, May 28, 1967. — San Salvador. ELIASSON 1390, north-east side, around small salt lagoon, sea level, Feb. 22, 1967.

Linum cratericola ELIAS. **spec. nov.** — Fig. 4.

Holotypus: ELIASSON 905 (S).

Descriptio holotypi: Suffrutex, 4—5 dm altus, glaber. Caules et rami numerosi ascendentes vel erecti, rami striati. Folia numerosa, caulem obtegentia, alterna, anguste oblongo-lanceolata, ad apicem subacuta, basim versus angustata, 1-nervata; intermedia 7.5—10 mm longa, 1.0—1.3 mm lata, basi glandulis carente. Inflorescentia cymatoides. Flores in apice ramulorum solitarii. Sepala subovata vel subrhomboidea, acuminata, 3—3.5 mm longa, 1.9—2.1 mm lata, obscure 3—5-nervata, nervo medio prope basim prominente; glandulae desunt. Petala late obovata, flava, circ. 8 mm longa et 5 mm lata. Filamenta basim versus dilatata, singulis staminodiis dentiformibus inter filamenta dispositis. Styli usque ad basim liberi. Capsula globosa, diametro circ. 2.5 mm, pallide fusca. Semina subelliptica, compressa, circ. 1.6 mm longa et 1.0 mm lata, fusca, nitida.

Fig. 3. *Salicornia fruticosa* L. from the locality shown in Fig. 2. In the background *Batis maritima* L. Photo: U. E. 22.2.1967.

Suffrutescent, 4—5 dm high, glabrous. Stems and branches numerous, ascending or erect; branches striated. Leaves (Fig. 4 A) numerous, covering the stem, alternate, narrowly oblong-lanceolate, subacute at apex, narrowed at base, 1-nerved; the intermediate 7.5—11 mm long, 1.0—1.3 mm wide; leaf glands absent. Inflorescence cyme-like. Flowers solitary (Fig. 4 F) at branchlet tips. Sepals (Fig. 4 F) subovate to subrhomboid, acuminate, 3—3.5 mm long, 1.9—2.1 mm wide, obscurely 3—5-nerved; the midnerve prominent near base; glands absent. Petals (Fig. 4 B) broadly obovate, yellow, about 8 mm long and 5 mm wide. Filaments (Fig. 4 C, D, E) wider near base, alternating with tooth-shaped staminodes. Styles (Fig. 4 D, E, F) free to the base. Capsule (Fig. 4 F) globose, about 2.5 mm in diameter, light brown. Seeds (Fig. 4 G) subelliptical, flat, about 1.6 mm long and 1.0 mm wide, brown, shining.

This species was collected in two localities, close to each other, on the island of Floreana. The type locality is a small, strongly weathered crater north-east of Floreana Peak and about 100 m north-east of the trail leading from Black Beach to the Wittmers' farm. This crater is very small, less than 100 m in diameter, and about 10 m deep. *L. cratericola* was found on the south-western part of the crater rim, where it was growing together with bushes or small trees of *Zanthoxylum*, *Croton*, *Cordia* and *Darwiniothamnus*. The second locality is a larger crater some hundred metres north-east of the type locality. This crater has a diameter of several hundred metres and a depth of about 60 m. *L. cratericola* was found on the north-eastern part of the steep inner wall of the crater. Other genera growing in the vicinity were *Tillandsia*, *Boussingaultia*, *Pisonia*, *Zanthoxylum*, *Croton*, *Cordia*, *Darwiniothamnus*, *Lecocarpus*, *Scalesia* and *Macraea*.

COLLECTIONS STUDIED: Floreana. ELIASSON 905, the rim of a small crater north-east of Floreana Peak, alt. 370 m, Dec. 16, 1966 (holotypus). ELIASSON 964, north-eastern wall of a larger crater north-east of Floreana Peak and some hundred metres from the type locality, alt. 380 m, Dec. 21, 1966. ELIASSON 2100, the type locality, May 6, 1967.

Linum Harlingii ELIAS. **spec. nov.** — Fig. 5.

Holotypus: HARLING 5367 (S).

Syn.: *L. oligophyllum* sensu ROBINSON 1902 p. 156 et STEWART 1911 p. 80, non WILLDENOW 1820 p. 758.

Descriptio holotypi: Suffrutex, 3—5 (—6) dm altus, glaber, virgatus, ramis numerosis plus minus erectis. Rami striati. Folia alterna, sparsa, caulem non obtegentia, lanceolata, ad apicem subacuta, basim versus angustata, 1-nervata; intermedia (4—) 5—10 mm longa, (0.8—) 1.0—1.2 mm lata, ad basim binis glandulis globosis fusco-purpureis praedita. Inflorescentia cymatoides. Flores in apice ramulorum solitarii. Sepala rhomboido-elliptica, acuminata, 2.9—3.3 mm longa, 1.5—1.7 mm lata, obscure 3-nervata, nervo medio prominente, ad basim binis glandulis globosis fusco-purpureis praedita. Petala obovata, circ. 10 mm longa et 5 mm lata, in vivo flava, in siccitate albescentia. Filamenta basim versus dilatata, singulis staminodiis dentiformibus inter filamenta dispositis. Styli usque ad basim liberi. Capsula globosa vel subglobosa, diametro 2.5—2.7 mm, subflava, supra saepe purpurea. Semina subelliptica, compressa, circ. 1.7 mm longa et 1.0 mm lata, fusca, nitida.

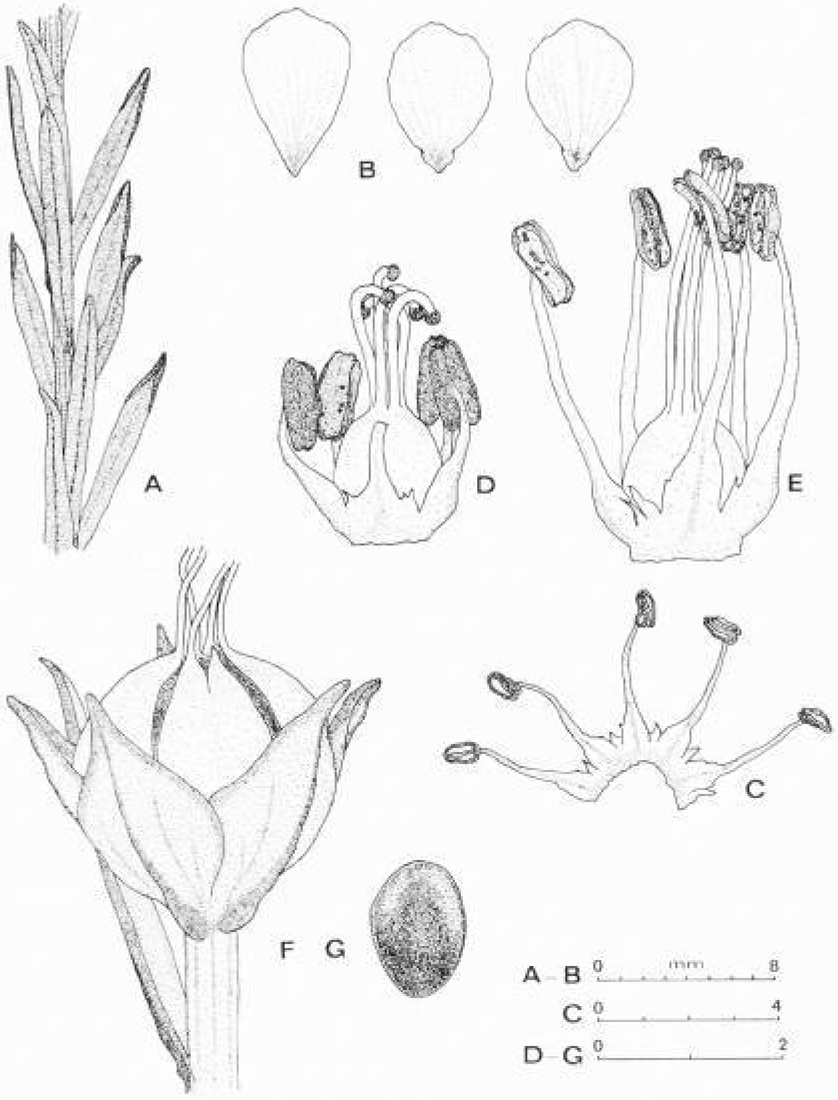

Fig. 4. *Linum cratericola* Elias. (holotypus). — A: Part of stem with leaves. — B: Petals from a bud. — C: Stamen-tube opened, showing fertile stamens alternating with staminodia. The anthers are emptied. — D: Androecium and gynoecium from a young flower. One of the anthers has been cut away. The styles are free to the base. — E: Androecium and gynoecium from a mature flower. The anthers are emptied. — F: Ripe capsule opening. — G: Seed.

Suffrutescent, 3—5 (—6) dm high, glabrous, twiggy with more or less erect numerous branches. Branches striated. Leaves (Fig. 5 A) alternate, sparse, not covering the stem, lanceolate, subacute at apex, narrowed at base, 1-nerved; the intermediate (4—) 5—10 mm long, (0.8—) 1.0—1.2 (—1.5) mm wide, at base with two globose glands, dark reddish brown. Inflorescence cyme-like. Flowers solitary (Fig. 5 F) at branchlet tips. Sepals (Fig. 5 F) rhomboid-elliptical, acuminate, 2.9—3.3 mm long, 1.5—1.7 mm wide, obscurely 3-nerved; the midnerve prominent; at base of sepal two globose glands (Fig. 5 F), dark reddish brown. Petals (Fig. 5 B) obovate, about 10 mm long and 5 mm wide, yellow, when dried almost white. Filaments (Fig. 5 C, D, E) wider near base, alternating with tooth-shaped staminodes. Styles (Fig. 5 D, E, F) free to the base. Capsule (Fig. 5 F) globose or nearly so, 2.5—3 mm in diameter, yellowish, above often reddish brown. Seeds (Fig. 5 G) subelliptical, flat, about 1.7 mm long and 1.0 mm wide, brown, shining.

L. Harlingii grows on the upper part of the western slope of Volcán Darwin on the island of Isabela. Other genera growing in the neighbourhood are *Froelichia, Acalypha, Dodonaea, Opuntia, Cordia, Lippia, Darwiniothamnus, Scalesia* and *Macraea*. The plant was first collected by SNODGRASS and HELLER in 1898—1899. It was referred by ROBINSON (l. c.), and later by STEWART (l. c.), together with his own material, to "*L. oligophyllum* WILLD.". I have examined type material (WILLDENOW No. 6233) of the last-named species from the Willdenowian herbarium (B) and found it to be specifically distinct from the Galápagos plant. Compared to the Galápagos plant, *L. oligophyllum* has larger sepals, 4.0—4.1 mm long, without basal glands. Also the leaves seen by me lack glands, although these may be present in additional type material of which I have only seen pictures. According to MACBRIDE (1949 p. 623) the presence or absence of leaf glands seem to be a variable character in several species of the genus.

The original description of *L. oligophyllum* (WILLDENOW 1820 p. 758) is very poor, and the characters mentioned in the description match many species of *Linum*. The origin of the type is unknown. ROBINSON (l. c.) states, on grounds unknown to me, that *L. oligophyllum* is distributed in the Andes of Ecuador and Peru. I have been unable to identify any of the plants in MACBRIDE's Flora of Peru with *L. oligophyllum*. There seem to be some resemblances to *L. Weberbaueri* KRAUSE (1908 p. 277), but that species has (ex char.) smaller sepals, 2.0—2.3 mm long, with basal glands. Since a description as well

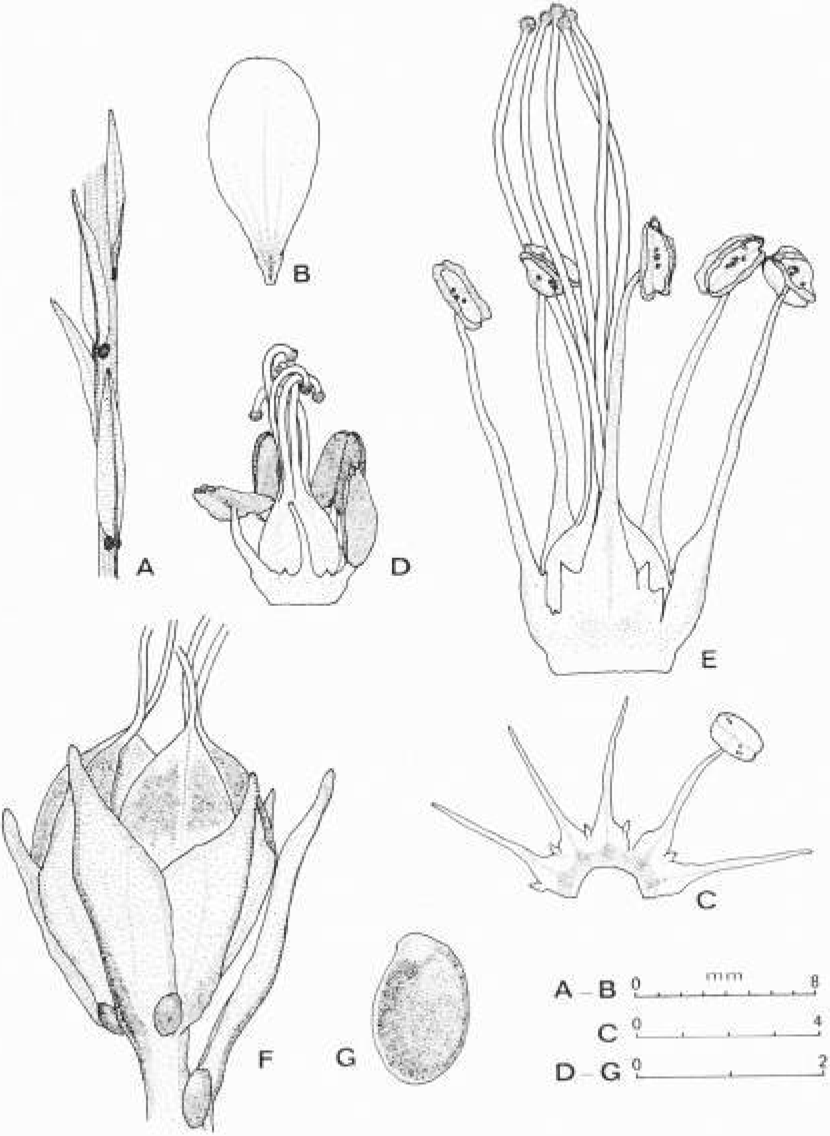

Fig. 5. *Linum Harlingii* ELIAS. (ELIASSON 1762). — A: Part of stem with leaves. — B: Petal from a mature flower. — C: Stamen-tube opened, showing filaments alternating with staminodia. Four of the anthers have fallen away. — D: Androecium and gynoecium from a young flower. One of the anthers has been cut away. The styles are free to the base. — E: Androecium and gynoecium from a mature flower. The anthers are emptied. — F: Ripe capsule opening. — G: Seed.

as a type specimen of *L. oligophyllum* exist, it is not possible to drop the name as a nomen nudum, as suggested by MACBRIDE (op. cit. pp. 626—627).

L. Harlingii is named for Professor GUNNAR HARLING, who collected this plant in Galápagos in 1959 and who introduced me to the problems of the flora of the Galápagos Islands.

COLLECTIONS STUDIED: Isabela. HARLING 5367, Volcán Darwin, between alt. 800 m and 1100 m, June 7, 1959 (holotypus). ELIASSON 1762, Volcán Darwin, western slope, alt. 1180 m, March 29, 1967.

Key to the Galápagos species of Linum

Glands absent at base of leaves and sepals; leaves numerous, covering the stem .... *L. cratericola*

Glands present at base of leaves and sepals; leaves sparse, not covering the stem .... *L. Harlingii*

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Pubescence in the Sanguisorba Group (Rosaceae)

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ABSTRACT

Five main hair types occur in the *Sanguisorba* Group, comprising the genera *Sanguisorba* (incl. *Dendriopoterium* and *Marcetella*), *Sarcopoterium* and *Bencomia*. These are: unbranched, unicellular and thick-walled; unbranched, multicellular and eglandular; unbranched, multicellular and with a unicellular gland; unbranched, small, multicellular and with a multicellular gland; and branched, multicellular and eglandular. No hair type is restricted to a single taxon. However, the five types are not randomly distributed, but occur in certain combinations within genera, subgenera and sections. *Sanguisorba* sect. *Poterium* has been studied in detail on specific and subspecific level. All three hair types occurring in the section are represented in most taxa, even if the density may be rather different.

The genera studied are *Sanguisorba* L., *Sarcopoterium* SPACH and *Bencomia* WEBB. et BERTH., i.e. the *Sanguisorba* group as defined by NORDBORG 1966. The genera *Marcetella* SVENT. and *Dendriopoterium* SVENT. (SVENTENIUS 1948 pp. 255 and 263) are included in genus *Sanguisorba* (NORDBORG op. cit.).

In my previous paper dealing with the genera of the *Sanguisorba* group the pubescence has been discussed in those cases where it is of taxonomic importance (NORDBORG 1966 p. 21 and NORDBORG 1967 p. 20). Only macroscopically visible hair types and their frequency and distribution were treated, i.e. a revision was made of characteristics previously used in floras. In more penetrating morphologic studies in the genus *Sanguisorba* microscopic glandular hairs were also observed, however, as well as branched hairs, hitherto not described in the genus. Glandular hairs, corresponding to type D below, have been described by REINKE (1876 pp. 136—137) in *Sanguisorba officinalis*.

Five hair types are found, Fig. 1.

The indumentum was studied on the stems, petioles and leaflets. The distribution of the different hair types in the genera of the *Sanguisorba* group may be found in Table 1.

A. Unicellular, eglandular, thick-walled, acuminate, long and slender. The cell is empty and accordingly appears white. Length 0.6—1.0 (—1.6) mm. Long hairs corresponding to the value given in parentheses are found only in *Sanguisorba vestita* (section *Poterium*) and in *Bencomia exstipulata*, see below. Fig. 1 A—C.

B. Multicellular, eglandular, thin-walled, unbranched, acute or obtuse, composed of one cell row. The number of cells in fully developed hairs varies between 6 and 26 with the mean value 18 (the cells of 200 hairs from 16 species were counted). The length of the cells often varies between and also within taxa. The hairs are usually of the appearance seen in Fig. 1 D—F, but all cells of the hair may also be quite short and broad, as in section *Marcetella* (genus *Sanguisorba*) and in *Bencomia exstipulata*. The cells are usually practically empty, only in *B. exstipulata* are they ± mucilaginous. The colour is white or sometimes brownish. In dried material this hair type has a characteristic chain structure, the cells being ± flat with every other cell or at least some cells in the row turned vertical to horizontal. Length 1.2—2.2 mm.

C. Multicellular, thin-walled, unbranched, composed of 3—20 cells in one row, terminated by a unicellular gland. Although of the same basic type, the appearance is rather different in the two species where these hairs occur, see Fig. 1 G—J and pp. 646—648. The number and shape of the cells vary and also the shape and the size of the gland. The colour is pale yellow to greyish. Length 0.6—1.3 mm.

D. Multicellular, thin-walled, unbranched, composed of 2—12 cells: the stalk with a single or sometimes in the upper part double row of cells, terminated by a multicellular gland. These hairs are very small, not visible without lens. The colour is yellow to ± brownish. Length 0.1—0.3 mm. Some variation is found between taxa, especially in the shaping of the gland, see Fig. 1 K—L.

Fig. 1. Hair types in the *Sanguisorba* group. — A—C: One-celled, thick-walled hairs, type *A*. — D—F: Multicellular, non-glandular and unbranched hairs, type *B*. — G—J: Multicellular hairs with one-celled apical gland, type *C*. — K—L: Multicellular hairs with apical gland or capitulum of several ± distinct cells, type *D* — M—R: Multicellular, non-glandular, ± branched hairs, type *E*.

A: *Bencomia exstipulata*. — B: *Sanguisorba vestita*. — C—D: *Sanguisorba minor* ssp. *minor*. — E—F: *S. minor* ssp. *magnolii*. — G—H: *S. hybrida*. — I—J: *Sarcopoterium spinosum* (I from petiole, J from stem). — K: *Sanguisorba ancistroides*. — L: *Bencomia exstipulata*. — M—N: *Sanguisorba menendezii*. — O—R: *Sanguisorba moquiniana*. (Scales as indicated at the bottom of the figure.)

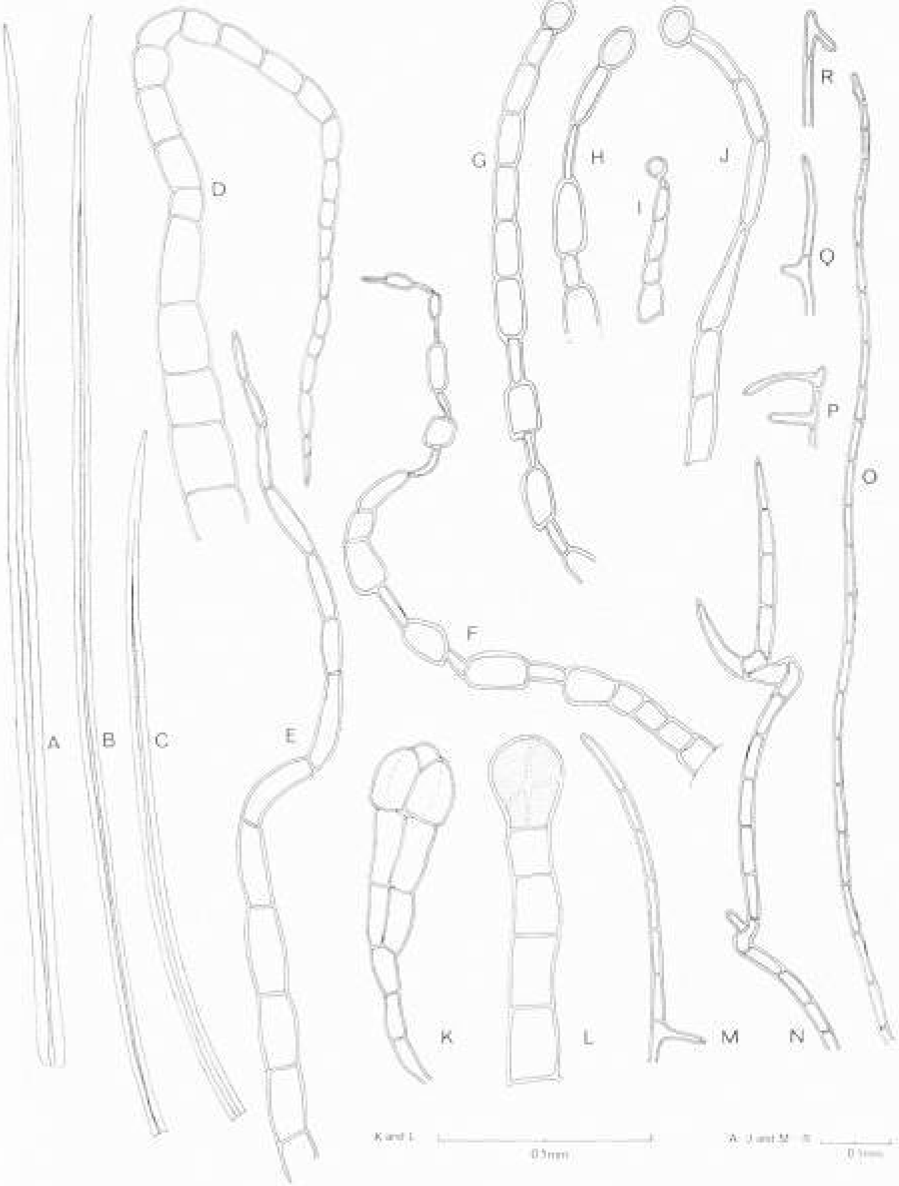

Fig. 1.

E. Multicellular, eglandular, thin-walled, branched, usually with short branches or with merely protuberances from a cell. The hairs are often curved just beneath the branching points. The number of cells varies from 2 to c. 30. The cell sap is colourless or intensely red. Length 0.1—1.4 mm. Fig. 1 M—R.

GENUS SANGUISORBA

Subgenus Sanguisorba

Most species of the two sections *Sanguisorba* and *Pterachaenium* are glabrous or subglabrous. The three hair types A, B and D occur in the sections, but when existing they are ± sparsely scattered, very sparsely on stem and petioles, somewhat more densely on the lower side of the leaflets. Usually all three types are found, if pubescence occurs at all.

Section Sanguisorba. The percentage of hairy plants in species of the *S. officinalis* group, the *S. canadensis* group, and the *S. tenuifolia* group of section *Sanguisorba* lies within the limits 23 to 35 %. In the *Sanguisorba obtusa* group, *S. obtusa* MAX. itself is distinguished by having densely placed brown hairs of type B on the stem and the midvein of the lower side of the leaflets. Such hairs are lacking in other species of that group.

Section Pterachaenium CES. No hairs whatsoever have been observed in *S. dodecandra* MOR. In *S. diandra* (HOOK.) NORDB. there are sparse hairs of type A, on leaves also rarely of B, and in two of twelve plants studied, of D.

Subgenus Poteridium (SPACH) A. BR. et BOUCHÉ

The only species of this subgenus, *Sanguisorba annua* (NUTT. ex HOOK.) TORR. et GRAY can be classed as almost glabrous. In single plants there are sparse hairs of the multicellular acuminate type on the stems, and unicellular as well as microscopic glandular hairs on the leaflets.

Subgenus Poterium (L.) A. BR. et BOUCHÉ

Section Poterium. The greatest variation in pubescence is found in section *Poterium* where quite glabrous to densely villous taxa are met with. The variation within taxa is also great (NORDBORG 1967 pp. 20—21). The three hair types A, B and D are found in the section. Their distribution among taxa, the percentage of hairy plants in each of the taxa, and the degree of pubescence can be seen in Table 2.

Table 1. Distribution of Different Hair Types within the Sanguisorba Group.

Taxon	Hair type (parentheses=occurring rarely)				
	A	B	C	D	E
Genus *Sanguisorba*					
Subgenus *Sanguisorba*					
Section *Sanguisorba*	×	×	—	×	—
Section *Pterachaenium*	×	×	—	×	—
Subgenus *Poteridium*	×	×	—	×	—
Subgenus *Poterium*					
Section *Poterium*	×	×	—	×	—
Section *Agrimonioides*	×	—	×	—	—
Subgenus *Dendriopoterium*					
Section *Dendriopoterium*	(×)	×	—	×	×
Section *Marcetella*	×	×	—	×	×
Genus *Sarcopoterium*	×	(×)	×	—	×
Genus *Bencomia*	×	×	—	×	—

S. ancistroides (DESF.) CES., *S. cretica* HAYEK, *S. filiformis* (HOOK. F.) HAND.-MAZZ., and forms of *S. minor* SCOP. ssp. *rupicola* (BOISS. et REUT.) NORDB. appear glabrous at a first sight. Other subspecies of *S. minor* vary from glabrous to ± hairy. *S. lateriflora* (COSS.) A. BR. et BOUCHÉ is always hairy, and *S. vestita* (POM.) NORDB. is quite villous.

The dominant hair type in *S. ancistroides* is the microscopic glandular one, D, which is found in more than 90 % of the plants investigated and in the same degree on stem, petioles and leaflets. Hairs of types A and B can be found very sparsely on the lowermost part of the stem and on the petioles, type A also on the lower side of the leaflets. If type B occurs on the leaflets, these hairs are always restricted to the midrib.

No unicellular hairs are found in *S. cretica*, and the other hair types occur sporadically and very sparsely. In *S. filiformis* the multicellular eglandular hair type is lacking.

The dense, white pubescence on the lower part of the stem of *S. lateriflora* consists of the chain-like hairs, of type B, and were found in all the plants studied of this species. Colourless unicellular hairs, type A, have not been observed on the stem, only together with the multicellular ones, on the petioles and leaflets of many plants.

In *S. minor* SCOP., the subspecies *minor*, *magnolii* (SPACH) BRIQUET and *muricata* (GREMLI) BRIQUET largely follow the same pattern in regard to hair types and percentage of hairy plants, except that ssp. *muricata* has somewhat lower values than the others. It should also be stated, that the values are not the same as those given for the pubescence in NORDBORG 1967 because these referred to distinctly hairy contra glabrous plants: in the present investigation all plants have been classed as hairy where any hairs can be seen under the microscope, even if occurring very sparsely. Ssp. *muricata* includes the whole variation from extremely sparsely to very densely pubescent, while the degree of hairiness in ssp. *minor* and *magnolii* is somewhat less variable.

In ssp. *lasiocarpa* (Boiss. et Hausskn. in Boiss.) Nordb. the frequency of plants with unicellular hairs is greater than with multicellular ones, but when present the latter hairs dominate in density. More than half the plants studied are almost glabrous. The glandular hair type is often lacking in this subspecies.

Most plants of ssp. *rupicola* look glabrous. Very few hairs exist except for microscopic glandular ones.

In all plants of *S. vestita* the stems are densely covered with up to 1.5 mm long hairs of type A. Type B is rarely found. Small glandular hairs are as common as in *S. minor* ssp. *minor*, *magnolii* and *muricata*.

Section Agrimonioides Spach. The single species, *S. hybrida* (L.) Nordb. is constantly hairy. The dominant type is C, i.e. ± long, glandular hairs, which occur on the whole stem but also on the petioles and the leaflets. Usually the number of cells varies between 6 and 20. Even when composed of few cells, these hairs are easy to distinguish from the small glandular ones because of their one-celled glands. They replace type B, which is lacking in this species. The unicellular hair type occurs sparsely on the stem and ± closely on the petioles and the leaflets, although sparsely in relation to the glandular one.

Subgenus Dendriopoterium (Svent.) Nordb.

Hairs of type E characterize this subgenus, but also hairs of types A, B and D have been found.

Section Dendriopoterium. Only one species, *S. menendezii* (Svent.) Nordb. belongs to this section. Except at seedling stage, the hairs are very sparse. When present they are concentrated to the stipule bases and a zone of the petiole just above these, and to the lower side of the leaflets. The branched hairs of type E are colourless and short, occurring on the petioles as well as the leaflets, and there mainly on the veins. Rarely some hairs are unbranched, consisting of several cells and reminiscent of type B but without a chain-like structure. The limit between the types B and E seems diffuse here. Unicellular hairs, of type A, occur very sparsely on the petioles, more frequently together with the branched hairs on the midveins of the leaflets.

Table 2. The Pubescence in section Poterium.
Italics: dense pubescence; parentheses: sparse pubescence.

Taxon	Percentage occurrence of the three hair types:									Number of plants studied
	Stem			Petiole			Leaflets			
	A	B	D	A	B	D	A	B	D	
S. ancistroides	(67)	(38)	*93*	69	26	90	71	(12)	93	42
S. cretica	—	(50)	(50)	—	50	(67)	—	—	(50)	6
S. filiformis	(47)	—	(32)	(32)	—	(42)	(68)	—	(21)	19
S. lateriflora	—	*100*	53	59	*76*	76	71	12	71	17
S. minor										
ssp. *minor*	(14)	77	71	29	68	66	73	(18)	70	56
ssp. *lasiocarpa*	(52)	33	37	(37)	26	30	93	(7)	52	27
ssp. *magnolii*	(20)	86	77	(32)	82	59	68	(4)	70	44
ssp. *muricata*	(10)	48	70	(38)	48	70	44	—	72	50
ssp. *rupicola*	—	(63)	100	(25)	50	100	63	(25)	94	16
S. vestita	*100*	(18)	73	*100*	(36)	73	*100*	—	(45)	11

Section Marcetella (SVENT.) NORDB. There is some difference between the two species of this section. Hairs of type E are always found in *S. moquiniana* (WEBB. et BERTH.) NORDB., also at the adult stage. They occur on the young parts of the stem, the petioles, and more densely at the base and on the veins of the lower side of the leaflets. They are variable in length but very characteristic because of their intensely blood-red colour. Also single hairs of type A have been observed on the petioles and leaflets. Short glandular hairs of type D and also multicellular hairs of type B occur on the petioles, although less frequently than the red, branched hairs. The hairs of type D are similar to those in genus *Sanguisorba* but sometimes have indistinct walls between the cells of the gland. In the limited material of *S. maderensis* (BORNM.) NORDB. studied, branched hairs have not been found. Hairs of type A cover the petioles and the lower side of the leaflets, but occur extremely sparsely on the stem, where there are also short glandular hairs of type D.

GENUS SARCOPOTERIUM

Multicellular hairs, generally with an apical, capitate gland-cell, corresponding closely to type C, which is characteristic of section *Agrimonioides*, occur on the stems and thorns of *S. spinosum* (L.) SPACH, although they are shorter and consisting of only 4—8 cells, and often more sparsely scattered. Occasionally the longest of these hairs lack an apical gland cell and thus agree with type B, every other cell being generally twisted at right angles to the other in dry condition. Very exceptionally also the unicellular hairs of type A have been found on the stems.

On the petioles hairs of type B and type C occur together. The latter are much shorter than on the stem and consist of 2—6 cells. The lower side of the young leaflets has a caducous cover of relatively short, colourless, branched, multicellular hairs. These resemble the longer similar hairs, of type E, found in section *Dendriopoterium*. Sparse unbranched, unicellular, thick-walled hairs of type A also exist on the leaflets.

GENUS BENCOMIA

The plants usually appear densely hairy. The dominant hair type on petioles is B, and type D is also frequent ("petiolo . . . pubescente glanduloso et albido-piloso" according to SVENTENIUS 1960 p. 25). Type A occurs more or less sporadically. Hairs of this type are found on both sides of the leaflets, although more densely on the lower side, where they often form a villous layer. Sometimes, e.g. in *B. caudata* (AIT.) WEBB et BERTH. hairs of type D follow the midvein and the larger lateral veins on the upper side of the leaflets. In *B. exstipulata* SVENT. the glandular hairs have a somewhat deviating appearance from those observed in other taxa with this type. The gland is small, with ± indistinct cell-walls and filled with secretory products. Usually there is only a single cell row beneath the gland. The hairs of type A are very long, and those of type B have relatively short and broad cells with somewhat mucilaginous contents.

TAXONOMIC IMPORTANCE

Combinations of Hair Types in Taxa

The hairs of type A occur in all taxonomic groups presented in Table 1. Their structure is the same in all taxa, although the length is variable. The hairs are usually between 0.6 and 1.0 mm long, only in *S. vestita* (section *Poterium*) and in the genus *Bencomia* do they reach a length of 1.2—1.6 mm. Especially in *B. exstipulata* the hairs are consistantly long. The presence of this hair type accordingly cannot be used as a taxonomic characteristic, but the density can have some taxonomic importance, viz. in the *Sanguisorba minor* complex and related species, see below.

The hairs of type B are absent in the monotypic section *Agrimonioides* of *Sanguisorba* subgenus *Poterium*, and occur extremely sparsely in the monotypic genus *Sarcopoterium*, but they are found in all other groups. The occurrence of the glandular hairs of type C is common to the two taxa mentioned; moreover, they are restricted to these taxa and apparently replace the hairs of type B. The microscopic glandular hairs of type D are also lacking only in these two taxa.

The branched hairs of type E occur in the genus *Sarcopoterium* and in two species of *Sanguisorba* subgenus *Dendriopoterium*. In the third species of this subgenus, *S. maderensis*, no branched hairs have been observed in the limited material studied.

The other subgenera of *Sanguisorba* and the genus *Bencomia* have the same hair types, viz. A, B, and D.

Variation within the Hair Types

The appearance of the hairs of each type is usually rather similar in different taxa. Some deviation has been observed, however, mainly in the genus *Bencomia*, where the hairs of type A are distinctly longer than in other taxa (*S. vestita* excepted), and those of type B often have shorter cells than normally, although this short-celled type occurs also in the section *Marcetella* of *Sanguisorba*. The hairs of type D in *Bencomia* consist of a single cell row, often with smaller cells upwards and a small gland not or only slightly broader than the cells of the row and generally indistinctly multicellular.

The hairs of type D in *Sanguisorba* section *Marcetella* can also be distinguished from those of this type found in the other subgenera. They may be described as intermediate between the latter and those of *Bencomia*. Furthermore, the hairs of type C in *Sanguisorba* section *Agrimonioides* and in the genus *Sarcopoterium* are somewhat different in length and appearance. In the latter genus the limit between type C and type B is diffuse. In section *Agrimonioides* the gland is always present on the hairs of type C but the cells of the stalk occasionally have "chain structure" (Fig. 1 G) and thus there seems also to be relationship between the two hair types in this group.

Speculatively, it might be possible that type A and type B are the original hair types. From type B the evolution has probably proceeded to gland hairs of type C, and possibly further to variants of type D with a stalk of a single cell row, as in *B. exstipulata*. From this type the development should have gone to the type in subgenus *Dendriopoterium* and to the more differentiated one, i.e. the one in section *Poterium*. More probable is, however, that the hairs of type D have developed independently. Finally the branched hairs of type E may have developed from type B. More penetrating studies of the indumentum in related genera in Africa and S. America could be of importance in solving such phylogenetic problems.

Distribution of the Hair Types in Section Poterium

The more penetrating analysis of the pubescence in section *Poterium* (Table 2) shows that hairs of type A are absent in *S. cretica*, and of type B in *S. filiformis*. They occur in all other taxa, although those of type A are lacking on the stem of *S. lateriflora* and *S. minor* ssp. *rupicola*, and those of type B on the leaflets of *S. lateriflora*, *S. minor* ssp. *muricata* and *S. vestita*. Hairs of type D have been observed in all the species. However, the density and distribution on stem, petiole and leaflet are variable. Thus hairs of type A are very sparse on the stem, except in *S. vestita*, where they cover the lower parts entirely. Such hairs are dominant on the petioles in *S. vestita* but occur also in 69 and 59 per cent of the studied material of *S. ancistroides* and *S. lateriflora* respectively, although rather sparsely. Hairs of type B dominate on stem and petioles of *S. lateriflora* and occur also in as much as 70 % or more of *S. minor* ssp. *minor* and ssp. *magnolii*, although not densely. Hairs of type D are characteristic of *S. ancistroides*, but were also found ± sparsely in 70 % of the studied material of the subspecies of *S. minor*, except in ssp. *lasiocarpa* with values between 30 and 50 %.

Conclusions

No taxon can be distinguished by the occurrence of any specific hair type. However, two hair types, C and E have a very limited distribution. Thus type E (branched hairs) has only been found in *Sarcopoterium* and in two of the three species of *Sanguisorba* subgenus *Dendriopoterium*. Type C is restricted to *Sarcopoterium* and *Sanguisorba* section *Agrimonioides*, where it apparently replaces type B.

In *Sanguisorba* section *Poterium* the qualitative differences are few. Type A does not occur in *S. cretica*, nor does type B in *S. filiformis*. Other differences are quantitative. Thus, *S. vestita* differs from other taxa by the density of hair type A, and *S. lateriflora* by type B, although the difference is not great in this respect from forms of *S. minor* sspp.

minor and *magnolii*. Glandular hairs of type D occur densely in *S. ancistroides*, but are found ± sparsely also in a variably high percentage of the other taxa. The variation in pubescence in the *Sanguisorba minor* group follows a similar pattern as the variation of most other morphologic characteristics and only combined with these can the hair types and the density of hairs be used in the taxonomic treatment.

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Brief Articles and Reports

Notes on Filago vulgaris Lam. (F. germanica) in Scania, Sweden

ABSTRACT. — A new locality of *Filago vulgaris* from Gabeljung in the parish of Gärdslöv in Scania is reported. The species has become very rare in the province. The chief reason for this is that the ecology of the previous localities has changed and that many suitable localities disappear in consequence of the agricultural re-organization taking place in recent time.

Filago vulgaris LAM. (*F. germanica* L. non HUDS., *F. canescens* JORDAN) is a species which now stands on the limit of extinction in Scania, the only province in Sweden where it has occurred regularly. Another species of the same group of *Filago*, viz., *F. lutescens* JORDAN (*F. apiculata* G. E. SMITH nom. provis.), occurred in Scania previously. It is now extinct. According to H. WEIMARCK (Bot. Notiser 1958 p. 120) it was seen the last time in 1927 at "Svinaberga backar" in the parish of S. Mellby in eastern Scania. It had a distribution similar to that of *F. vulgaris* but was more rare. The distributional similarities of the two species are probably connected with their similar ecology. The decline in their occurrences has probably the same reasons and has been almost simultaneous in time, though the rarest species has become extinct first.

F. vulgaris was reported from Scania the first time by LECHE in 1744 (Sv. Vet. Akad. Handl. 1744 pp. 261—285). He found the species at Hälsingborg, "torra backar utom Helsingborgs kulleport". Since that time it has been reported from about 40 different localities in the province (cf. the map). All localities except one somewhat dubious report (from Höör) are confined to areas near to the coast. The localisation of some of the older findings may sometimes be inexact because of the incomplete reports. In most localities the species has been seen only once or for a few subsequent years and then it has disappeared. But in some localities it has been observed for a considerable time, viz., Nyhamnsläge in Brunnby 1926—1958, Ven 1884—1917, Svarte in Balkåkra 1824—1892, Stenshuvud 1866—1928. The species is often irregular in its occurrence. In one year it may be common in a locality, the next year it is very sparse or has disappeared and then it can be refound some years later in the same place, a type of meteoric occurrence. The species has been

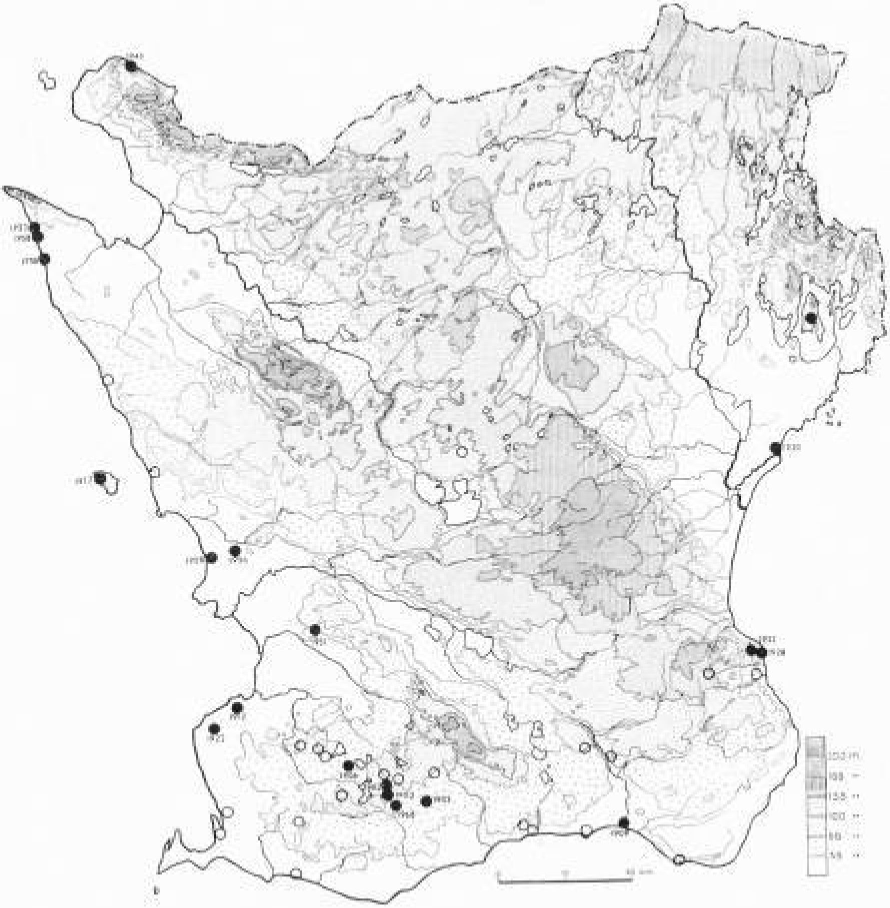

Fig. 1. The distribution of *Filago vulgaris* LAM. in Scania, Sweden. Dots represent findings after 1900, and rings findings before 1900. The year of the latest known find has been indicated. For one locality (Ivön) no year was available.

reported from about 20 localities during this century. In the last twenty years it is known from only five localities, although the province during this time has been floristically thoroughly investigated. From these figures it is evident that the known localities of the species have decreased in number rapidly in recent years. According to a statement by G. WAGENITZ, Berlin, the same tendency holds true in Central Europe.

In Scania *F. vulgaris* reaches the northern limit of its distribution in Europe. It has probably never been a common species in the province. It is hardly possible to decide whether the Scanian population has been stable within the province with only seasonal fluctuations depending on external factors or if it has had to rely on a ± occasional supply of diaspores from abroad for its existence.

The species grows on dry, sandy or gravelly ground in a ± open vegetation in fallow fields, hillsides, and grass-fields. It also occurs on disturbed and ruderal places. Some of the Scanian localities are of this latter type, viz., Lund 1951 (SYLVÉN, Skånes Natur 1952 pp. 22—24), Höganäs 1958 (RICKMAN), Malmö 1912 (GERTZ, Bot. Notiser 1913 p. 118). The species was found in a new locality, a gravel-pit, last summer by the author. The locality is situated at Gabeljung in the parish of Gärdslöv. About one hundred specimens were seen. The new locality is situated within an area where the species seems to have had a distribution centre in the province.

This kind of localities are depending on a certain clearing influence mainly from man in order to keep the vegetation open. If they are left alone which now take place very often the vegetation will soon be too dense to allow plants like *F. vulgaris* to thrive. Many fields and hillsides have now also been afforestated. This recent change in the exploition of the land is probably the most important factor responsible for the rapidly decreasing distribution of *F. vulgaris*.

The distribution map of *F. vulgaris* is mainly based on reports in the archives of "Skånes Flora" at the Institute of Systematic Botany in Lund.

ÖRJAN NILSSON

"Sporomorphae" and "Trophomorphae" Terminological Contours

The increased amount of pollen and spore research has, i.a., entailed the establishment and swift growth of a "new" branch of science, palynology, sometimes referred to as sporology.

With regard to many characteristics such as size, wall (sporoderm), chemistry, plasma organellae (as far as investigated) sporomorphs (pollen grains and spores sensu lato) are often very uniform and, paradoxically, at the same time often extremely diversified. The uniformity makes them exquisite objects in comparative research by means of special methods, e.g. electron microscopy. Their diversity on the other hand, can make them serve as "fingerprints" in the identification of the plants which produced them. Pollen grains and spores, particularly certain parts of their resistant walls, have probably a wider distribution, both in time and space, than any other biological objects. They are not necessarily bound to special units or subunits of the plants. They thus constitute a very minute part of the n-generation in such mosses as *Polytrichum*. With regard to the male gametophyte in the flowering plants, e.g. *Narcissus*, conditions are different. Yet the sporomorphs in these two disparate genera have certain gross characteristics in common.

Nor does the trophic status of the plants have an apparent influence upon the sporomorphs. The pollen grains in heterotrophic plants, *Balanophora*, *Cynomorium*, *Orobanche* and *Rafflesia*, to take but a few examples, do not in principle deviate from those in autotrophic plants. It may be added, as a mere curiosity, that pollen grains from a specimen of *Plantago lanceolata*, more than three feet high, growing on the margon of the crater of an extinct volcano in Curepipe, Mauritius [ERDTMAN s.n., 1966 (S)], were as large (diameter 26—28 μ) as those of "ordinary", i.e., much smaller, specimens from Scandinavia.

In the lower plants, algae fungi, etc. the condition is more intricate. It may not be insuperable, though, to extract, also here, characteristics separating the "sporomorphs" from the "other parts of the plants". Short and trenchant, in order to avoid a lengthy explanation: the former are chiefly concerned with the reproduction. They are, as a rule, small, agile, or easily transported. The latter are larger, usually neither agile nor adapted to locomotion (except ensily distributed diaspores etc.). They are chiefly connected with the livelihood, the nourishment, of the plants. In contradistinction to the sporomorphs they can be referred to as "trophomorphs" (Greek *trophon*, food, that which feeds).

In taxonomy descriptions of higher plants are almost exclusively based upon the trophomorphs, e.g. gametophytes and sporophytes in the mosses, sporophytes in the flowering plants, etc. Why not let the sporomorphs acquire the significance and credit they justly deserve? The same may be contended in morphology. In ecology, including palaeobotany, the sporomorphs are increasingly exploited or resorted to in their capacity of guide-fossils and/or indicators of plant and climate history through the ages.

A tentative enumeration of "morphae" would perhaps be as follows: abiomorphae, biomorphae; zoomorphae, phytomorphae; trophomorphae (rhizo-, phyllo-, xylo-morphae, etc.) and sporomorphae. The latter can be classified according to the NPC-system or in other ways. To these groups can be added palynomorphae, spore-like bodies incertae sedis. This term is not new; it has, i.a. been used in geological and/or palaeobotanical context.

From this collocation, be it superfluous or not, at least one point of some significance seems to emerge, viz. the logical limitation of the main domains and precincts of palynology, and "non-palynology".

G. ERDTMAN

Meddelanden

Utmärkelse

Professor Nils Hylander, Uppsala, har av Kungl. Fysiografiska Sällskapet i Lund tilldelats Linnépriset i botanik.

Fria transoceana resor

har av Kungl. Fysiografiska Sällskapet i Lund tilldelats

professor Erik Åkerberg för deltagande i den 11:e int. botanistkongressen i Seattle, USA, för överläggningar rörande resistensförhållanden, samt för besök vid den amerikanska genbanken för vilda potatisarter.

fil. mag. Gun Romée för fortsatt inventering av floran i Libyska öknens oaser.

P. F. Wahlbergs minnesfond

Kungl. Vetenskapsakademien har ur P. F. Wahlbergs minnesfond utdelat ett bidrag på kr. 6.400 till intendent Ove Almborn för en botanisk studieresa till USA inkluderande bl.a. deltagande i botanistkongressen i Seattle.

Botanisk litteratur
(Botanical Literature)

RECHINGER, K. H.: **Flora Iranica.** Flora des Iranischen Hochlandes und der umrahmenden Gebirge. Persien, Afghanistan, Teile von West-Pakistan, Nord-Iraq, Azerbaidjan, Turkmenistan. — Fasc. 16—57, 1966—68. — Akademische Druck- u. Verlagsanstalt, Graz, Austria. Price per 16 pp. ÖS 38.— (DM. 6.—, U.S. $1.50).

Since the previous review of 'Flora Iranica' in this journal [Bot. Notiser 120(1), 1967] another 42 fascicles have appeared, each comprising one family. Altogether more than 1250 species are treated. The size of the fascicles is much varying, and no less than 21 contain one or two pages only. Many families are represented in the area by a single species (e.g., *Platanaceae*, *Punicaceae*, *Aquifoliaceae*, *Ebenaceae*, *Myrtaceae*, *Loganiaceae*). RECHINGER himself is the author of most fascicles, but he has managed to get several collaborators in Vienna and other parts of the world.

Among the somewhat larger families treated we find *Papaveraceae* (by J. CULLEN) with 7 genera and 48 species. Its largest genus in the area is *Papaver* with 30 species, 8 of which are endemic. *Rutaceae* (by C. C. TOWNSEND) is practically entirely represented by the genus *Haplophyllum* (26 spp.: 12 endemics). *Gentianaceae* (9 genera, 46 spp.) is treated by H. SCHIMAN-CZEIKA. Largest genus is *Gentiana*, and it is noteworthy that of its 25 species in the Flora Iranica area only 4 are endemic. Comparable figures are found in *Saxifraga*, which with 21 species and 4 endemics (21: 4) makes up the major part of *Saxifragaceae* (by E. SCHÖNBECK-TEMESY). Even more striking is *Hypericum*, the only genus of *Guttiferae* (by N. K. B. ROBSON) in the area. Of its 21 species only 2 are endemic.

Polygonaceae (by RECHINGER and SCHUMAN-CZEIKA) forms a sizeable fascicle (88 pp.). There are 123 species belonging to 9 genera, largest of which are *Polygonum* (53 spp.: 14 endemics) and *Rumex* (26: 4).

The two largest fascicles will attract much attention from taxonomists and phytogeographers. One of them deals with *Boraginaceae* (281 pp., 46 genera, 368 spp.), and presents the results of H. RIEDL's very careful studies in the gross as well as detail taxonomy of the family. *Ehretiaceae* is not treated as a separate family but included as subfam. *Cordioideae* and *Ehretioideae*. Many genera show a high degree of endemism, e.g., *Heliotropium* (74: 40) and *Onosma* (59: 32). The genera *Mattiastrum* (25: 22) and *Paracaryum* (16: 9) are of special phytogeographical interest, having more or less pronounced centres within the area.

The largest fascicle treats *Cruciferae* (372 pp., 126 genera, 476 spp.) with Rechinger and I. Hedge as main authors. Many of the genera are small, and no less than 66 genera are represented by a single species. Several of these are widespread weeds, whereas others are phytogeographically more interesting. Thus there are 11 endemic monotypic genera, viz. *Pseudofortuynia, Acanthocardamum, Brossardia, Cyphocardamum, Straussiella, Alyssopsis, Pyramidium, Micrantha, Zerdana, Dielsiocharis,* and *Nasturtiicarpa.* Seven or eight of these are represented in southweastern Iran, an area with some significance as an evolutionary centre within the family.

The largest genera of *Cruciferae* are *Alyssum* (36:9) and *Erysimum* (41:25). Of special interest is the nearly endemic genus *Pseudocamelina* (7:7) with a pronounced centre in SW. Iran. A nomenclatural detail may be mentioned in this connection. *Pseudocamelina campylopoda* was originally published as *Cochlearia campylopoda* Bornm. & Gauba, and the authors gave as a synonym "*Pseudocamelina campylopoda* Bornm. & Gauba in litt." This does not constitute valid publication of the latter combination, since it was not accepted by its authors and merely mentioned as a synonym (Article 34 of the International Code of Botanical Nomenclature). It seems that the valid combination under *Pseudocamelina* still remains to be done, and I leave the matter to the editor of the flora.

Some inconsistencies in author citation may be pointed out. The following examples will illustrate the point.

p. 153: *Alyssum dasycarpum* Steph. ex. Willd. in L.
p. 224: *Tetracme quadricorne* (Steph. in Willd.) Bge. — Basionym: *Erysimum quadricorne* Steph. in Willd.
p. 295: *Erysimum leucanthemum* (Steph.) B. Fedtsch. — Basionym: *Cheiranthus leucanthemum* Steph. in Willd.
p. 324: *Torularia contortuplicata* (Willd.) O. E. Schulz — Basionym: *Cheiranthus contortuplicatus* Steph. ex. Willd. in Willd.
p. 331: *Arabidopsis pumila* (Steph.) N. Busch — Basionym: *Sisymbrium pumilum* Steph. apud. Willd.

All these species were originally published in Willdenow's Species Plantarum 3: 1 (1800). The epithets attributed to "Steph." merely appeared in synonymy, although Willdenow adopted the same epithets. E.g., under *Erysimum quadricorne*, Willdenow gave the synonym "*Sisymbrium quadricorne* Stephan. in litt." Clearly the latter name was not validly published, and there are no reasons to cite the basionym otherwise than *Erysimum quadricorne* Willd. The same holds true in all cases quoted above, even if the wording "Steph. ex Willd." may seem admissible in some cases (but not "Steph. in Willd."!). In all later combinations "Willd." should be cited as the name-bringing author.

The larger fascicles are provided with illustrations in various techniques, viz. pencil drawings, ink drawings, and photographs in black and white and even some in colour (*Boraginaceae*). The quality varies considerably, and generally the drawings are to be preferred. Especially those of the last fascicle

(*Cruciferae*) are excellent, and it is to be hoped that future emissions will contain many more drawings of that standard. Accompanying the key to genera in *Cruciferae* there are numerous drawings of fruits, providing an excellent aid in the identification.

Five years have elapsed since the publication of Flora Iranica was started, and about one fifth of the species have now been treated. This would seem to indicate a period of another 20 years for completion of the flora. There are reasons to take a more optimistic view, however, and to predict a more rapid publication rate. Even the taxonomic difficulties presented by the large families *Leguminosae* (*Astragalus*!) and *Compositae* (*Cousinia*!) will no doubt be overcome successfully by RECHINGER and the entire great undertaking will be brought to a happy end. With this *magnum opus* Professor RECHINGER is doing an immeasurable service to contemporaneous and future botanists.

BERTIL NORDENSTAM

SHETLER, STANWYN G.: The Komarov Botanical Institute. 250 Years of Russian Research. — Smithsonian Institution Press, Washington, D.C., 1967. XIV, 240 pp. with two maps and numerous photos. Price $5.95.

Some of the cultural and scientific institutions founded by the czars in St. Petersburg have survived in modified form until present time. One of them, the Pharmaceutical Garden (Aptekarsky Ogorod) was founded by PETER THE GREAT in 1714 on an island in the Neva Delta, chiefly for the purpose of supplying medical plants and products to his army. This institution was a forerunner of the Botanical Garden, established in 1823. The Garden passed from one jurisdiction to another and changed names accordingly until 1931. This year the Garden and the Botanical Museum of the Academy of Sciences were merged into a single institution, the Botanical Institute, within the framework of the Academy. The Museum, established in 1835, was an outgrowth of the botanical collections in the old "Kunstkammer" — a gallery of arts and curios — founded by Czar PETER in 1715. In 1940 the Botanical Institute was named in honour of V. L. KOMAROV, distinguished botanist and editor-in-chief of the "Flora S.S.S.R.".

The Komarov Institute, situated near the center of Leningrad on the same island as Czar PETER's Aptekarsky Ogorod, is now the leading centre of the Soviet botanical research with vast resources: a staff of ca. 700 persons (including ca. 200 scientists), 24 major laboratories, a large greenhouse and outdoor garden complex, a 450,000-volume library with some 2,000 domestic and 3,000 foreign journals and serials, and a herbarium with nearly 6 million specimens.

After a short outline of the founding of St. Petersburg and a personalized description of modern Leningrad, the author tells the story af the Komarov Institute and its predecessors, which at the same time is the story of the major part of Russian botany. Biografical notes on the directors (especially V. L. KOMAROV, B. A. KELLER, B. K. SCHISCHKIN, V. F. KUPREVICZ, P. A. BARANOV, and AL. A. FËDOROV) are included in the text. There are also detailed descriptions of the pre- and post-war organisation and the research activity in the various departments. A very useful section is the enumeration of the serial publications of the Institute and its predecessors.

The author, active in the North American Flora project, has payed special attention to the "Flora S.S.S.R.", the most outstanding taxonomic achievement of the Komarov Institute and the Russian botany down to the present time, and gives an interesting account of the background, history, problems and general significance of this gigantic project.

Before a concluding chronological table of significant events the author discusses the national and international role of the Institute and gives his opinion of its intellectual milieu.

Most of the facts given in this book has no doubt been published earlier in Russian books and journals. It is, however, of great values that they now are available also to those botanists who do not read the Russian language.

Kurt Lindberg

Wardlaw, C. W.: Essays on Form in Plants. — Manchester University Press. Manchester 1969. XIV, 399 S. mit 30 Fig. (52 Teilfig.). Preis geb. 55 sh.

Professor emeritus C. W. Wardlaw, Manchester, hervorragender Kenner der Pflanzenmorphogenese, hat in dem vorliegenden Buche 30 Aufsätze gesammelt, die er 1944—1966 in verschiedenen Büchern und Zeitschriften veröffentlicht hat. Ihr Inhalt ist also schon bekannt — die Aufsätze sind fast unverändert neugedruckt — und ich kann mich hier auf einige formale Bemerkungen beschränken. Einige lateinische Namen sind leider misshandelt worden, z.B. *Aegopodium podograria* (S. 180), *Nymphaea micranthra* (S. 198) und *Cryptogramme crispa* (S. 322) statt *Ae. podagraria*, *N. micrantha* und *Cryptogramma crispa*. Da dieselbe Schreibweise auch im Stichwortregister vorkommt, kann es sich kaum um Druckfehler handeln. Weiter kann man sich fragen, warum einige unscharfe und skizzenhafte Figuren (z.B. Fig. 3 b S. 90 und Fig. 4 S. 217) nun nicht reingezeichnet worden sind.

In dem neugeschriebenen Einleitungskapitel gibt der Verfasser eine Übersicht über die Entwicklung der Pflanzenmorphogenese seit 1769 und einen Bericht über seine eigene Tätigkeit. In dem ebenso neuen Schlusskapitel sucht er die künftige Entwicklung innerhalb seines Faches vorauszusagen.

Die neugedruckten Aufsätze sind ursprünglich in etwa 20 Büchern und Zeitschriften erschienen, von denen einige in den Bibliotheken der botanischen Institute nicht immer zugänglich sein dürften. Es ist daher sehr wertvoll, dass die Artikel nun in einem einzigen Band gesammelt sind.

Kurt Lindberg

Lunds Botaniska Förening 1968

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