DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE SKRIFTER, BIND VI, NR. 2

THE MARINE ALGÆ OF DENMARK

CONTRIBUTIONS TO THEIR NATURAL HISTORY

VOL. II. PHÆOPHYCEÆ

IV. SPHACELARIACEÆ, CUTLERIACEÆ, AND DICTYOTACEÆ

BY

SØREN LUND

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
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INTRODUCTION

The present publication constitutes Part 4 of the work, commenced in 1941, on the Danish marine Phæophyceæe: "The Marine Algæ of Denmark. Vol. II. Phæophyceæ." It comprises the 3 orders: *Sphacelariales*, *Cutleriales*, and *Dictyotales*, each with 1 family, *Sphacelariaceæ*, *Cutleriaceæ*, and *Dictyotaceæ*. Since from the beginning, as a title for the individual parts of the series, family names were used instead of the more comprehensive names of the orders (the family *Ectocarpaceæ* in Part I composes only part of the order of *Ectocarpales*), I have been compelled to continue on this principle, and the title of the present work therefore is: *Sphacelariaceæ*, *Cutleriaceæ*, and *Dictyotaceæ*.

The 3 families like the families *Ectocarpaceæ* and *Acinetosporaceæ*, published in Part I, belong to the class of *Isogeneratæ* KYLIN (1933 p. 91), for the basis of which there is primarily an alternation of generations on the model of the *Dictyota*-type, i. e. an alternation between 2 generations morphologically identical. However, the alternation of generations of the members of *Isogeneratæ* may be modified in various ways just as it may possibly be discontinued. In the family *Sphacelariaceæ* it was demonstrated, or made probable, in a very few cases. In *Cutleria* the alternation of generations differs in the sexual generation being morphologically different from and more vigorously developed than the sporophyte. KYLIN (l. c. p. 79), however, regards the *Cutleria*-type as an anomaly of the *Dictyota*-type, referring to the fact that the genus *Zanardinia*, closest related to *Cutleria*, follows the *Dictyota*-type.

The work comprises in all 18 species. 16 of these belong to *Sphacelariaceæ*, distributed into 5 genera: *Sphacelaria* with 11 species, *Chætopteris* with 1, *Stypocaulon* with 1, *Cladostephus* with 2, and *Disphacella* with 1 species. *Cutleriaceæ* and *Dictyotaceæ* both are only represented by 1 genus, *Cutleria* and *Dictyota*, respectively, each with one species.

The material on which the work is based is chiefly, as was the case of the previously published parts, due to ROSENVINGE's very comprehensive collections, but it also includes collections made by others (especially LYNGBYE and CAROL. ROSENBERG). In addition I myself have collected material by which I succeeded in finding several species new to the Danish waters: *Sphacelaria britannica*, *S. saxatilis*, and *Dictyota dichotoma*. Besides, going through ROSENVINGE's herbarium also disclosed a species until now not recognized in Denmark, *Sphacelaria tribuloides*. The occurrence of these species in the Danish waters has already been published in a few temporary reports (LUND 1949 and 1940).

A small selection of the *Sphacelariaceæ* herbarium, particularly that due to the collections of LYNGBYE and CAROL. ROSENBERG from Hofmansgave on the north coast of Funen, at one time was lent to the French algologist SAUVAGEAU, who on the basis of it made several of the species the object of a thorough description. This applies to *Halopteris spinulosa* (var. *patentissima*—which in the present work is regarded as a form of *Stypocaulon scoparium*), *Cladostephus verticillatus* (var. *patentissimus*) and *Disphacella reticulata*, the latter of which was even established on the material from Hofmansgave, representing a new genus *Disphacella*. Concerning the two last-mentioned species I thought it sufficient to give a short summary from and for the rest refer to SAUVAGEAU's treatment (Remarques, 1900—14, and Recherche de la paternité du Cladostephus verticillatus, 1906).

Unlike what was the case with the former publications of the series, ROSENVINGE has not contributed by posthumous manuscripts, notes, or drawings to the present work, and therefore I have not included him as an author.

I wish to express my respectful thanks to the direction of the Carlsberg Foundation for the subsidy granted for the treatment of the Danish Phæophyceæ and to the Botanical Travelling Fund for a grant towards collecting *Sphacelariaceæ*. Finally I am indebted to the Rask-Ørsted Foundation for having made possible the translation into English by a pecuniary support.

SØREN LUND.

Sphacelariales.

Sphacelariaceæ.

The members of this family have especially been made the object of investigation by GEYLER (1866), PRINGSHEIM (1873), MAGNUS (1873), REINKE (1891 and Atlas, H. 2 1892), KUCKUCK (1894), and SAUVAGEAU. More than any one else, however, the last-mentioned investigator through his meritorious studies, whose results chiefly are embodied in the "Remarques sur les Sphacélariacées", has contributed to throwing light on the group. The following account is in part based upon this work. The references are to the complete edition 1900—14. After many of the references to the "Remarques" there are references added in brackets. These are to the "Journal de Botanique", in which pp. 1—348 were first published.

The Danish representatives of the family generally have an erect, branched thallus; they usually form tufts of a few mm high to well over 12 cm, more rarely indefinitely extended mats reaching a height of a few mm to about 1 cm. The erect thallus is polysiphonous, but in *Sphacelaria bipinnata* the young generations of shoots are frequently monosiphonous at a long stretch. The great majority are perennial; annual are *S. bipinnata* and perhaps *S. Plumula* and a few other species of *Sphacelaria*.

The family is primarily characterized by all the shoots, which are rather stiff, terminating in a very large apical cell, in which the longitudinal growth takes place. Downwards the apical cell by a transverse wall cuts off a long cell, a primary segment, which is afterwards divided by a transverse wall into 2 secondary segments. In the latter longitudinal walls henceforth occur, by which a central part and a cortex are formed in some species. Whereas the secondary segments of some species of *Sphacelaria* are not subjected to transverse septation, transverse walls develop in other species of this genus as well as in the representatives of the other Danish genera. With the exception of *Cladostephus*, whose long shoots have a secondary growth in length and thickness, the secondary segments in the Danish species are not further enlarged and with increasing septation the cells become increasingly small. In some species the limit between the individual secondary segments is distinct in the whole plant, in others only in part of it, for a larger or smaller portion of the plant may be covered by a rhizoidal cortex. In the long shoots of *Cladostephus* the limits are invisible owing to the secondary growth of the segments.

The cells contain a single nucleus and numerous small, discoid chromatophores without pyrenoids. In the apical cell fucosan and tannin occur, causing a brownish

or blackish colour. The older layers of the cell wall are transiently coloured by Eau de Javelle (which mainly consists of potassium hypochlorite). This colour reaction, which was discovered by REINKE, may sometimes be of diagnostic importance, e. g. to distinguish a sterile or fructifying basal part without erect shoots of *Sphacelaria cæspitula* (the so-called *Sphaceloderma* stage) from other crustaceous phæophycean algæ.

In certain species there is in the upper secondary segments frequently a conspicuous big cell containing fucosan, yellowish brown or dark brown, light or not deviating by its colour. In others similar cells occur in a number of four (or fewer), not only in the upper secondary segments but also in the lower ones. SAUVAGEAU calls the cells in question pericysts. They generally occupy the whole height of the secondary segment, whereas the other pericentral cells of the segment divide by transverse walls. They are to be regarded as branch-initials, which either remain inactive or do not develop until a late stage. They may give rise to branches, rhizoids, or sporangia. In Danish species they occur in *Sphacelaria cæspitula*, *S. radicans*, *Stypocaulon scoparium*, and *Disphacella reticulata*. Perhaps the pericysts are not different from the branch-initials occurring in other species, in which they are not or less conspicuous. Many of these, too, remain resting, either temporarily or for ever.

Sheathed hairs of an endogenous origin are found in most species. They occur singly or in pairs or several together. The growth comes off through a growing zone in the basal part.

The branching takes place in various ways, and on the basis of this it is possible to divide the family into subdivisions. Of the groups entered in SAUVAGEAU (Remarques, p. 605) the following are represented in the Danish waters: *Hemiblasteæ* (with the genera *Sphacelaria* and *Chætopteris*), *Holoblasteæ* (with the genus *Stypocaulon*), *Polyblasteæ* (with the genus *Cladostephus*), and *Dichoblasteæ* (with the genus *Disphacella*).

In *Hemiblasteæ* (SAUV. op. c. p. 267 (1903 p. 332)) the branches arise typically as protrusions from the upper secondary segment in the whole height of the latter, with the basal part occupying half of the height of the original primary segment. Thus they are inserted between 2 secondary segments, and the basal part is limited above by a primary wall, below by a secondary wall. SAUVAGEAU calls these branches *rameaux hémigènes* or *hémiclades*.

The hairs in this group are founded by a small lenticular cell, which is cut off from the apical cell of the shoot through a watchglass-formed wall near the tip of the apical cell. The latter continues its growth in the longitudinal direction of the shoot, and hence the lenticular cell, soon beginning to develop into a hair, will come to be placed laterally. When the apical cell of the shoot thereafter forms another primary segment through a primary transverse wall, the latter will lean to the watchglass-formed wall of the hair-initial. On certain occasions, however, the apical cell does not grow after the cutting off of the lenticular cell, and the hair will then be terminal as it may sometimes be seen e. g. in *Sphacelaria Plumula* and *S. tribuloides*; in others the hair-cell is laid out in the middle of the uppermost part of the apical

cell, which also causes the hair to be terminal. The formation of hair is regarded by MAGNUS (1873) and SAUVAGEAU, who in the lenticular cell see the actual apical cell, as a sympodial process, while other investigators, such as GEYLER and PRINGSHEIM interpreted the hairs as lateral shoots. A hair-bearing filament according to the first conception therefore is composed of as many parts of shoots as generations of hairs exist.

In *Holoblasteæ* (SAUV., op. c. p. 270 (1903 p. 335)) the branches like the hairs in *Hemiblasteæ* are started in the apical cell itself. The process is initiated by the apical cell by means of a steep wall cutting off a lenticular cell, which soon after by a transverse wall is divided into 2 cells of unequal size, an upper, small one and a lower, large one. The upper small cell according to SAUVAGEAU is to be regarded as the apical cell of a diminutive generation, while the lower one represents its only primary segment. The latter does not divide in the usual way by a secondary transverse wall into 2 secondary segments, but behaves as a *sphacèle raméal*, growing out in its whole height in a lateral direction into a branch. The diameter of these branches at the base thus is identical with a primary segment in its whole height—in contradistinction to the branches in *Hemiblasteæ*, which are inserted on half a primary segment (= a secondary segment). SAUVAGEAU terms the former branches *rameaux hologènes* or *holoclades*. When the original apical cell of the axis after the cutting off of the lenticular cell forms a new primary segment through a primary wall, the latter will hit the mother cell of the branch. Therefore a branch at base will lean to a primary wall in the axis and be inserted at the lower part of a lower secondary segment and the upper part of the upper secondary segment occurring below. The branches, in their turn, ramify in the same way as the mother shoot.

The hairs are always in the axils of the branch; they develop from the upper, small cell, formed by the transverse division of the lenticular cell. This *sphacèle axillaire* may produce one or more hairs, but it may also remain unchanged or develop into a branch or one or more sporangia.

In *Polyblasteæ* (SAUV., 1906 a, p. 94) the branches are of very different origin. In the only genus belonging here, *Cladostephus*, whose erect, vegetative thallus is differentiated into long shoots and verticillate, more or less divaricate short shoots (ramuli), no less than 5 different kinds of shoots are found. The long shoots, the so-called *pousses plagioblastiques* (SAUVAGEAU, Remarques p. 528), rise from an upper secondary segment as a kind of synclade having a peripheral origin. The first whorls of ramuli rise from upper secondary segments a little behind the apex of the long shoot; these ramuli occupy the whole height of the segment, being hemiblastic as in *Hemiblasteæ* (*rameaux hémiblastiques*, SAUV.). The bases of the ramuli become part of the segments, which are subject to numerous divisions, at the same time stretching, and gradually the hemiblastically formed branches come to be placed in the uppermost part of the upper secondary segments. Behind the primary whorls of ramuli the peripheral cells of the upper secondary segments produce another (or more), more or less distinct whorl(s) of ramuli. As these take up only part of the height of the secondary segments, SAUVAGEAU calls them *rameaux mériblastiques*.

To begin with only the upper secondary segments are fertile, but gradually the peripheral cells of the lower secondary segments, which also have been subject to numerous divisions, having stretched, likewise produce more or less complete whorls of meriblastic ramuli.

The long shoots are differentiated into a cortex and a medulla. Through the cell divisions of the cortex a vigorous, secondary cortex is gradually formed which surrounds the lower part of the ramuli. From surface cells in the secondary cortex *pousses microblastiques* (Sauv.), normally bearing sporangia, arise between the whorls of ramuli. In the lower part of the plant the outer cells of the secondary cortex produce hyphae, which form a thick continuous *couche cortico-rhizoïdale* (Sauv.). This layer envelops the basal part of the microblastic shoots which occur here; from its surface microblastic branches also may issue.

Finally the verticillate ramuli, the microblastic shoots as well as short shoots issuing from the basal part, may branch in a holoblastic manner, by which *ramules holoblastiques* (Sauv.) arise. From the axillary apical cells hairs develop in pairs.

In the fourth group, *Dichoblasteæ* (Sauv. Remarques p. 272 (1903 p. 338)) the branching is made through a dichotomizing of the apical cell. Each of the two cells becomes the apical cell of a new branch. Further, late developed branches from the pericysts may develop, as e. g. in *Sphacelaria radicans.*

In most of the species both unilocular and plurilocular sporangia are known (*Disphacella,* however, is only known in the sterile state). They are stalked or sessile on the erect shoots, more rarely they may in addition develop directly out of or from the basal part (*Sphacelaria cæspitula* and *S. saxatilis*). In *Cladostephus* and *Chætopteris* they occur on special short shoots, issuing from the cortex of the axis. In the former the cortex of the axis, as appears from what is mentioned above, is a secondary cortex formed by the secondary growth of the segments (in the lower part of the plant it is, as mentioned above, surrounded by a rhizoidal layer); in *Chætopteris* it is of rhizoidal origin. Certain of the rhizoid-bearing *Sphacelarias* (*S. radicans, S. britannica, S. bipinnata,* and *S. racemosa*) may also produce sporangia on the rhizoids, and any real difference between the genera *Sphacelaria* and *Chætopteris,* which are, indeed, both hemiblastic, does not actually exist.

The unilocular sporangia are generally more or less spherical, while the plurilocular ones are cylindrical, broadly cylindrical, pyriform, or nearly spherical. The latter, which in some species may be of two kinds, partly with numerous small compartments, partly with fewer, larger compartments, in most of them have a separate aperture for each compartment. In *S. olivacea,* which according to my examinations is identical with *S. cæspitula,* however, septa are stated by Sauvageau (Remarques p. 75 (1901 p. 59)) to disappear prior to maturity, the contents coming out through a joint apical opening. This experience I have not made in the Danish material of *S. cæspitula.*

In certain species of the genus *Sphacelaria,* in addition to sporangia, propagules of different shape are found, which may vegetatively multiply the species. In

S. bipinnata and *racemosa* I observed detached fragments which at any rate in the former gave rise to new plants. In *Stypocaulon scoparium*, too, a vegetative propagation by detached parts of the plant occurs.

Among the Danish species *Disphacella reticulata* and *Cladostephus verticillatus* occur only in the loose state in our waters, the latter as f. *patentissimus*. On the whole, the former is only known as a loose form. *Sphacelaria cirrosa*, *S. plumigera*, and *Stypocaulon scoparium* occur partly in the attached state, partly in a loose form, f. *patentissima* (*um*). The former two, however, each occur also in another loose form, f. *ægagropila* and f. *pinnata*, respectively.

Common to the f. *patentissima* (*um*) of the three last-mentioned species is the fact that the frond is reduced, consisting of thinner filaments with divaricate branches, issuing at a wide, often right angle, besides being sterile. This form was originally described for *Sphacelaria cirrosa* by GREVILLE (Scottish Cryptogamic Fl., VI, 1828, pl. 317)—whose plant to judge from the figure, however, was attached. Later it was described for a number of other *Sphacelariaceae* by SAUVAGEAU (Remarques). Both authors interpret it as a variety; I myself prefer to use the term *forma*.

Key to the Danish genera.

1. Plant with secondary growth in length and thickness. With verticillate, vegetative ramuli ..... *Cladostephus.*
1. Plant without secondary growth in length and thickness. Without verticillate vegetative ramuli.
   2. The normal branches formed by dichotomizing of the apical cell..... *Disphacella.*
   2. Branches not formed by dichotomizing of the apical cell.
      3. Branches inserted between two transverse walls.
         4. Sporangia occur on special short shoots issuing from an axial cortex formed by rhizoids; propagules lacking ..... *Chætopteris.*
         4. Sporangia generally not of rhizoidal origin; propagules occurring in some species ..... *Sphacelaria.*
      3. Branches leaning against a transverse wall..... *Stypocaulon.*

Hemiblasteæ.

Sphacelaria (Lyngb.). J. Ag.

J. AGARDH, Spec. Alg., I, 1848, p. 29.

The Danish species of this genus most frequently form small tufts, the height of a few mm to about 2 cm. In *S. racemosa* the height of the tufts, however, amounts to 4 cm, in *S. plumigera* even up to 11 cm. The frond of some few species is expanded in low mats of a height of a few mms to about 1 cm. To the naked eye some of the species may bear a resemblance to *Ectocarpus*, from which, however, particularly in the living state, they usually are easily distinguished owing to their stiff shoots. As a rule they are epiphytic on other algae or growing on stones, shells, wood, or the like. The basal part of three of the species, *S. cæspitula*, *S. furcigera*, and *S. bipin-*

nata are partly endophytic; the first two of them may, indeed, also grow on stones and similar hard substrata.

The basal part of the frond in some species consists of simple or branched, creeping stolons, which here and there generally form small disks consisting of one layer. In others the basal part exclusively consists of a single disk, which may have one or more layers. *S. cæspitula* and *S. plumigera* both have a single, several-layered disk, which in the former is vigorously developed; in the latter the disk is strengthened by the descendent rhizoids issuing from the axes. In *S. radicans* and *S. racemosa* stolons spring from the margin of the disk; they may produce additional disks. In *S. cirrosa* and *S. bipinnata*, too, runners are found, but in the former lower lateral branches are involved, which become prostrate, while the runners in *S. bipinnata* are rhizoids.

The erect thallus is in some species differentiated into main axes and branches, while such a separation is only very little visible or lacking in others. In some of the latter (*S. cæspitula*, *S. radicans*, *S. britannica*, and *S. saxatilis*) the branching is scanty and irregular, while the former are richly branched, often pinnate.

The secondary segments in some species are divided by transverse walls, in others the latter are lacking. This character is of taxonomic significance. In *S. radicans* and *S. racemosa* generally only one series of transverse walls are found, whereas *S. cæspitula* and *S. plumigera* generally have more series. In the species whose secondary segments undergo transverse septation, the formation of transverse walls, however, fails to appear in the upper secondary segments in the cells representing branch-initials. In the main axes with a pinnate branching the initials of branches generally grow out into branches immediately after their formation, but apart from these cases many branch-initials remain resting temporarily or for ever. The initials of branches in *S. cæspitula* and *S. radicans*, the so-called pericysts, which in the latter seem to occur in almost every upper secondary segment, have previously been mentioned. The branches produced from them must be regarded as adventitious shoots.

In all the Danish species with the exception of *S. cæspitula*, *S. britannica*, and *S. saxatilis* hairs are known. The growth of these three species is monopodial, whereas the hair-bearing shoots in the others according to the view of Magnus and Sauvageau have a sympodial growth. In *S. Plumula* and *S. plumigera* the hairs are often lacking; if they are present they are terminal or occurring near the apex of some of the pinnae, but not on the main axes, which are monopodia. In most of the species the hairs occur singly, but in *S. radicans* they are found 2(-4) together. In *S. racemosa* and *S. plumigera* the hairs may also be found some few together.

Rhizoids are lacking or rare in some species (e. g. *S. cæspitula*); in others they are numerous. They may either be divaricate, as for instance in *S. radicans*, or descendent. In the latter case they may either be closely apposed to the axes, sometimes being so numerous that they form a thick investment of cortex in the lower part of the axes (*S. plumigera*), or they do not adhere to the axes as in *S. bipinnata*, where they frequently are spirally coiled round the lower part of the latter. In this species,

too, they may form a cortex. In *S. racemosa* both divaricate and descendent rhizoids occur, the latter forming a thin cortex.

In about half of the Danish species propagules occur. In *S. Plumula* and *S. tribuloides* the shape of the propagule is a wedge with 3 small horns; *S. cirrosa* and *S. bipinnata* have trifurcate, *S. furcigera* bifurcate propagules. When the propagule falls off a short sterigma remains, and from here another propagule with its sterigma may develop, etc. The detached propagule leaves a collar-formed scar around the sterigma, and when gradually more consecutive propagules have been produced, more sterigmata, each having a collar, may be observed. The propagules—as well as the sporangia-bearing branches—issue from resting branch-initials, only the whole length of the initial is not used for it.

The detached propagules germinate by the apex or apices of the arm(s) or (and) the stalk which come into contact with the substratum, producing a short filament, which spreads into a disk from which afterwards erect shoots issue. Each disk causes a plant to be formed. The apices which do not get into touch with the substratum, on the other hand, do not produce new plants, but they may develop hairs.

Unilocular sporangia are known in all the Danish species. The same applies to the plurilocular sporangia with the exception of *S. britannica, S. Plumula,* and *S. plumigera.* In the Danish waters unilocular sporangia, however, are only observed with certainty in *S. radicans, S. britannica, S. cirrosa, S. bipinnata, S. racemosa,* and *S. plumigera,* whereas the plurilocular sporangia have only been met with in *S. cæspitula, S. saxatilis,* and *S. bipinnata.* The fact that the latter are not found in *S. racemosa* in Denmark, is no doubt accidental and due to an extremely slight material of this species being collected in winter. In fact, only two plants from this season exist, one of which is provided with unilocular sporangia, while the other is sterile and no more than one cm high.—The plurilocular sporangia are generally of the same type in the same species. In *S. furcigera,* however, they are of two kinds, one of which contains many small loculi, the other fewer, larger ones. The former are possibly antheridia, the latter oogonia.

According to PAPENFUSS's (1934) investigations an alternation of generations betweén 2 morphologically identical generations seems to occur in *S. bipinnata.* The sporophyte bears unilocular sporangia in which meiosis takes place (CLINT 1927)—sometimes in addition plurilocular sporangia with diploid swarmers. The gametophyte, on the other hand, exclusively bears plurilocular sporangia, whose swarmers are isogametes, which copulate, reestablishing the diploid generation.

Key to the Danish species.

(Mainly on the basis of SAUVAGEAU's key in "Remarques", pp. 264—66 (1903, pp. 94—95)).

1. Secondary segments divided by transverse walls.
   2. Basal part of thallus partly endophytic..... 1. *S. cæspitula.*
   2. Basal part of thallus external.

3. Branching pinnate.
4. Rhizoids formed in the plane of branching ..... 11. *S. plumigera.*
4. Rhizoids formed without any order ..... 10. *S. racemosa* f. *arctica.*
3. Branching not pinnate.
4. Unilocular sporangia sessile, in pairs ..... 2. *S. radicans.*
4. Unilocular sporangia stalked, single ..... 1. *S. cæspitula.*
4. Unilocular sporangia in racemes ..... 10. *S. racemosa* f. *typica.*

1. Secondary segments generally not divided by transverse walls.
2. Propagules occur.
3. Propagules broad, wedge-formed.
4. Branching pinnate ..... 9. *S. Plumula.*
4. Branching not pinnate ..... 8. *S. tribuloides.*
3. Propagules narrow, with radiating arms.
4. Propagules bifurcate ..... 5. *S. furcigera.*
4. Propagules trifurcate.
5. Basal part of plant partly endophytic in *Halidrys siliquosa*; rhizoids numerous; propagules rare ..... 7. *S. bipinnata.*
5. Basal part of plant not endophytic; rhizoids rare; propagules very common ..... 6. *S. cirrosa.*
2. Propagules lacking.
3. Indistinct difference between creeping threads and erect filaments; erect filaments 25—30 μ thick; unilocular sporangia only ..... 3. *S. britannica.*
3. Distinct difference between creeping threads and erect filaments; erect filaments 17—21 μ thick; both unilocular and plurilocular sporangia ..... 4. *S. saxatilis.*

1. **Sphacelaria cæspitula** Lyngb.

Lyngbye, Tent. Hydr. Dan., 1819, p. 105, tab. 32 A; Batters, Mar. Alg. of Berwick-on-Tweed, 1889, p. 59, pl. 9 figs. 5—8; Reinke, Sphacelariaceen, 1891, p. 13, pl. 4 figs. 1—4; Kylin, Phaeophyceen schw. Westküste, 1947, p. 26, fig. 24 A; Lund, Nye Alger for de danske Farvande, 1949, pp. 241, 250, fig. 3 A.

Sph. olivacea "Pringsh.", Kuckuck, Bemerkungen [I], 1894, p. 232, fig. 5; Zur Fortpflanzung d. Phaeosporeen, 1912, p. 180, Taf. VIII (19) fig. 4. — Not *Sph. olivacea* Reinke, Atlas, H. 2, 1892, pl. 46.

Sph. olivacea Pringsh. emend. Sauvageau, Remarques, p. 70 (1901, p. 54), fig. 17; Kylin, Algenfl. schw. Westküste, 1907, p. 63.

Sph. olivacea var. *cæspitosa* Pringsheim, Sphacelarien-Reihe, 1873, p. 166, p. p., pl. 9 figs. 1—3, pl. 11 figs. 2—4.

Not *Conferva olivacea* Dillwyn, British Confervæ, 1809, p. 57, pl. C.

Sphaceloderma helgolandicum Kuckuck, Bemerkungen [I], 1894, p. 232, fig. 7.

Sphacelaria helgolandica (Kuck.) Wærn, Remarks on some Swedish Sphacelariaceae, 1945, p. 399.

This alga, characteristic by a thick, several-layered, partly parasitic basal disk and thin, stiff, slightly branched erect filaments which are provided with pericysts and during winter bear large plurilocular sporangia, was first described by Lyngbye on sterile material from the Faroes and Norway. Later it was studied by Batters,

REINKE, and KYLIN. BATTERS described the plurilocular sporangia, but it was with doubt that he referred his plants to *cæspitula*. REINKE confirmed the identity of BATTERS' plants with LYNGBYE's, drawing attention to the parasitic nature of the basal disk. REINKE's mention of the species is accompanied by instructive figures by KUCKUCK. KYLIN calls the species epiphytic, with the basal disks penetrating into the host-plant. KYLIN's plants like LYNGBYE's (which are kept in the Botanical Museum of Copenhagen) and those of BATTERS were growing on the stipe of *Laminaria hyperborea* (= *Cloustoni*), but the species has also been found on *Saccorhiza bulbosa* (cf. REINKE pp. 13 and 37).

In the Danish material the species did not seem to be represented, but with KYLIN's finding from the Swedish west coast being borne in mind, it was to be supposed that it could also be found in Denmark. Hence I made an excursion on March the 4th, 1948, to Tyskerens Rev and Nordvestrevet at Hirsholmene in the northern Kattegat, gathering a lot of specimens of *Laminaria hyperborea* at depths between 4 and 10 m. I succeeded, indeed, in finding the species on the stipe of *Laminaria*, where it seems to be rather common, particularly on the lower part of the stipe, partly in company with *Rhodochorton Rothii*. The species formed low, brush-like tufts, at most 2 mm high, growing so closely together that they apparently formed confluent mats. In section across the stipe of the *Laminaria* the individual plants, however, proved separated.

The basal part was vigorously developed, consisting of a several-layered, parenchymatous disk with marginal growth. The disk penetrates into the cortex of the host, as was easily observed in slides treated with *Eau de Javelle*. From the basal part numerous erect, simple, or slightly and irregularly branched filaments issue, 23—30 μ in diameter. The branches of these are of about the same diameter as that of the mother shoot, so that there is no differentiation in axes and branches. The secondary segments, besides by longitudinal walls, are also divided by transverse walls. A surface view generally shows 1—3 longitudinal walls and (1—)2—3 series of transverse walls.

In several filaments a pericyst occurs in the upper secondary segments (cf. SAUVAGEAU, Remarques, p. 268 (1903 p. 334)). In living material and in material preserved in alcohol they were generally characterized only by their size, but not by their colour, which was like that of the other cells or lighter. When in the microscope they were not turned towards the observer, it was therefore not always easy to perceive them. If with the micrometer screw one adjusts to lower levels, however, they are often disclosed.—Also in LYNGBYE's original material from the Faroes, with which my plants agree excellently regarding vegetative structure, I have found pericysts, which completely agreed with those of my material; but KYLIN, who also examined an original specimen from the Faroes, did not mention pericysts.

Plurilocular sporangia (fig. 1 *A*), which practically were all emptied, occurred in considerable numbers, especially on the lower part of the erect filaments. They were 86—135 μ long and 62—90 μ in diameter, in most cases ovate, borne on a stalk

consisting of 2—3 segments. When the pericysts develop into sporangia, they are generally divided by 1 or 2 transverse walls (fig. 1 *A*).

Later I succeeded in ROSENVINGE's posthumous herbarium to find a small number of small tufts of a species of *Sphacelaria*, which by a comparison with the above-mentioned typical plants proved to belong here. They were collected on January the 5th, 1895, at nearly the same place, but are stated to have grown on *Fucus serratus*. An examination of the host-plant was difficult, since it was only represented by some quite thin chips, but as far as I could decide, the stipe of *Laminaria hyperborea* is involved here, too.

The plants concerned agree completely with those mentioned above. However, the pericysts here were yellowish brown and commoner; in several cases they occurred almost right up to the apices of the filaments. Besides, the plants in the lower part of the filaments bore numerous mature, stalked plurilocular sporangia, which measured 94—156 $\mu \times$ 66—131 μ, and which could be observed by a magnifying glass when the material was soaked and it was placed on the slide.

Finally, completely corresponding plants were found by the author on Sept. 30th, 1948, on the stipe of *Laminaria hyperborea* washed ashore near Kandestederne on the coast of the Skagerak. These plants, however, were sterile, but the sporangia-stalks in several cases were still preserved.

A species which is closely related to *S. cæspitula* is the alga known in the literature under the name of *S. olivacea* PRINGSH., chiefly only divergent by the basal disk growing externally on the substratum (usually stones, shells, and the like, but also *Laminaria*) and by having both unilocular and plurilocular sporangia. This species can originally be traced in PRINGSHEIM (1873), partly under the name of *S. olivacea* var. *cæspitosa*, but this investigator does not separate it from his very comprehensive *olivacea*-complex (which has nothing to do with DILLWYN's *Conferva olivacea*, as was supposed by PRINGSHEIM). After PRINGSHEIM's work the misleading designation of *S. olivacea* PRINGSH. was attributed to it by KUCKUCK, who is the first to have given a precise description of it. Later it was made the object of a thorough investigation by SAUVAGEAU and henceforth got the designation *S. olivacea* PRINGSH. emend. SAUV. This investigator, however, uses the specific name of *olivacea* from the view that PRINGSHEIM was the first to use it for a new species in such a way that it is possible to recognize it (SAUVAGEAU, Remarques p. 56 (1901 p. 27)). On the other hand DILLWYN's *olivacea* is said to be too insufficiently described for a safe recognition for which reason it ought to be forgotten. In his treatment SAUVAGEAU (Remarques p. 71 (1901 p. 56)) further calls attention to the fact that the crustaceous *Sphaceloderma helgolandicum*, established by KUCKUCK, represents nothing but the basal disk of *S. olivacea*. Consequently, WÆRN proposes to alter the name of the latter to *S. helgolandica*, stating that the name of *olivacea* applies to DILLWYN's *olivacea*.

This species has in the Danish waters been found in the North Sea (at a depth of 27 m), in the Skagerak (in 8—10 m and 23 m) and in the northern Kattegat (from 6—8 to 19 m). It has been collected during the months of March, May, July,

August, and October and has been found on shells and concretions. The present plants, which in the dried state are dark green or olive green, were not, with the exception of a few specimens, more than 0.6 cm high, but in all the plants from summer and autumn the erect filaments were broken off at a greater or smaller distance from the apex. In the plants from May, collected on the 5th, two generations of erect shoots could be observed; partly old, brown, branched, broken remnants, having wintered and still bearing sporangia-stalks, partly newly formed, light, long, branched, intact, sterile filaments issuing from the old ones. These plants measured 0.8 cm in length, which almost exclusively applies to the newly formed shoots.

Common to the present specimens was the fact that below they have a several-layered, parenchymatous disk growing marginally. The cells of the disk in the radial section are arranged in vertical series. In continuation of the latter the erect filaments issue, which are 21—30 μ (—33 μ) thick, simple or sparingly or irregularly branched without any differentiation in axes and branches. The secondary segments are provided with transverse walls; often up to three series of them occur in each secondary segment. Pericysts are seen now and then in the upper secondary segments, but they are generally characteristic by their size only, not by their colour (*p* in fig. 1 *B*).

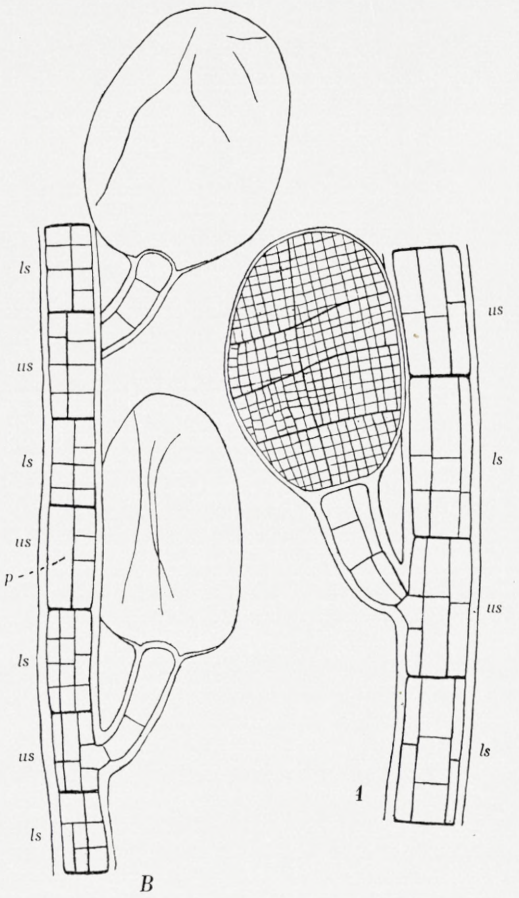

Fig. 1.
Sphacelaria cæspitula from the northern Kattegat. *A*: erect filament with an emptied, plurilocular sporangium. *B*: erect filament of *Sph. olivacea* "Pringsh." with emptied unilocular or plurilocular sporangia. *us*: upper, *ls*: lower secondary segments; p: pericyst. — *A*: Tyskerens Rev, 4—10 m; on stipe of *Laminaria hyperborea*, 4-III-1948 (S. L.). *B*: between Laurs Rev, Marens Rev and Deget, 6—8 m, on *Modiolaria*, 4-VII-1904. — *A-B*: ×355.

In a single case I observed two short rhizoids, which arose beside one another from an erect shoot in a place where the shoot—probably as a consequence of an injury—was somewhat bent.—According to Sauvageau (l. c. p. 73 (1901 p. 58)) rhizoids are absent in the species. Still this author later (1909 p. 26) mentions that he found long, very divaricate rhizoids on some plants collected by Kuckuck in the month of May near Heligoland.

The great majority of the plants examined were sterile. On the plants from March, collected on the 4th, however, numerous emptied, plurilocular sporangia

occurred. Also in a plant from July many emptied, usually rather well preserved sporangia borne on a stalk consisting of three or, more rarely, two segments were found (fig. 1 *B*). The sporangia of this plant were roundish, short cylindrical, or ovoid, 82—107 μ long and 66—78 μ in diameter. While some of them were distinctly plurilocular, a whole network of septa occurring in them, it was doubtful, whether others were unilocular or plurilocular, as they did not show septa. That the 2 kinds of sporangia may occur on the same plant is known from PRINGSHEIM's description. On the other hand septa apparently often disappear at an early time in the plurilocular sporangia. According to SAUVAGEAU they disappear already before maturity.

Finally a few emptied sporangia—without networks of septa—were observed in the above-mentioned specimens from May as well as in a plant from the beginning of October. In most cases only the stalks were left in these individuals.

Besides the plants mentioned, a few sterile specimens from the Little Belt and the South Funen waters are found in the herbarium. They have been examined by SAUVAGEAU, who with some reservation refers them here. One (No. 1385) bears the signature "probablement *S. olivacea*", the other (No. 2109) "peut-être *S. olivacea*". The former is mentioned by SAUVAGEAU in Remarques p. 212 (1902 p. 400) and later in "Sur le développement échelonné de l'Halopteris . . . et Remarques sur le Sph. radicans", 1909 p. 26, and in the list of errata in Remarques p. 629. According to the view expressed in the last-mentioned places a new species or *S. olivacea* with holoblastic branches is perhaps involved.

A more detailed study of *S. cæspitula* and *S. olivacea* PRINGSH. emend. SAUV. now has convinced me that the two species are really identical. It appears first from a comparison between LYNGBYE's original material of *S. cæspitula* from the Faroes, and a plant which by SAUVAGEAU is determined as *S. olivacea* PRINGSH. and which therefore must be a perfectly valid expression of what this author means by *S. olivacea* PRINGSH. emend. SAUV. The latter specimen originates from Mosterhavn south of Bergen on the Norwegian west coast, where it was growing on the stipe of *Laminaria hyperborea;* it was collected by STRÖMFELT and later by FOSLIE sent to SAUVAGEAU, who mentioned it in Remarques p. 212 (1902 p. 400). Thanks to Professor ROB. LAMI's kindness I had an opportunity to borrow it from Muséum national d'Histoire naturelle in Paris. Since it was not attached to its substratum, I have not, however, been able to decide whether the basal part was parasitic, but apart from this it seems to agree excellently with LYNGBYE's plants. In both cases the basal part is discoid; the erect filaments are slightly branched, about 25—33 μ in diameter, showing transverse walls in the secondary segments, frequently with periçysts in the upper secondary segments. On the Norwegian plant emptied unilocular sporangia occurred attached to unbranched stalks generally consisting of three segments; LYNGBYE's plants were sterile, but similar stalks of sporangia were still preserved in several cases.

Secondly my observations in nature also confirmed the identity of the two species. During the above-mentioned excursion to Hirsholmene I found on shells

of *Balanus*, occurring between the haptera of *Laminaria hyperborea*, some tufts, up to 6 mm high, provided with plurilocular sporangia which—apart from their size and external basal part—in every respect corresponded with the partly parasitic specimens of *S. cæspitula* growing on the very *Laminaria*-stipe. There is no doubt that they also are identical with *S. olivacea* PRINGSH. emend. SAUV.

Thus it is the nature of the substratum which actually decides whether the basal part penetrates into the substratum or grows externally. If the plant grows on a relatively soft substratum like the stipe of *Laminaria hyperborea*, the basal part will generally be partly parasitic, and *S. cæspitula* is involved; if on the other hand it grows on shells, stones, or other hard substrata the plant is regarded as *S. olivacea* PRINGSH. emend. SAUV.

In this connection it is not without interest that KYLIN, who in 1907 (p. 64) recorded *S. olivacea* PRINGSH. emend. SAUV. from the Swedish west coast as growing on stones, shells, and the stipe of *Laminaria Cloustoni* (= *hyperborea*) in 1947 (p. 26) referred the specimens from the host-plant mentioned to *S. cæspitula*. In the work of 1947 the author does not enter *S. olivacea* at all and he gives no information about the identity of the *S. olivacea*-plants from stones and shells mentioned in the paper of 1907. On the basis of my examination it is to be concluded that they, too, belong to *S. cæspitula*.

Localities. **Ns:** eQ (Dana Station 2856), 8 miles NW by W $^1/_2$ W of Lodbjerg lighthouse, 27 m. — **Sk:** Dana St. 2904, 13$^1/_2$ miles NE $^1/_2$ E of Hanstholm lighthouse, 23 m (C. A. Jørgensen); ZK°, Mellemgrund off Lønstrup, about 1 mile from the shore, 8—10 m, on *Buccinum*; Kandestederne, on stipe of *Lamin. hyp.* washed ashore (S. L.). — **Kn:** fC (Dana St. 2870), 3 miles SW by S of Skagen lighthouse, 15 m, on shells of *Turritella*, October 4th, with sporangial stalks and a few empty sporangia; N of Græsholm, 9—10 m, on stipe of *Lamin. hyp.*(?), January, with mature pluriloc. sporang.; Tyskerens Rev or Nordvestrevet at Hirsholmene, 4—10 m, on stipe of *Lamin. hyp.* and shells of *Balanus*, March, empty pluriloc. sporang. (S. L.); ibid. May, on shells of *Balanus*, with preserved sporangial branches and a few empty sporangia (S. L.); between Laurs Rev, Marens Rev, and Deget, 6—8 m, on *Modiolaria*, July, with empty pluriloc. sporang.; Trestens Rev, on concretions, July; IX, Trindelen lightship NE $^2/_3$ E 4 miles, 19 m, on *Buccinum*. — **Lb** and **Sf:** 2 questionable localities, see above (No. 1385: N of Fænø Kalv, 13 m, on stones, and No. 2109: CC, south side of Hornenæs, 8 m, on *Mytilus*).

2. **Sphacelaria radicans** (Dillv.) C. Ag.

C. AGARDH, Systema Alg., 1824, p. 165; HARVEY, Phycol. Brit., II, 1849, pl. 189; TRAILL, On the fructification of Sph. radicans, Harvey, and Sph. olivacea, J. Ag., 1889, p. 77, pl. 2 fig. 1; REINKE, Sphacelariaceen, 1891, p. 8, pl. 3 fig. 1; KUCKUCK, Bemerkungen [I], 1894, p. 229 fig. 4; SAUVAGEAU, Remarques, p. 56 (1901, p. 27), fig. 14 A—B, E—J, fig. 15; Sur le développement échelonné de l'Halopteris (Stypocaulon Kütz.) scoparia Sauv. et Remarques sur le Sph. radicans Harv., 1909, p. 64, figs. 11—12; JÓNSSON, Mar. Alg. Iceland, II, 1903, p. 159; KYLIN, Algenfl. schw. Westküste, 1907, p. 62; Phaeophyceen schw. Westküste, 1947, p. 27, fig. 24 C; WÆRN, Remarks on Some Swedish Sphacelariaceae, 1945, p. 400.

Conferva radicans DILLWYN, Brit. Confervæ, 1809, p. 57, Sup Plate C; English Botany, Vol. 30, 1810, tab. 2138.

Species growing gregariously, forming dense, often rather extensive dark brown mats or velvety coatings. The height generally amounts to about 1 cm. The colour in the dried state at times almost black.

The plant has especially been studied by KUCKUCK and SAUVAGEAU (Remarques and 1909). The horizontal part consists of many small, thin disks formed by coalescent filaments. Seen from below the disks remind of e. g. a *Myrionema*; seen from above the structure of the disks—consisting of radial threads—are more indistinct. Some of the radial threads extend farther than the margin of the disks, developing into simple or branched stolons which in structure correspond with the erect filaments; they form new disks.

From the basal disks issue erect filaments. They are rather stiff, slightly and irregularly branched and not differentiated into main axes and branches, in Danish plants 33—about 50 μ in diameter. The secondary segments as a rule are of the same height as the diameter, provided with transverse walls. Usually one series of transverse walls occurs, but in other cases the secondary segments contain at any rate up to three series—or some of the secondary segments may entirely be devoid of transverse walls. Generally 2—5 longitudinal walls are observed when the secondary segments are seen in a surface view. In most of the upper secondary segments one yellowish brown to dark brown pericyst occurs (fig. 2 F), which may develop branches, rhizoids, and sporangia, mainly the latter. A great number of the pericysts, however, never develop. When the longitudinal growth of the filaments ceases, the apical cell is divided by walls variously directed. From the lower part of the erect filaments numerous, divaricate rhizoids issue.

The erect filaments sometimes bear hairs. The latter were first described by SAUVAGEAU (Remarques p. 60 (1901 p. 31)), who later (1909) also made them the object of a special study. They are characteristic by occurring in pairs or up to 4 together; they arise by the lenticular cell dividing into 2—4 cells, each growing into a hair. They seem to be rare and are supposed—at least in France—to occur only in summer, when the species is sterile. Referring to the fact that JÓNSSON found hairs neither in Icelandic (1903) nor in Greenlandic plants (Mar. Alg. East Greenl., 1904, p. 40), the latter being sterile and originating from June and July, SAUVAGEAU concluded that the hairs perhaps do not occur in all latitudes.—In this connection, however, it should be mentioned that I observed hairs on a specimen collected in northern Norway near Tromsø at about 70° N. lat. on August 8th 1949 by Mr. ERIK JAASUND, Gothenburg.

The hair-bearing individuals, which SAUVAGEAU mentioned in his paper from 1909 (p. 66), originated from an aquarium culture which KUCKUCK had established at Heligoland. They were taken out in December and were sterile and intact, the upper part of the erect filaments not being broken off, as is generally the case in nature at this time of the year. The hairs were particularly found on the upper half or uppermost third of the filaments, occurring in pairs of 4 together; in the latter case the lower pair seemed to be placed in the axil of the upper one. In some cases

the longitudinal wall, which divided the lenticular cell into two hairmother-cells was oblique so that these were of unequal size. SAUVAGEAU interprets this arrangement as a special case of sympodial branching, comparing the phenomenon with the holoblastic method of branching in *Halopteris* and *Stypocaulon*, where the lenticular cell, being cut off from the apical cell of the axis, is divided by a transverse wall into a small apical cell and a larger, lower cell developing into a branch. The two hairs in *S. radicans* would correspond to the shoots produced by these cells.

In the aquarium plants in question SAUVAGEAU further found several holoblastic branches. In some cases the paired hairs were in the axil of the branch, in others a little above the axil of the branch, in others again placed laterally, possibly even on the opposite side of the axil of the branch. It was characteristic of the branches that their angle to the axis was small.

In the Danish waters I have, with certainty, met hairs within three collections only, all from April, originating from the northern Kattegat, the Samsø area, and the Sound (Saltholm), respectively. In the two first cases the plants were sterile (in a single plant, however, two paired sporangia occurred on a rhizoid), growing on the lower, thick, stalk-like part of *Fucus* together with *S. cirrosa* and other epiphytes. The hairs occurred only in the upper part of the filaments formed during the spring. They mainly occurred four together, in some cases, however, in pairs (fig. 2 A). In a few cases holoblastic branches, too, occurred, in accordance with the statements in SAUVAGEAU. The plants from the Sound bore a few emptied besides some incompletely developed unilocular sporangia; they were growing on stones and chiefly consisted of old, dark filaments. Only a single, rather young filament bore two paired hairs.

On a plant collected on a piece of cinder in the northern Kattegat in July twin hairs, too, occurred, or four hairs together, but as the plant in several respects deviates somewhat from the present species I refer it here with some doubt. Below, it had several small basal disks provided with stolons. The former issued erect filaments, up to well over 1 cm high, somewhat lengthened and flaccid. Rhizoids were absent or occurred only in an extremely small number. The erect filaments were 29—35 μ in diameter, slightly branched, the secondary segments often remarkable long; the upper secondary segments not infrequently possessed a pericyst. The secondary segments on an average showed one or two longitudinal walls in surface view, but only in half of them, at most, transverse walls were observed. Most branches seem to be of holoblastic origin, the twin hairs being placed in the axil or laterally. These branches were of considerable length, issuing similar branches themselves.

In *S. radicans* both unilocular and plurilocular sporangia are known, but of the latter up till now only a single one has been observed by KUCKUCK at Heligoland. It was stalked, occurring together with a few-celled shoot as a proliferation of an emptied unilocular sporangium. On the other hand propagules are not known.

The unilocular sporangia are ovoid or spherical. According to the literature they are generally sessile on the erect filaments, the basis partly enclosed in the filament,

although they also may be found on the rhizoids. They most frequently occur in pairs, but one of them may now and then be suppressed. Sometimes some of the sporangia are stalked, but in such cases, too, they may occur in pairs. In specimens from Falmouth Holmes (1889 p. 80) found sessile sporangia in the upper part of the plant, stalked ones below. At Heligoland Kuckuck noticed short shoots bearing

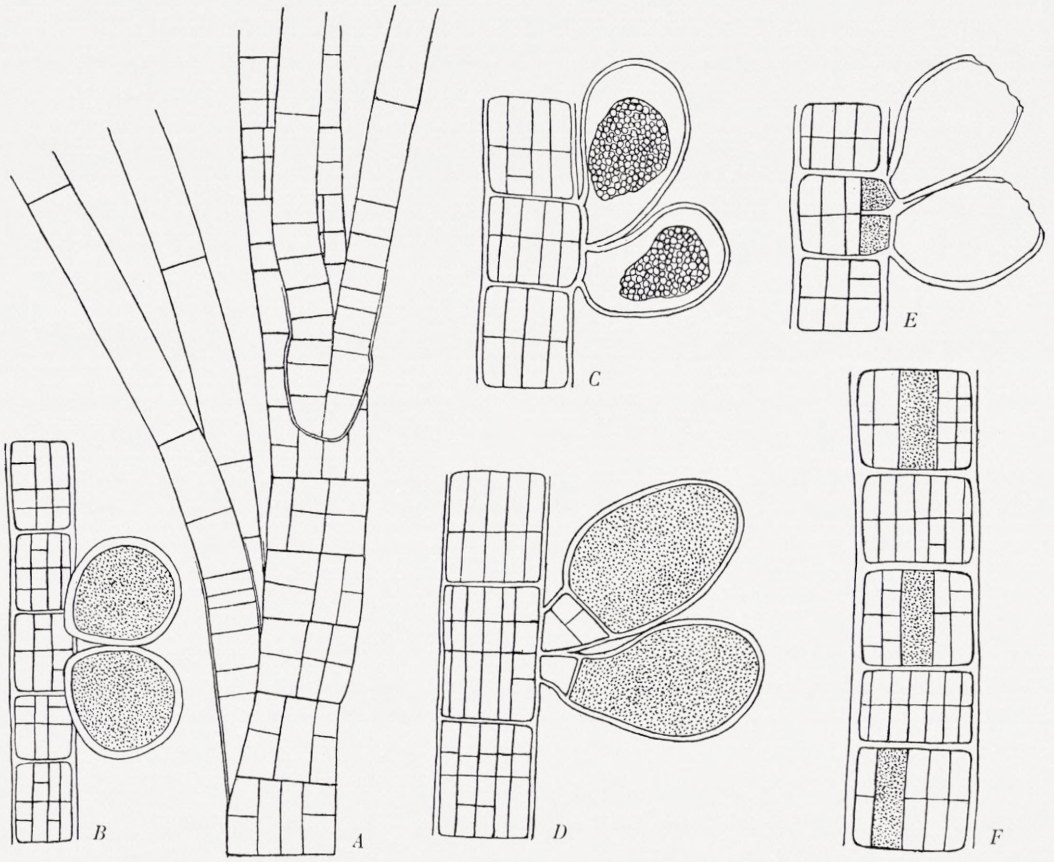

Fig. 2.
Sphacelaria radicans. *A*: upper part of a hair-bearing filament from the spring. *B-E*: unilocular sporangia. *F*: filament with pericysts. — *A*: Northern Kattegat, Frederikshavn harbour, on stalk of *Fucus*, 28-IV-1897 (F. Børgesen); *B*: Saltholm near Copenhagen, on stones, 24-I-1948 (S. L.); *C-F*: north coast of Sjælland. *C*: Gilleleje, on wood, 17-II-1906; *D-F*: between Hundested and Spodsbjerg, 1 m, on stones, 22-I-1948 (S. L.). — *A-F*: ×355.

up to four sporangia at the apex as well as emptied sporangia, which were proliferated by other stalked sporangia. Additional to the erect filaments rhizoids were inhabited by sporangia. During the fructification the upper part of the erect filaments and the longest branches are broken off in nearly the same plane (Sauvageau 1909 p. 65).

The time of fructification is generally given in the literature as falling in the winter. Jónsson (1903), however, in his Icelandic plants observed sporangia both in December and June.

In the Danish material I have met with unilocular sporangia—and only unilocular ones—in plants which were collected in January, February, April, July, and August. However, the sporangia only had any contents in the plants from the two first months, while those from the other months were always empty, apart from a few rhizoidal sporangia from April. The fructifying plants from January were collected by the author at Hundested on the north coast of Sjælland on the 22nd and at Saltholm near Copenhagen on the 24th; in both cases the fertility was relatively small. The plants from February originate from Gilleleje on the north coast of Sjælland, where they were collected by ROSENVINGE on the 17th; they were abundantly supplied with unilocular sporangia.

In most cases the unilocular sporangia were sessile on the erect filaments (fig. 2 B—C, E), but numerous of them, however, were short-stalked (fig. 2 D), mostly fastened to a unicellular stalk. The two categories occurred mixed together. In some cases one of the sporangia was suppressed, while the other was stalked and might laterally bear a sessile sporangium. In some cases the sporangium occurred on rather a long stalk, indeed, once I saw a sporangium terminally upon a polysiphonous branch, consisting of up to 10 secondary segments (I regard it as out of the question that an attack of a chytridiaceous fungus might have been involved). Still more forms of insertion of sporangia might be mentioned. The mature ones occurring on the erect filaments measured in the plants from February 53—66 × 45—60 μ (the measurings carried out on plants, which had been kept as a glycerine micropreparation).

Besides on the erect filaments unilocular sporangia were common on the rhizoids. One of the two above-mentioned rhizoidal sporangia from April measured 41×45 μ, while the other, which was spherical, was 53 μ in diameter.

According to KUCKUCK the upper sporangium develops from an upper pericentral cell of a secondary segment; the lower one does not develop direct from the lower pericentral cell of this segment, but only from an upper daughter pericentral cell. According to SAUVAGEAU the twin sporangia often develop from a pericyst, which divides transversally.

In the Danish plants the twin sporangia frequently seem to occur as described by KUCKUCK (cf. fig. 2 B, D). In a number of cases, however, I have observed that the sporangia did not originate from casual pericentral cells, but just from a pericyst divided transversally (cf. fig. 2 E), and I suppose that they always—or nearly always—have this origin (apart from the rhizoidal sporangia). This would, indeed, seem natural considering that the sporangia always develop from the upper secondary segments, in which, exactly, the pericysts are found. During the formation of sporangia the pericyst may be further divided transversally, a fact which may explain KUCKUCK's description of the position of the lower sporangium.

Sphacelaria radicans undoubtedly has rather a wide distribution in the Danish waters, generally occurring in shallow water, usually at the ordinary water-mark or a little below, more rarely a little above. At Saltholm I saw it in the company of *Sphacelaria britannica* at a depth of 1 m. In one case it was found down to a depth of 3—5 m,

in another case to 8 m. Besides on stones it has been observed on wood and, as mentioned above, as an epiphyte on *Fucus*. It generally retains a lot of grains of sand, particles of oozy bottom and the like.—I have only examined part of the material available. Therefore the following list of localities is not exhaustive.

Localities. **Kn:** Busserev and Kolpen, near Frederikshavn; Marens Rev and outside the latter, on cinder, with hairs in July (determination uncertain); Frederikshavn harbour, on *Fucus*, with hairs in April (F. Børgesen). — **Ke:** Gilleleje, on wood at the ordinary water-mark. — **Ks:** Between Hundested and Spodsbjerg, 1 m, on stones (S. L.); mole at Tisvilde Leje. — **Sa:** PA, near Albatros on the western side of Sjællands Odde, 8 m, on *Fucus*, with hairs in April; Juelsminde. — **Su:** Saltholm near Copenhagen, January, April, and November (S. L.). In the plants from April a hair-bearing filament was noticed.

3. **Sphacelaria britannica** Sauv.

Sauvageau, Remarques pp. 56, 66 ff. (1901, pp. 27, 50 ff.), fig. 16; Jónsson, Mar. Alg. Iceland, II, Phæophyceæ, 1903, p. 159, fig. 16; Wærn, Remarks on some Swedish Sphacelariaceae, 1945, p. 402, pl. 2; Lund, Nye Alger for de danske Farvande, 1949, pp. 244, 251, fig. 3 C—D.

Sphacelaria olivacea J. Ag. partim, Traill, On the fructification of Sph. radicans, Harvey, and Sph. olivacea, J. Ag., 1889, p. 78, pl. 2 fig. 2; Holmes, Remarks on Sph. radicans, Harv., and Sph. olivacea, J. Ag., 1889, p. 79.

Sph. olivacea (Dillw.) Ag., Kylin, Phaeophyceen schw. Westküste, 1947, p. 27 fig. 24 B.

Conferva olivacea (?) Dillwyn, British Confervæ, 1809, p. 57, Sup Plate C.

Sph. radicans (Dillw.) Harv., *f. olivacea* (Dillw.) Batters, Mar. Alg. Berwick-on-Tweed, 1889, p. 60; Traill, Mar. Alg. Orkney Islands, 1891, p. 312.

In 1809 (p. 57, Sup Plate C) Dillwyn described a new alga from the Orkneys under the name of *Conferva olivacea*. The description, which was made on the basis of sterile material, was, however, too insufficient for a safe recognition. This, among other things, caused that later it was confused with *Conferva radicans*, described at the same time by Dillwyn. A further confusion took place in 1873, when Pringsheim erroneously thought that he had found the species at Heligoland, besides extending *S. olivacea* to include several distinct species. In what follows some features of the use of the specific name of *olivacea* are given, reference at the same time being given to the detailed compilations in Sauvageau (Remarques p. 51 (1901 p. 22)) and Wærn (1945 p. 397).

After Dillwyn's description *Conferva olivacea* was re-described and depicted in English Botany (Vol. 31, 1810, tab. 2172), but without any better result. In 1828 it was by C. Agardh (p. 30) referred to the genus *Sphacelaria*. Later J. G. Agardh (1848 p. 31) extended *S. olivacea* to comprise *S. radicans*, too, which is entered as a special variety. About the same time Harvey (Phycol. Brit., II, 1849, pl. 189) likewise united *olivacea* and *radicans*, but he retained *radicans* as the specific name, giving *olivacea* as a synonym.

Harvey's course of procedure was followed by other authors, but in 1889 Traill (p. 77) again entered *S. olivacea* and *S. radicans* as 2 distinct species. Simultaneously this author described and depicted for the first time unilocular sporangia for the

supposed *S. olivacea*. They are stalked unlike those in *S. radicans*, which generally are sessile. HOLMES (1889 p. 79) agreed in this taxonomic view, while BATTERS (1889 p. 60) again united the two species under the name of *S. radicans*, entering *S. olivacea* as a variety, a method which TRAILL (1891 p. 312) himself followed later. *Olivacea* sensu TRAILL, HOLMES, and BATTERS was later interpreted by SAUVAGEAU (Remarques p. 56 (1901 p. 27)) as a new species, *S. britannica*, with the argument that DILLWYN's *Conferva olivacea* is not recognizable.

In PRINGSHEIM (1873) *S. olivacea* includes no less than three species, viz. *S. radicans*, *S. furcigera*, and the alga later known under the name of *S. olivacea* PRINGSH. Apart from the fact that the last-mentioned species has nothing to do with DILLWYN's *Conferva olivacea* either, PRINGSHEIM has thus made the conception of *olivacea* still more obscure by referring the two first, distinct species here.

In his monograph on the *Sphacelariaceae* REINKE (1891 p. 6) partly follows PRINGSHEIM, entering *S. olivacea* with the latter as the author, but in contradistinction to PRINGSHEIM, he separates *S. radicans* from *S. olivacea*. On the other hand REINKE also added to the confusion about *S. olivacea* by referring here a plant which he found in the Baltic (Atlas, H. 2, 1892, pl. 46). The latter, however, has nothing to do with *S. olivacea*. By SAUVAGEAU (Remarques p. 246 (1903 p. 75)) it was referred to *S. racemosa* f. *typica*, by LEVRING (1940 p. 44) to *S. racemosa* f. *arctica*, while WÆRN (l. c. p. 398) regards its identity as obscure. I myself regard it below (p. 47) in the same way as LEVRING.

In KUCKUCK (1894) the specific name of *olivacea* is used about *S. olivacea* "PRINGSH." (cf. above, p. 14). SAUVAGEAU (Remarques p. 70 (1901 p. 54)) also employed it in this way although on other grounds.

Thus it will be seen that the conception of the specific name of *olivacea* by KUCKUCK and SAUVAGEAU does not correspond with the interpretation of it by British algologists. Whereas the latter by *S. olivacea* understand the supposed *Conferva olivacea* in DILLWYN, the former use the name for *S. olivacea* PRINGSH. sensu KUCK. Since the last-mentioned species, as appears from my examination pp. 16—17, is identical with *S. cæspitula* the designation *S. olivacea* PRINGSH. must be dropped.

In his flora of Phaeophyceae from the Swedish west coast KYLIN (1947 p. 27) after the fashion of the English algologists uses the specific name of *olivacea* for the supposed DILLWYN-plant. Owing to the insecurity of the recognition of *Conferva olivacea* I prefer to use the name *S. britannica* SAUV. for the species in which TRAILL described the unilocular sporangia. Therefore the specific name of *olivacea* in my opinion ought to be left out completely from the taxonomy of *Sphacelaria*.

S. britannica has been thoroughly described and depicted by SAUVAGEAU (l. c. p. 66 (1901 p. 50)) on the basis of an examination of a couple of specimens from Berwick-on-Tweed on the British North Sea coast, collected by BATTERS. Later the species was made the subject of comment by, among others, JÓNSSON (1903 and 1904 p. 41) and WÆRN (1945), who both furnished pictures.

In the present Danish material of the genus *Sphacelaria* it was not represented. However, it must, after WÆRN's finds, among other places at Kullen on the Swedish coast of the Kattegat and in Höllviken a little SSW of Malmö in the Swedish part of the Sound, be taken for granted that Danish plants might also be found. During a search for the species on April 17th, 1947, at Saltholm near Copenhagen I actually succeeded in finding it. It grew here on stones (partly flint) at a depth of 1 m quite close to the jetty, forming—partly together with *S. radicans*—rather characteristic low mats, 2—3 mm (up to 5 mm) high, dense, velvety, sand-binding, to an extent of up to about 5—6 cm^2.

The horizontal part of the thallus consists of more or less irregular, branched stolons, which are entangled in one another and which often issue lateral excrescences forming small irregular parts of cells or marginally growing disks of varying size. The basal part thus is more vigorously developed than in SAUVAGEAU's plants and seems to correspond to those of JÓNSSON's. Also in WÆRN's Swedish plants disks occurred (cf. pl. 2 on the right). Rhizoidal attaching threads issuing from the stolons as seen in this figure, also occurred in my plants. The stolons generally are a bit thicker and more irregular than the erect filaments (in *S. saxatilis* this difference is more distinct); frequently they are sinuous.

The erect filaments are very flexible; they issue partly from the actual basal part (stolons, disks, and irregular parts of cells), partly from stolons projecting outwards. In most cases they issue at a wide angle, frequently rectangularly. They are not differentiated into main axes and branches. The branching is most frequently slight, irregular, scattered, rarely opposite. In a few cases somewhat appressed branches were observed. In other, rare cases divaricate branches, slightly sinuous, issued almost rectangularly; they were to be interpreted as intermediate between branches and rhizoids. The diameter of the filaments usually amounts to 25—30 μ, while the thinner branches only are 16—18 μ, the thicker filaments on the other hand up to 33 μ in diameter. Local swellings of the filaments, as mentioned by SAUVAGEAU and shown in WÆRN's figure, are rather common; they measured 37—45 μ in diameter.

The secondary segments in many cases are a little longer than broad, or the length is equal to the breadth, more rarely the breadth greater than the length. In surface view generally 1—2 longitudinal walls may be observed, or longitudinal walls are completely lacking in some secondary segments. More rarely 3 longitudinal walls are seen. In most cases transverse walls are lacking, although they are not uncommon (fig. 3 D-E). In this connection it should be mentioned that WÆRN (l. c. p. 403, footnote) mentioned a *Sph. britannica*? with transverse walls in the secondary segments from the Swedish west coast.

In numerous cases erect filaments occurred in which a larger or smaller part was broken off. In this species, too, the great capability of regeneration of the *Sphacelariaceæ* is confirmed, 1—4 new branches frequently issuing from the truncation. In other cases a branch and a sporangium are involved (fig. 3 A), two branches and a sporangium or a branch and several (up to 4 ?) sporangia. In the truncated filament depicted

in fig. 3 A, the upper part of the branch was decaying and almost colourless. From the lowermost secondary segment of the decaying part a long rhizoid of the same thickness and appearance as the branch was given out. From a filament which was broken off below, two rather long rhizoids issued; from another similar filament a single, long rhizoid developed.

For that matter rhizoids are not uncommon on intact, erect filaments either; they chiefly occur on the rather old filaments. They are either somewhat divaricate

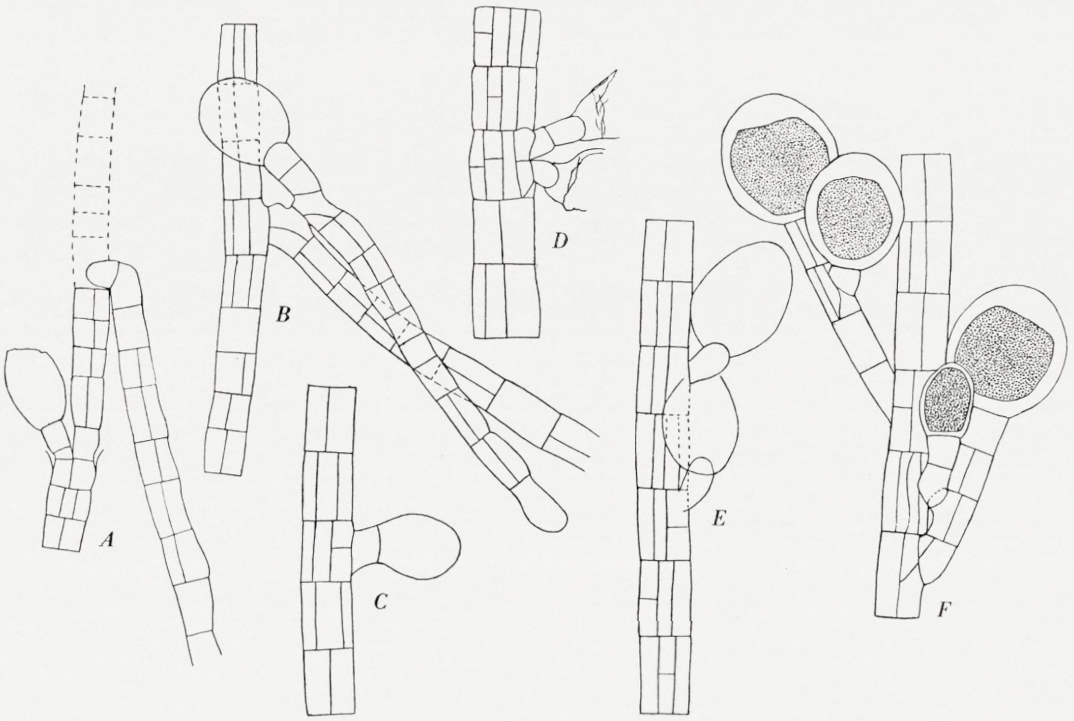

Fig. 3.
Sphacelaria britannica. *A*: part of an erect filament, which from a truncation has sent out a unilocular sporangium, now emptied, and a branch, which at a little distance higher up is decaying (the dotted part). From the lowermost secondary segment of the decaying part a rhizoid is issued. *B*: erect filament with rhizoid, which from its uppermost cell sends out another rhizoid, in its turn issuing a stalked unilocular sporangium from its uppermost cell. *C-E*: emptied, unilocular sporangia. *F*: fragment of erect filament with unilocular sporangia, nearly mature. — Saltholm near Copenhagen, 1 m, on stones. *A-E*: 17-IV-1947; *F*: 24-I-1948 (S. L.). — ×284.

or descendent. In the first case they were simple, usually almost straight, often of a considerable length. They frequently bear the greatest resemblance to the erect filaments and may possess longitudinal walls in many of the secondary segments, so that an examination of the direction of growth in relation to the erect filaments in numerous cases is necessary to prove the rhizoidal character. A few divaricate rhizoids, however, were thin and irregular, having a typical rhizoidal appearance. The descendent rhizoids generally were short, sometimes branched; they did not adhere to the erect filaments.

In the divaricate rhizoids as well as in the descendent ones an erect shoot might develop from the uppermost cell of the rhizoid. In a single case a rhizoid of the second order arose from the uppermost cell of a rhizoid, the former in its turn bearing a stalked sporangium on its uppermost cell (fig. 3 *B*). The erect filament in this case had developed after a truncation and the rhizoid of the first order issued from the 13th secondary segment above the truncation. Rhizoidal sporangia issuing from the uppermost cell of a divaricate rhizoid have, for that matter, been observed in several cases.

The erect filaments, frequently already at a short distance above the base, bear numerous ovoid, oval, or spherical unilocular sporangia, which practically all were emptied, but frequently well preserved. The emptied sporangia measured 45—66 μ in length and 33—45 μ in diameter. Three sporangia possessing contents measured 49—57 × 41—45 μ. The sporangia generally are born on a short monosiphonous, 1—2-celled stalk or on a stalk consisting of several cells just as they may be terminal on a rather long branch some of which secondary segments are divided longitudinally. They are usually scattered (fig. 3 *E*), but they may issue from the same secondary segment, either beside one another or nearly opposite or one below the other (fig 3 *D*). In one case I noticed an erect filament in which 3 consecutive secondary segments bore a unilocular sporangium. At times divaricate sporangia are observed (fig. 3 *C*).

In many cases the emptied, unilocular sporangia were proliferated by a shorter or longer sporangial stalk, bearing itself an emptied, unilocular sporangium. In other cases the emptied, unilocular sporangia were proliferated by long, vigorous branches, which sometimes bore lateral, stalked, emptied, unilocular sporangia.

Hairs and propagules were not observed and they are not known. Neither did I succeed, in spite of going through numerous preparations, in detecting plurilocular sporangia, which are likewise unknown.

On Januar 24th of the following year I collected additional material of the species in the same locality. On the whole these plants, which chiefly bore mature unilocular sporangia, agreed excellently with those from April, but on an average they were not so high, a large number of the erect filaments having been truncated a little distance above their base. They formed quite low mats, which owing to numerous retained grains of sand were rather hard. The truncation of the erect filaments probably were caused by the waves during rough weather. The plants from April for a long time had not been exposed to a similar mechanical influence, the locality having been ice-bound for about three months until shortly before the collection. The fructification in these plants thus had mainly taken place under the ice.

Moreover, the fertility of the fresh plants were considerably poorer, a fact which not only may be explained through the numerous broken, erect filaments, but perhaps is due to the sporangia being not very numerous in this month. At any rate the sporangia on those plants with intact, erect filaments which were observed in a few cases, were rather infrequent. However, it should be noted that when emptied, unilocular sporangia were so numerous in April, some of them may very well originate from January,

others from February or March, for they are capable of being preserved long in the empty state.

Most of the unilocular sporangia like those in the material from April were borne on a short stalk. In a few cases the sporangial stalk was branched as shown in fig. 3 *F*. The largest mature unilocular sporangia measured 57—62 $\mu \times 49$—53 μ (measured in a glycerine preparation). Nor did I find any plurilocular sporangia in these plants.

S. britannica is probably widely distributed in the Danish waters, but no doubt often disregarded, as its fructification takes place during the winter, when few collections of algae are made. In all probability it prefers somewhat sheltered localities. On the exposed coast of North Sjælland I searched for it between Hundested and Spodsbjerg on January 22nd, 1948, on stones at a depth of 1 m, but in vain.

Localities. **Su:** Barakkebro, Saltholm, near Copenhagen, 1 m, on stones, January 1948 and April 1947 (S. L.).

4. **Sphacelaria saxatilis** Kuck. emend. Sauv.

Sauvageau, Remarques, pp. 5, 69, 152, 254, and 265 (1900, p. 217; 1901, pp. 53, 376; 1903, pp. 83, 94); Kylin, Phaeophyceen schw. Westküste, 1947, p. 28; Lund, Nye Alger for de danske Farvande, 1949, pp. 245, 251, fig. 3 B.

Sph. saxatilis Kuckuck in litt. apud Sauvageau, Remarques p. 5 (1900, p. 217), Note 2.

Sph. furcigera var. *saxatilis* Kuckuck, Bemerkungen, II, 1897, p. 373, fig. 1, p. p.; Wærn, Remarks on Some Swedish Sphacelariaceae, 1945, p. 401 p. p.

Sphacelaria sp., Kuckuck, Bemerkungen [I], 1894, p. 232, fig. 6.

In 1897 Kuckuck on the basis of material from Heligoland described a variety of *S. furcigera* Kütz., var. *saxatilis*. Both plants with unilocular sporangia, plants with plurilocular sporangia, and plants with bifurcate propagules and hairs are mentioned. The sporangia-bearing plants formed extensive mats on rocks and stones. Although the two kinds of sporangia always occurred in distinct individuals, they were often observed in the very same mat. The plants bearing propagules were likewise growing on rocks and stones—in a single case, however, epiphytically on *Cladostephus spongiosus*—but mostly they formed small tufts.

Later Kuckuck, however, changed his systematic view, now using the designation *S. saxatilis* for his plants (*in litt.* in Sauvageau, Remarques, p. 5, Note 2 (1900, p. 217)). Probably it is, however, only the plants with sporangia to which he wishes to attribute this name, for in a letter from Sauvageau to Børgesen (Mar. Alg. Færöes, 1902 p. 433) occurs the following passage: "Récemment M. Kuckuck (in litt.) revenait à l'opinion que ces propagules appartenaient au *S. olivacea* . . . ."

That Kuckuck's complex consists of two species was, for that matter, emphasized later by Sauvageau (Remarques pp. 69, 152 (1901 pp. 53, 376)) and Kylin (1947 p. 29), a view shared by the present writer. Sauvageau names the two species *S. furcigera* and *S. saxatilis*, while Kylin uses the designation *S. solitaria* for the plants bearing propagules.

Besides at Heligoland *S. saxatilis* has been found on the Swedish west coast at Kristineberg in Bohuslän by WÆRN (1945 p. 402). In the plants concerned, which were collected at the end of July, two old remnants of stalked, unilocular sporangia were observed. Together with the plants of *S. saxatilis* very small tufts of *S. furcigera* occurred, bearing propagules and hairs; the latter plants were attached to the former. Both species are entered under the designation of *S. furcigera* KÜTZ. var. *saxatilis* KUCK. without their taxonomy being discussed.

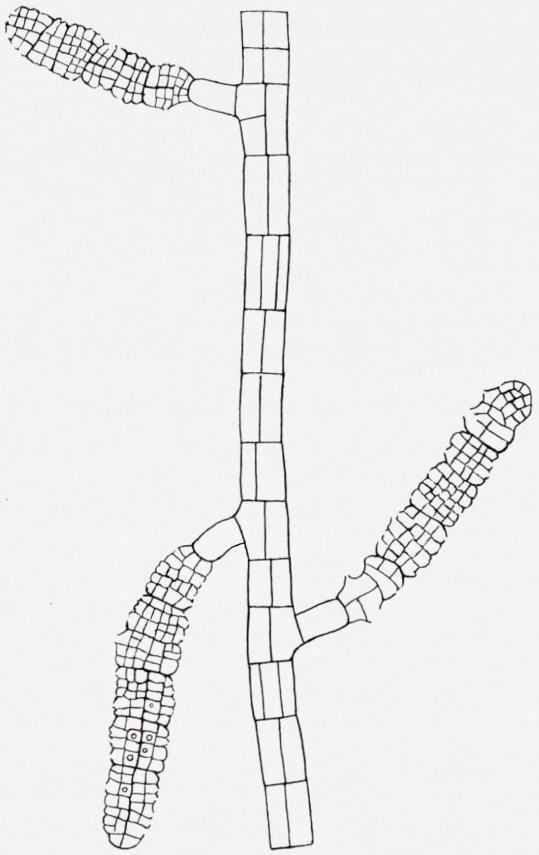

Fig. 4.
Sphacelaria saxatilis. Erect filament with emptied, plurilocular sporangia. — The northern Kattegat: Tyskerens Rev or NV. Revet, 4—10 m, on stipe of *Laminaria hyperborea*, 4-III-1948 (S. L.). × 355.

In ROSENVINGE's posthumous material of the genus *Sphacelaria* the present species was not represented, but during an excursion to Tyskerens Rev and Nordvestrevet at Hirsholmene in the northern Kattegat on March 4th, 1948, I succeeded in finding it in a small quantity. The plants concerned, which were only a few mm high, growing with *S. cæspitula* on the stipe of *Laminaria hyperborea* from a depth of 4 to 10 m, bore numerous emptied and very few mature plurilocular sporangia (fig. 4).

The basal part corresponds to that in *S. britannica*, consisting of a felt of more or less irregular, often sinuous, creeping threads, which issue stolons and form small disks. However, the disk formation was more pronounced than in this species, just as generally there was a distinct difference between the basal threads and the erect filaments (cf. WÆRN, 1945 p. 402).

From the basal part numerous, often crowded, slightly and irregularly branched erect filaments issued almost rectangularly, which are slightly attenuated below, mostly 17—21 μ in diameter. In surface view the secondary segments generally contain 1—2 longitudinal walls, rarely 3, or longitudinal walls may, although exceptionally, be lacking completely. Transverse walls are usually lacking, but they occur now and then. In some filaments the secondary segments at shorter distances were rather short and somewhat barrel-shaped. In a single case a long divaricate rhizoid was observed.

The plurilocular sporangia are cylindrical, often somewhat curved. They issue

from the erect filaments, especially from the lower part of the latter, being fastened on a monosiphonous stalk, which consists of 1—2, rarely 3 cells. They are usually given out at an acute angle, sometimes, however, at a wider, possibly right angle, so that they become divaricate; more rarely they are directed downwards slantingly (fig. 4). In numerous cases they were issued directly from the basal portion of the frond, fastened on shorter or longer shoots. Usually it was easy in the sporangia to distinguish the original secondary segments of the fertilized shoots. The swarmers are liberated individually, each compartment having its separate aperture, a phenomenon already noted by KUCKUCK. The dimensions of the emptied, plurilocular sporangia amounted to 33—125 $\mu \times 16$—25 μ.

Unilocular sporangia did not occur in my material. According to KUCKUCK they are almost spherical, 33—45 μ in diameter, borne on short stalks, united in small clusters or occurring terminally on a long branch. In rare cases they were sessile.

S. saxatilis is closely related to *S. britannica*, but like KYLIN (l. c.) I have been unable to decide whether these two species are really distinct or not. The fact that the erect filaments in my plants of *S. saxatilis* were a little thinner than those of *S. britannica* from Saltholm and the difference between the creeping threads and the erect filaments are more marked in the former than the latter, need not necessarily be an expression of a specific difference. It may, for that matter, be mentioned that KYLIN in both species gives the diameter of the erect filaments as 20—35 μ. I wish, however, to call attention to the fact that in spite of a very thorough examination of a large material of *S. britannica* from both January and April, I succeeded in detecting only unilocular sporangia and further, that *S. saxatilis* from the northern Kattegat only bore plurilocular sporangia.

Localities: **Kn:** Tyskerens Rev or Nordvestrevet at Hirsholmene, on stipe of *Lamin. hyperb.* from the depth of 4—10 m (S. L.).

5. **Sphacelaria furcigera** Kütz.

KÜTZING, Tab. phycol., V, 1855, p. 27, pl. 90 II; ASKENASY, Algen d. Forschungsreise "Gazelle", 1888, p. 21; REINKE, Sphacelariaceen, 1891, p. 14, pl. 4 figs. 5—13; SAUVAGEAU, Remarques, p. 145 (1901, p. 368), fig. 35.

Sph. furcigera var. *saxatilis* KUCKUCK, Bemerkungen, II, 1897, p. 373 p. p., fig. 1 K, N, O; WÆRN, Remarks on Some Swedish Sphacelariaceae, 1945, p. 401 p. p.

Sph. olivacea var. *solitaria* PRINGSHEIM, Sphacelarien-Reihe, 1873, pl. 10 figs. 11—13.

Sph. solitaria (PRINGSH.) KYLIN, Phaeophyceen schw. Westküste, 1947, p. 28, fig. 24 D.

Sphacelaria sp. KUCKUCK, Bemerkungen [I], 1894, p. 229, fig. 3.

This alga, particularly widely distributed in warmer seas, has been described by KÜTZING and later studied by ASKENASY, REINKE, KUCKUCK, SAUVAGEAU, and others. PRINGSHEIM, too, has discussed it (under the name *S. olivacea* var. *solitaria*). In the Danish waters it has been met with a few times, viz. in the Skagerak and the northern Kattegat. The specimens from the Skagerak consist of tufts, 1.2 cm high, which according to ROSENVINGE's journal had grown on *Laminaria hyperborea*. From the

northern Kattegat plants exist which form tender growths to a height of some millimetres, partly on the stipe of *Laminaria digitata* and *hyperborea*, partly on an old shell of *Buccinum*.

The basal part of the thallus is given in the literature to be endophytic (REINKE), completely or partly, or creeping outside the substratum if the latter is hard (SAUVAGEAU). In the plants mentioned from *Laminaria digitata* and *hyperborea* from the northern Kattegat, it was, owing to the very small quantity of material, impossible to decide whether the basal part was epiphytic or endophytic. On the other hand, in the plants from the Skagerak from *Laminaria hyperborea*, in spite of the latter in the herbarium being represented only by some thin, superficial scrapes of the stipe, it was easily observed that the basal part actually penetrated into the tissue of the host. It was especially distinctly seen, when the slides were treated with Eau de Javelle. In the plants from the shell of *Buccinum* the basal part of the thallus consisted of creeping threads, here and there forming small, irregular disks.

The erect filaments in the present material are slightly and irregularly branched. A differentiation into axes and branches is not found, and on an average the branches and the mother shoots are of the same diameter. In some cases main filaments, however, were recognizable in the greater part of their length. The diameter of the erect filaments in the plants from the Skagerak amounted to 17—29 μ, in the plants from the northern Kattegat to 21—35 μ. The length of the segments as a rule vary between the length = the diameter and the length = twice the diameter. A surface view generally reveals 1—2, more rarely 3 longitudinal walls. Transverse walls are not found.

Hairs occurring singly are common on the plants from the Kattegat; they were especially numerous and well preserved on those growing on *Buccinum*. On the other hand, under a relatively superficial examination, I did not see them in the herbarium material from Skagerak. If they really are present here, they cannot at any rate be very numerous. The diameter of the hairs amounted to 12—16 μ.

Narrow, bifurcated propagules are common both on the plants from the Skagerak and those from the Kattegat (fig. 5). They are borne on a sterigma and consist of a cylindrical stalk with two cylindrical arms. However, the stalk is often tapering downwards just as the arms may taper somewhat towards their free end. Usually the 2 arms are of equal length, but in some cases one is shorter than the other. Still I have not seen any cases in which one arm is not developed at all as in plants from the Faroes (SAUVAGEAU l. c. p. 152 (1901 p. 375)). In some propagules one arm was forked (fig. 5 *C*). In a single case the arms of a propagule were much lengthened, behaving like vegetative branches, bearing hairs and new propagules. The propagules have been observed in July, August, and January.

Both unilocular and plurilocular sporangia are known, but not observed in Danish plants; they were first described by ASKENASY and later mentioned and depicted in REINKE and SAUVAGEAU, in all three authors on material from warmer seas. The plurilocular sporangia have also been depicted by YAMADA (1941 fig. 3) in specimens from Formosa, belonging to var. *tenuis*. The unilocular sporangia

occur in distinct plants or in individuals, which in addition bear propagules; in the latter case they may be found even on the stalk or arms of the propagules. They are spherical, borne on a one-celled stalk, more rarely on a several-celled one, 50—70 μ in diameter. The stalk may later issue a fresh sporangium given out laterally.

The plurilocular sporangia occur on distinct individuals whose branches are tenderer than those of the plants which bear propagules or unilocular sporangia.

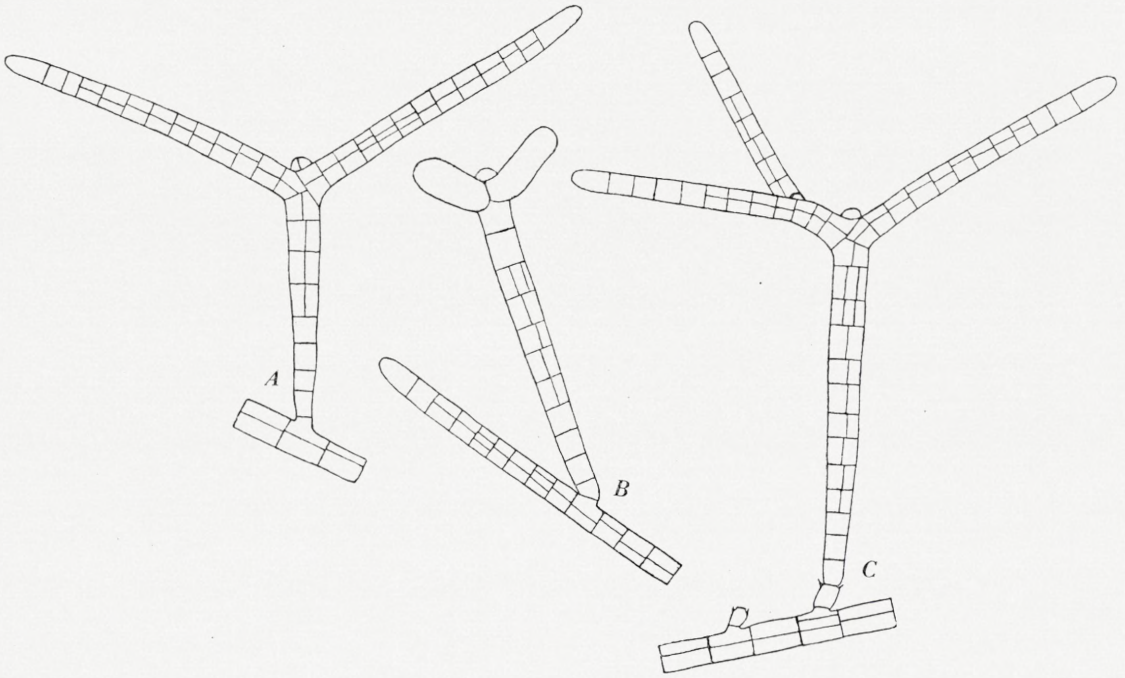

Fig. 5.
Sphacelaria furcigera. Propagules, *B* young one. In *C* one arm of the propagule, developed in continuation of the sterigma of a cast-off propagule, has become forked. Below the propagule in *C* the sterigma of another cast-off propagule is seen. — The northern Kattegat: Laurs Rev, on stipe of *Laminaria digitata*, 12-VII-1926. ×173.

Generally they are fastened to a one- or two-celled stalk which may produce another sporangium laterally. The plurilocular sporangia are of two kinds, one of which contains many, small loculi, the other fewer, larger loculi. The former, which possibly are antheridia, are cylindrical, 45—65 μ long and 24—28 μ in diameter, while the latter, possibly representing oogonia, are shorter and more irregular, usually amounting to 30—45 μ in length and 28—40 μ in diameter.

Kylin (1947 p. 29) thinks that the propagule-bearing component of the complex of Kuckuck's *S. furcigera* var. *saxatilis* is not identical with the typical form of *S. furcigera* distributed in warmer seas on *Fucaceae*. He establishes it as a new species under the name of *S. solitaria*, declaring that it was first described as *S. olivacea* var. *solitaria* by Pringsheim. *S. furcigera* and *S. solitaria*, it is true, are considered to be closely related, but whereas the basal part of the former is parasitical in the host,

the latter is an epiphyte. With the expression "epiphytisch" is apparently meant only that the basal part occurs externally. KUCKUCK at any rate emphasizes that he found his plant epiphytic only once (on *Cladostephus*), but otherwise always on rocks and stones.

Bearing in mind the statement above of my experience of the character of the basal part in Danish plants and referring to SAUVAGEAU's information (Remarques p. 147 (1901 p. 370)) of the different behaviour of the basal part on hard and softer substrata, I do not see any reason to separate *S. solitaria* from *S. furcigera*. The plants from the Skagerak which were growing on the stipe of *Laminaria hyperborea* behave like *S. furcigera*, while those from *Buccinum* correspond to *S. solitaria*. Circumstances are completely as in *S. cæspitula*, i. e. the character of the substratum determines whether the basal part of the plant becomes parasitic or external.

Localities. **Sk:** Off Hirtshals, 11—13 m, Aug., on *Lamin. hyperb.* — **Kn:** Laurs Rev, July, in company with *Ectocarpus* and other epiphytes on stipe of *Lamin. digit.*; Marens Rev, July, on shell of *Buccinum*; within the broom N of Græsholm (Hirsholmene), 9—10 m, January, in company with *S. cæspitula* and *S. cirrosa* on *Lamin. hyperb.*

6. **Sphacelaria cirrosa** (Roth) Ag.

C. AGARDH, Systema Alg., 1824, p. 164; KÜTZING, Tab. phycol., V, 1855, pl. 88 II; GEYLER, Zur Kenntniss d. Sphacelarieen, 1866, p. 513, pl. 36 figs. 18—21; JANCZEWSKI, Études anatomiques sur les Porphyra et sur les propagules du Sphacelaria cirrosa, 1873, p. 253; MAGNUS, Zur Morph. d. Sphacelarieen, 1873, p. 131, pl. 1 figs. 1—14; ARESCHOUG, Observat. phycol., III, 1875, p. 21 p. p.; HAUCK, Meeresalgen, 1885, p. 344 p. p.; REINKE, Algenfl. westl. Ostsee, 1889, p. 39 p. p.; Sphacelariaceen, 1891, p. 10 p. p.; Atlas, H. 2, 1892, p. 65 p. p., plates 42, 43 p. p.; SAUVAGEAU, Remarques p. 211 (1902, p. 399), figs. 44—46; Sur les variations du Sph. cirrosa . . ., 1903, p. 309; KYLIN, Algenfl. schw. Westküste, 1907, p. 64; Phaeophyceen schw. Westküste, 1947, p. 29, fig. 24 E; PRINTZ, Algenveg. Trondhjemsfjordes, 1926, p. 164; NEWTON, Handbook, 1931, fig. 118 p.p.; SCHINGNITZ-v. BÖSELAGER, Beitr. z. Kenntnis d. Sph. cirrosa, 1936, p. 285, fig. 1; TAYLOR, Mar. Alg. Northeastern Coast of N. Am., 1937, p. 131, pl. 17 figs. 1—6.

Conferva cirrosa ROTH, Catalecta bot., II, 1800, p. 214.

Sphacelaria pennata (HUDS.) LYNGB.; KÜTZING, Tab. phycol., V, 1855, pl. 91 II; GEYLER, l. c. p. 519, pl. 36 figs. 6—11.

Sph. irregularis KTZ.; KÜTZING, l. c. pl. 91 III.

f. **septentrionalis** SAUV., Remarques p. 227 (1902 p. 415).

f. **patentissima** GREVILLE, Scottish Cryptogamic Fl., VI, 1828, pl. 317; SAUVAGEAU, Remarques p. 230 (1903, p. 46).

f. **aegagropila** REINKE, Algenfl. p. 40; LAKOWITZ, Algenfl. Danziger Bucht, 1907, p. 27, pl. 3 fig. 3.

This species, which particularly has been studied by GEYLER, JANCZEWSKI, MAGNUS, REINKE, and SAUVAGEAU, consists of small, rather stiff tufts, up to well over a few cm in height (—2.5 cm), which is found both as an epiphyte on other algae and on shells and stones. In the dried state the available plants were dark brown, olive-brown or yellowish brown.

The basal part consists of a small one-layered disk, formed by radiating threads. Now and then one of these threads or one of the lower branches may lengthen and form a new disk. The erect filaments are always branched, presenting a distinct differentiation between main filaments and branches. The branching previously caused a distinction between 2 types (species or varieties), the *pennata-* and the *irregularis*-type, between which, however, numerous transition forms exist. The former has a chiefly pinnate, generally regular opposite branching, while in the latter the branches issue irregularly, possibly locally unilaterally. According to SAUVAGEAU these names ought not to be maintained, since the variation is not connected with differences of substratum, the station, or the geographical distribution.

The erect filaments according to SAUVAGEAU are 40—100 μ in diameter. Transverse walls are lacking in the secondary segments, although they may sometimes be found in the lower secondary segments in f. *septentrionalis* mentioned below, if the lower secondary segments are longer than the upper ones. Unlike *S. bipinnata* rhizoids are usually lacking or at any rate rare.

Hairs occur especially on the primary branches and the branches of the lower orders. In several of the Danish plants examined they were rather numerous.

A feature characteristic of the species is the propagules, usually numerous, which are narrow, radiating, generally trifurcated, in many cases bearing a hair. The arms of the propagules are slightly constricted at their bases.

SAUVAGEAU, on the basis of material from numerous localities, thus from the North European coasts and along the French and Spanish coasts down to Madeira, has carried out thorough investigations of the variation of the species. He came to the result that within this area it is possible to distinguish 2 forms, a northern and a southern one, f. *septentrionalis* and f. *meridionalis,* which are connected by intermediate forms. Not only do the 2 forms look different, but they also differ by the shape of the propagules. In the former, which occurs in North European waters, being found, however, down to Concarneau on the south coast of Brittany, the tufts are longer and more flexible, having relatively thin main filaments (40—60 μ thick) and rather long primary branches, bearing only few hairs. The secondary segments of the main filaments, which present relatively few longitudinal walls, are often of the same height as or higher than the breadth. The propagules as a rule have 3, more rarely 2, cylindrical arms.

The southern form consists of stiffer tufts, whose main filaments are thicker, having more longitudinal walls, and whose secondary segments are of the same height as or lower than the breadth. The primary branches are shorter, more divaricate, often provided with more hairs. The propagules have 3 spindle-shaped arms. This form has been observed from the Channel and southwards but is also found as far northwards as at any rate Heligoland (cf. KUCKUCK, Bemerkungen, 1894, fig. 2).

Finally it may be mentioned that SAUVAGEAU for the Mediterranean plants established f. *mediterranea,* which resembles f. *meridionalis,* only that it has 3—5-branched propagules with cylindrical or spindle-shaped arms.

From the Danish waters a very large material of *S. cirrosa* exists, comprising collections from all months except February, March, and December, chiefly, however, from May to October. In this material I have examined a great many random samples from the various areas, finding that propagules occur in all the months from April to November. In plants from January, too, I have observed propagules, but they

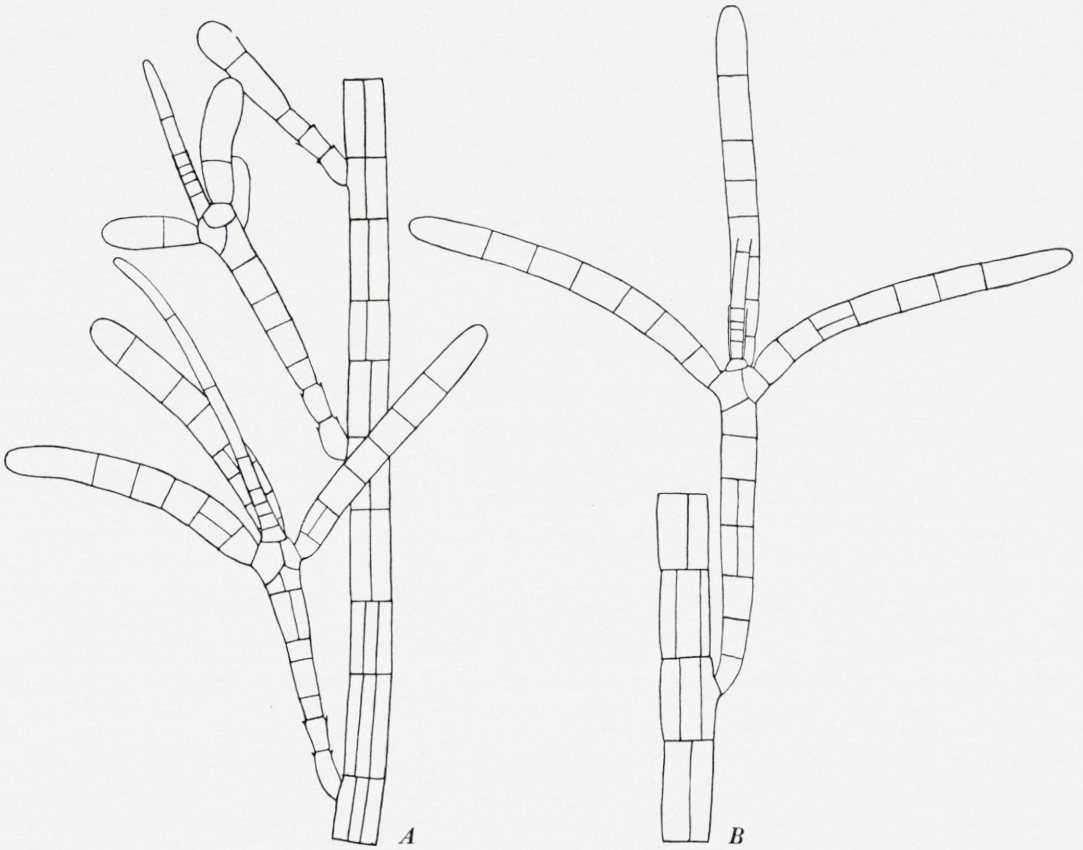

Fig. 6.
Sphacelaria cirrosa. Propagules of plants from the northern Kattegat. In *A* two consecutive sterigmata are seen at the base of both propagules and the propagule-initial. — *A*: Læsø Trindel, 16 m, on *Desmarestia aculeata*, 3-VIII-1922. *B*: east of the bell-buoy at Frederikshavn, 17—19 m, 26-VII-1922. ×173.

were only found in a very small quantity, their arms being partly broken off. The propagules are nearly always trifurcated, rarely bifurcated through suppression of one of the arms, which are slightly constricted at the base,—and usually issue a hair; when mature they have nearly always distinctly cylindrical arms (fig. 6). Hence I have referred the plants to f. *septentrionalis*. However, in some cases the diameter of the arms of the propagules was a little bigger at a little distance above the base just as the arms might taper slightly towards the apex. Not rarely they were somewhat recurved.

The reproduction of the species is mainly by propagules, but both unilocular and plurilocular sporangia are known. The unilocular ones are said not to be very frequent, still they cannot be considered rare in the Danish waters as is for instance the case on the Swedish west coast (cf. KYLIN, 1907 l. c.; 1933 p. 80; 1947 l. c.). The plurilocular sporangia are said to be very rare; they have not been noticed in Denmark.

In random samples from the present Danish material I have met with unilocular sporangia at the end of January, in the latter half of April (on a small, richly hair-bearing plant), at the beginning of June as also in the months of August—November. They are fastened to a one-celled stalk and are partly found on plants which in addition bear propagules. In most cases they were not very numerous, which is perhaps due to the fact that often they were still young, even on plants from such a late time as November. In some plants the sporangia—although comparatively well developed—were nearly empty, and it is doubtful whether such sporangia are able to produce spores. SAUVAGEAU, too, emphasized that at times the unilocular sporangia are almost empty. In some cases, however, I found plants in which the unilocular sporangia were rather common and mature or nearly mature.

This especially applies to some individuals from Læsø Trindel in the northern Kattegat, collected in August on *Desmarestia aculeata* at a depth of 16 m, where the unilocular sporangia were present even in a large number and, as far as a great many were concerned, possessed differentiated spores. These mature sporangia were spherical and had a diameter of 78—103 μ, most frequently 82—86 μ. Other sporangia, particularly those occurring near the apices of the branches, were still young and somewhat elongated. As far as could be decided these plants had no propagules, but in company with them other plants were growing which in a very large number bore propagules, generally young—and at any rate only unilocular sporangia in a small quantity.

Mature unilocular sporangia occur not only during summer, but they are also found in the autumn (e. g. in October) and in winter (January). In the latter month, where I observed them on a plant with partly truncated shoots, they were not very common. They measured about 85 μ in diameter occurring together with emptied and young unilocular sporangia.

The plurilocular sporangia according to SAUVAGEAU are stalked, cylindrical, 70—80 $\mu \times 60$—65 μ. They were observed by him on an individual which besides bore unilocular sporangia and propagules. The plant concerned had been collected on the Spanish north coast at Gijon, growing on *Cystoseira discors*.

Plurilocular sporangia, which are stated to belong to the present species, have been mentioned and depicted in the literature repeatedly. However, as *S. bipinnata* was not separated by SAUVAGEAU until the beginning of this century we cannot leave out of account the fact that at any rate some of the pictures prior to this time may have represented this species, in which plurilocular sporangia are common (cf. SAUVAGEAU, Remarques p. 224 (1902 p. 412)). Indeed, even after this time an example is known of plurilocular sporangia referred to *S. cirrosa*, actually belonging to *S. bipin-*

nata, viz. the plurilocular sporangia in NEWTON's Handbook (1931) fig. 118 *E-F*. For this writer does not enter *S. bipinnata* as a species but as a variety of *S. cirrosa*: var. *ægagropila* GRIFF. NEWTON's taxonomic view must appear rather antiquated, since her book was not published until nearly 30 years after SAUVAGEAU's establishment of *S. bipinnata*, and algologists after this time—among them CLINT (1927), who made plants of *S. bipinnata* from Isle of Man and Anglesey the object of an investigation—have followed SAUVAGEAU's example.

As for life-duration the species is regarded in different ways in the literature. From the Baltic REINKE (1889) and LAKOWITZ (1907 and 1929) give it as annual, whereas by KYLIN (1947) from the Swedish west coast (and by other investigators from other areas) it is said to be perennial. In the Trondheim fiord in Norway PRINTZ (1926) found that at any rate it could be perennial, being collected here at the end of March as creeping, hibernating basal threads, which were just issuing fresh shoots.

In the Danish waters it is no doubt mostly perennial, but apparently it often hibernates here in a considerably less reduced state than is the case with PRINTZ's plants. Thus on April 18th, 1933, on *Laminaria digitata* from Rosenvold in Vejle Fiord (The Little Belt) I found some old plants whose wintering part formed erect tufts. The main filaments and the great majority of the branches, it is true, were truncated at a distance above. The growth in these plants had been resumed some time ago by the issuing of a large number of new shoots, which particularly rose from the truncation of the main filaments and the more vigorous branches, or close by. As in PRINTZ's plants there was a conspicuous difference of colour between the new, light shoots and the old, hibernating, brown shoots, which were covered by a good number of Diatoms, *Cyanophyceae*, and other small epiphytes. In spite of a thorough search no propagules were noticed in these plants.

In ROSENVINGE's herbarium only some few plants exist from the winter period proper, collected in the northern Kattegat at the beginning of January 1895 on *Desmarestia aculeata*, *Furcellaria*, and *Fucus serratus*. They consisted of small tufts whose main filaments were truncated at a greater or smaller distance from the base. The remnants of the main filaments were provided with a good number of branches. Similar plants were collected by the author at Hundested on the north coast of Sjælland January 22nd, 1948, on *Fucus serratus* at a depth of 1 m; a single one of these specimens, however, bore unilocular sporangia.

I have further had an opportunity of studying the species at winter time in nature on Saltholm at the end of January 1948. In this locality, on stones at a depth of 1 m, numerous small plants were found of a height of a few mm to 1 cm; some were growing, however, on seedlings of *Fucus vesiculosus*, others on *Cladophora rupestris*. In a few cases propagules with arms partly broken were observed as well as empty, degenerated unilocular sporangia. Unlike the above-mentioned winter plants from the Kattegat the plants from Saltholm were young; probably they originate from the late autumn, but as in the former their growth had now been arrested and their main filaments in most cases were truncated.

Besides f. *septentrionalis* in the Danish waters two characteristic loose, sterile forms occur: f. *patentissima* GREV. and f. *aegagropila* RKE. The former is characteristic by its rather short, stiff, divaricate primary branches, issuing rectangularly from the main filaments in the same plane or in different planes. It is found e. g. in the Limfjord. F. *aegagropila* consists of roundish, densely branched, more or less dense balls, which measured well over 3 cm in diameter. It has been observed at Hofmansgave in the Samsø area.

S. cirrosa is a very common alga in all the Danish waters within the Skaw, where at any rate it descends to the depth of about 20 m. From the North Sea, on the other hand, only a single finding (Jydske Rev, 25 m) is on record. It is generally found as an epiphyte on various algae, e. g. *Fucus vesiculosus* and *serratus, Laminaria, Desmarestia aculeata, Furcellaria, Chondrus, Phyllophora Brodiaei* and *membranifolia, Cystoclonium,* and *Polysiphonia,* but it has also been found on *Zostera.* On *Halidrys* it has not been noticed in Denmark; all the *Sphacelarias* growing on this alga belong to *S. bipinnata,* but near Drøbak in Oslo Fjord I observed it during the summer of 1948 on *Halidrys,* too. Further it has been observed on shells of *Mytilus* and *Buccinum* as also on stones. Some of the small, reduced plants mentioned above, from January, were growing on *Desmarestia aculeata,* as reported; they had great habitual resemblance to the plant distributed by ARESCHOUG in Alg. Scand. exsicc., V, 1864, No. 219 under the name of var. *nana.*

Not all specimens from this host-plant, however, belong to the *nana*-type. On the contrary several extremely well developed tufts of *S. cirrosa* are just observed on *Desmarestia aculeata.* This applies e. g. to some plants which were collected in the Kattegat in July (N. of Læsø, 9 m, and Fladen, 18 m), and growing so densely that they nearly completely covered the host.

Localities. **Ns:** ZQ, Jydske Rev. Lodbjerg lighthouse E by S, $26^1/_2$ miles, 25 m. The **Limfjord**, the **Kattegat**, the **Belts**, the **Sound** and the **Baltic** to Bornholm: widely distributed.

7. **Sphacelaria bipinnata** (Kütz.) Sauv.

SAUVAGEAU, Remarques, p. 193 (1902, p. 381), figs. 41 L, 42; Variations du Sph. cirrosa, 1903, p. 313; KYLIN, Algenfl. schw. Westküste, 1907, p. 64; Phaeophyceen schw. Westküste, 1947, p. 30, pl. 1 fig. 3; CHEMIN, Sur le parasitisme de Sph. bipinnata Sauv., 1922, p. 244, fig. 1; CLINT, The Life-History and Cytology of Sph. bipinnata Sauv., 1927; PAPENFUSS, Alternation of Generations in Sph. bipinnata Sauv., 1934, p. 437, figs. 1—9.

Stypocaulon bipinnatum KÜTZING, Tab. phycol., V, 1855, p. 28, tab. 95.

Sphacelaria cirrhosa (ROTH); ARESCHOUG, Alg. Scand. exsicc., II—III, 1862, No. 108; Observat. phycol., III, 1875, p. 21 p.p.; KJELMANN, Handbok, 1890, p. 68 p.p.

Sph. cirrhosa var. *ægagropila* GRIFF. (cf. KNIGHT & PARKE, Manx Algae, 1931, p. 112).

Sph. amphicarpa LEBEL mscr.; SAUVAGEAU, Influence d'un parasite sur la plante hospitalière, 1900, p. 343.

Until SAUVAGEAU's thorough description and picture under the name mentioned above in "Remarques" this species generally has not been separated from *S. cirrosa.*

GRIFFITHS, however, distinguished it as *S. cirrosa* var. *ægagropila* (cf. KNIGHT & PARKE, l. c.), a method, which later was followed for instance by BATTERS (A Catologue of the British Mar. Alg., 1902, p. 39), even holding its ground in NEWTON's Handbook (1931, p. 190)! KÜTZING likewise recognized it, in 1855 describing and depicting it as *Stypocaulon bipinnatum*. REINKE (Sphacelariaceen, 1891, p. 10) and DE TONI (Sylloge Alg., Vol. 3, Fucoideæ, 1895, p. 504), however, do not admit KÜTZING's species, but enter it as a synonym for *S. cirrosa*. Finally it is mentioned as *S. amphicarpa* LEBEL mscr. in SAUVAGEAU 1900, p. 343, and *S. Lebelii* SAUV. in SAUVAGEAU, Sur les Sphacelaria d'Australasie (1902 p. 200).

The species consists of dense, supple tufts, in the mature state roundish, of a height of 2(—3) cm. It is bound to *Halidrys siliquosa* and, in more southern waters, *Cystoseira fibrosa*, in both of which it penetrates to some depth with its basal part, which forms "une sorte de pivot" (CHEMIN l. c. p. 244). By SAUVAGEAU it is named a parasite, by CLINT as at least partly parasitic, while CHEMIN designates it as "une algue Épiphyte-perforante". By it sendophytic basal part it differs together with *S. cæspitula* and *S. furcigera* (which, however, both may also be found on shells, stones, and similar hard substrata) from all the other Danish species of the genus. The colour of the herbarium plants from the Danish waters is brownish, at times yellowish brown. According to SAUVAGEAU the colour in the dried state is often reddish brown unlike *S. cirrosa*, which usually is tinged more olive-green. This difference is thought to be of importance at a macroscopic distinction of the two species when they are not attached to their substratum.

Besides its basal part being endophytic the species at the same time is epiphytic, for numerous, descending rhizoids become creeping on the surface of the host when reaching the latter. Here they form an entangled, sponge-like mass. Some of the rhizoids behave like stolons, sending out main filaments exactly like those which arise from the endophytic part.

The branching is opposite or scattered, at stretches pinnate or chiefly pinnate. The lowest branches are often rather vigorous, the character being almost like main filaments. The secondary segments of the main filaments generally are not provided with many longitudinal walls, and the branches of the highest order are frequently monosiphonous or chiefly so. The secondary segments of the main filaments are of the same height as the breadth or lower. Transverse walls are usually lacking; they may, indeed, occur in the lower secondary segments if the latter are longer than the upper ones, which is not rarely the case. The transverse walls not always occur rectangularly in the segment, but may be oblique or curved. The diameter of the main filaments in Danish plants amounted to 45—94 μ, the diameter, however, within the same filament often varying rather much.

Hairs are usually found abundantly, particularly on the rather young generations of shoots. In several cases a branch, rarely a sporangium, develops below the hair, so that the latter will be placed in the axil of the branch.

Rhizoids, which frequently dichotomize, are plentiful, especially on rather old

plants. They are descendent, often spiral, particularly occurring on the lower part of the main filaments, where they usually form a cortex. They are never adherent to the main filaments.

Propagules are very rare. They are narrow, with three radiating arms. They were observed by SAUVAGEAU on a specimen from the Norwegian south-west coast and in a specimen from Bohuslän on the Swedish west coast. In both cases the plants had grown on *Halidrys*. The former plant, moreover, bore unilocular sporangia, the latter both unilocular and plurilocular ones. Later they were mentioned by CLINT, who saw no more than three in all. These plants, too, were growing on *Halidrys*. The propagules have not been noticed by KYLIN (1907) on the Swedish west coast, nor observed by me in the Danish material.

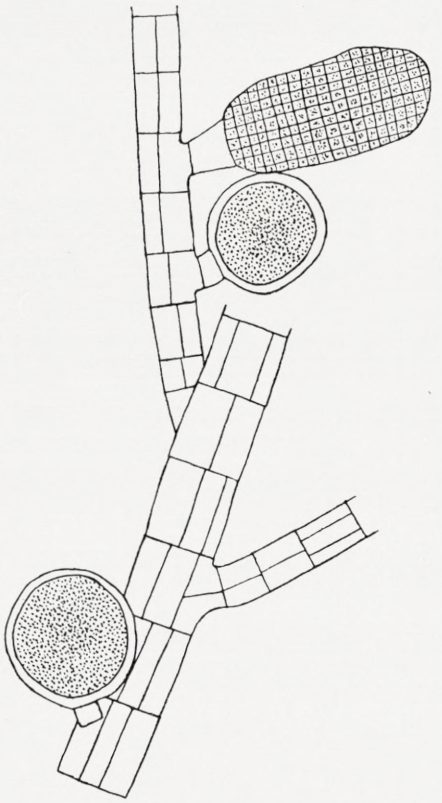

Fig. 7.
Sphacelaria bipinnata. Unilocular sporangia and a plurilocular one. — The Skagerak: Hirtshals lighthouse SSE. 2 miles, 14 m, on *Halidrys siliquosa*, 1-VIII-1901. ×473.

Of fructification organs both unilocular and plurilocular sporangia are known. The former are borne on a short, unicellular stalk and spherical or slightly flattened when mature (fig. 7). In the Danish material they measured in the rounded state (the spores, however, not being differentiated) 70—86 μ in diameter. In a specimen from the Skagerak, which was preserved in alcohol, the aggregate, mature spore-mass from the unilocular sporangia in many cases was ejected from the sporangium, when the plant was put into water. The spore-mass, which retained its spherical form, measured 74—98 μ in diameter, as a rule about 82 μ.

The plurilocular sporangia likewise are borne on a short, unicellular, possibly two-celled stalk (fig. 7). Sometimes the stalk, however, is formed of few—many cells, one or several of which may be divided by a longitudinal wall. In a single case I saw a stalked plurilocular sporangium issuing from the uppermost cell in the stalk of another plurilocular sporangium. The plurilocular sporangia are cylindrical, in my preparations being 70—107 μ, usually 86—94 μ long and (45—)49—53 μ in diameter.

The sporangia, for that matter, are not only restricted to the branches and the main filaments, but frequently also occur on the rhizoids.

The two kinds of sporangia, according to the literature, are found on the same or on different plants. On French plants from Roscoff on the Channel coast SAUVAGEAU (Remarques p. 199 (1902 p. 386)) generally found only one kind in the branching

ensemble of an axis, but nevertheless often both kinds on the same tuft—although rarely on the same branches. For English plants from the south-east coast of Isle of Man and Anglesey CLINT (p. 7) states that the two kinds usually occur on separate tufts, only it was not unusual that a few unilocular sporangia occurred on plants having chiefly plurilocular sporangia, and a few plurilocular sporangia on plants bearing chiefly unilocular sporangia. At Kristineberg in Bohuslän on the Swedish west coast PAPENFUSS as a rule found unilocular and plurilocular sporangia on different plants, but also exceptionally plants with both unilocular and plurilocular sporangia. Plants with unilocular sporangia exclusively were in great excess in this locality, constituting 90 per cent. of all the individuals examined.

Judging from the material available from the Danish waters unilocular and plurilocular sporangia apparently here generally occur on the same plants (but only rarely on the same branches). I dare not, however, express myself categorically on this question; for the tufts often grow so dense that it is impossible to define the individual specimens in the herbarium material. For a safe judgment it will be necessary to examine living plants or specimens preserved in alcohol. The fact that the two kinds of sporangia at any rate may occur on the same plant, was observed by me on a specimen from the Skagerak, where unilocular and plurilocular sporangia were found side by side on the same branches (fig. 7), corresponding to CLINT's fig. 7.

The time of fructification on the coast of the Isle of Man according to CLINT begins in early summer; at Anglesey, where the species is capable of surviving the winter, sporangia may also be produced during the winter. In Bohuslän on the Swedish west coast KYLIN (1907) found that the species commenced to become fertile at the end of August and that specimens from September were densely covered with plurilocular and unilocular sporangia. According to PAPENFUSS' observations at the zoological station Kristineberg in Bohuslän the unilocular and plurilocular sporangia there begin to be formed in the last half of July. They were found in the largest quantities from the middle of August to the last part of September. On the coast of Halland, according to KYLIN (1907), the species is fertile in July. At Kullen LEVRING (1935, p. 23) found that it began being fertile in August.

In the Danish material examined, which has been collected in May (1 collection), June 29th (1 collection), July (3 collections), August (5 colls.), September (2 colls.) and October 1st (1 coll.) practically all of the plants were fructiferous; only the specimen from May, which was growing luxuriantly, and an individual from July, were sterile.

Investigations of the swarmers from the unilocular sporangia were carried out by CLINT and PAPENFUSS; the latter also made examinations of the swarmers from the plurilocular sporangia. According to CLINT meiosis takes place in the unilocular sporangia and the swarmers from the latter are said to copulate. The swarmers from the plurilocular sporangia on the other hand are said to be diploid.

PAPENFUSS, who made his experiments on the Swedish west coast, found that the swarmers from the unilocular sporangia germinated direct without any copulation.

On the other hand the swarmers from the plurilocular sporangia from individuals which only bore plurilocular sporangia, copulated by isogamous copulation. The swarmers from the plurilocular sporangia, which occur on plants that in addition bear unilocular sporangia, are considered to be diploid. According to PAPENFUSS an alternation of generations between two morphologically identical generations takes place in the species.

Besides on *Halidrys* I have in the Danish material met with some small specimens, which were secondarily attached to *Stenorhynchus*, collected at Busserev near Frederikshavn in the northern Kattegat at the end of July, which owing to the complete accordance with the present species I think must be referred here. The plants concerned were at most 0.8 cm high, most of them were smaller. They all had a single main filament, broken below. Both from the place of the fracture and rather a long distance above numerous rhizoids rose, some of which did the attaching. In some cases it was apparently particularly the rhizoids from the place of the fracture which secured the plant, in others it was exclusively the rhizoids from above. The rhizoids which issued at a distance above the fracture were often very numerous; they were descendent, frequently winding and coiled round the main filament, generally having a diameter of about 30 μ. They sent out a number of erect shoots.

The plants were richly branched, partly pinnate, and in luxuriant growth. Some of the lower branches of the main filament were marked longitudinal shoots, which behaved like the main filament. The secondary segments of the main filament, which had no transverse walls, were approximately of the same height as the breadth or shorter than the breadth. The upper secondary segments were frequently shorte, than the lower ones. The diameter of the main filament was shortest in the lower part, longest near the growing apex of the filament. As a rule the diameter amounts to 41—66 μ (—78 μ).

Most of the plants bore unilocular sporangia, borne on a unicellular stalk. In some individuals they were rather scanty and young, in others very numerous and spherical, mostly mature or emptied. The spherical sporangia with contents measured 66—82 μ in diameter, most frequently about 70 μ. The emptied sporangia, which for that matter were very well preserved, were 53—78 μ in diameter. Besides through the length of the plant the unilocular sporangia also occurred on the erect filaments, which issued from the descendent rhizoids, as well as, in a few cases, direct on the rhizoids.

A few of the plants bore plurilocular sporangia (probably exclusively), which likewise were fastened to a unicellular stalk. They were cylindrical or a little thicker in the upper part. Some were mature or nearly so, others emptied. The former measured 57—78 $\mu\times$ 41—51 μ; the latter, which just as the emptied unilocular sporangia were very well preserved, 62—74 $\mu\times$41—45 μ. Propagules were not observed.

It might be of interest to record that *S. bipinnata*, which in Denmark otherwise is always bound to *Halidrys siliquosa*, may regenerate through isolated fragments of the frond in the way here indicated. Bearing in mind the conception of CHEMIN

according to which the species is not a true parasite, but only a perforating epiphyte, which merely uses the host as a substratum and not, or only very slightly, takes nourishment from it, circumstances really do not seem surprising.

S. bipinnata in the Danish waters has been found from the Skagerak to the Belts. It is commonest in the northern Kattegat, which is, indeed, the best examined area by far, but undoubtedly it will prove common at any rate in the whole area of the Kattegat. In the Skagerak it has been observed at a depth of 14—15 m, in the area of Kattegat in 4—6 m(—9 m), in the Little Belt at 13 m and in the Great Belt at a depth of 8 m. Without doubt it is annual in Denmark.

Localities. **Sk:** Off Hirtshals, 15 m; Hirtshals lighthouse in SSE 2 miles (the church in the brook), 14 m. — **Kn:** Nordvestrevet at Hirsholm; TX, just outside the broom N of Græsholm, 8—9 m; Marens Rev (L. K. R., H. E. Petersen); Laurs Rev (S. L.); TV, Krageskov Rev, 4 m; Frederikshavn; NG, W of Nordre Rønner, 4 m; TL, Nordre Rønner lighthouse in E to N $^1/_4$ N $1^1/_3$ mile, 7 m; GM, Engelskmands Banke, N of Læsø, 5—6 m. — **Ks:** FP, Jessens Grund, 4 m. — **Sa:** AS, western side of Meilgrund, 4—5 m; AT, eastern side of Svanegrund, 5 m; BB, Søby Rev, at the balloon. — **Lb:** N of Fænø Kalv, 13 m. — **Sb:** Between Slipshavn and Knudshoved, 8 m, May, sterile.

8. **Sphacelaria tribuloides** Menegh.

Meneghini, Lett. al Dott. Corinaldi, 1840, p. 2 (not seen); Alghe Italiane e Dalmatiche, 1842, p. 336; Kützing, Tab. phycol., V, 1855, pl. 89; Geyler, Zur Kenntniss d. Sphacelarieen, 1866, p. 516, pl. 36 figs. 12—17; Zanardini, Iconographia Phycol. Mediterraneo-Adriatica, III, 1870—76, p. 43, pl. 90 B; Pringsheim, Sphacelarien-Reihe, 1873, p. 166, pl. 8 figs. 7—23; Hauck, Beiträge z. Kenntniss d. adriatischen Algen, X, 1878, p. 291, pl. 3 fig. 16; Meeresalgen, 1885, p. 342, fig. 144; Reinke, Sphacelariaceen, 1891, p. 8; Sauvageau, Remarques, pp. 123 (1901, p. 233) and 237 (1903, p. 53), figs. 28—29, 47; Lund, Nye Alger for de danske Farvande, 1949, pp. 246, 252, fig. 3 E—F.

In Professor Rosenvinge's posthumous herbarium some small, brownish tufts, 1—1.5 cm high, of a *Sphacelaria* species are found, which temporarily by Rosenvinge was referred to *S. Plumula*. The specimens concerned, which were collected in 1933 in a locality in the northern Kattegat, where they probably were growing direct on concretions of sand, bear numerous propagules; the mature propagules are all of them broadly wedge-shaped, provided with three small horns. Apart from the form of the propagules, however, no resemblance to this species exists; thus the erect thallus is not differentiated into main axes and branches, the branching is scattered and the filaments much thinner than in *S. Plumula*. On the other hand the plants are in excellent accordance with the descriptions of *S. tribuloides*, which also possesses wedge-shaped propagules with three small horns, and I therefore do not hesitate to refer them here.

The basal part of the thallus consists of small, irregular disks, which appear on short, creeping stolons. From the disks numerous, crowded erect filaments and new creeping threads are issued. From the lower part of the erect filaments, at a little distance above the basis, in several cases horizontal, creeping threads occurred,

which undoubtedly, too, have sent out erect filaments and formed disks. The erect filaments are rather stiff, irregularly branched and of about the same length. The diameter amounts to 29—41 μ, usually 33—36 μ. The secondary segments as a rule are a little longer than broad, but otherwise the individual secondary segments vary

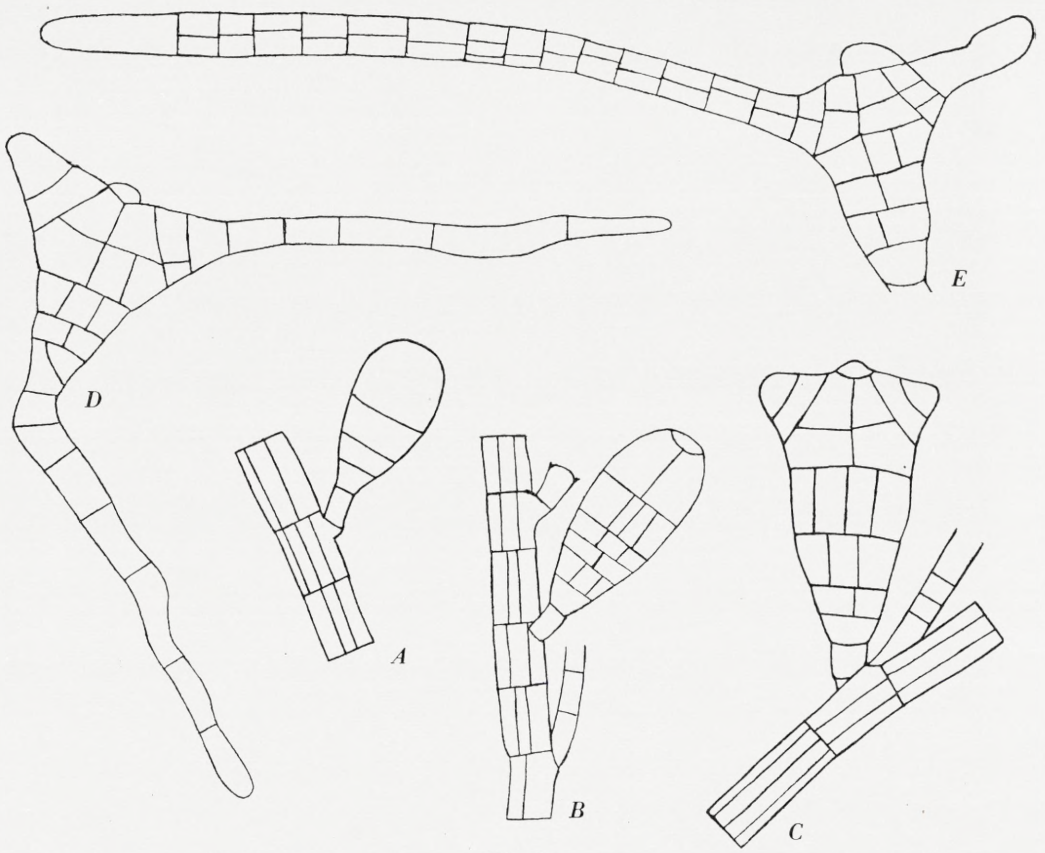

Fig. 8.
Sphacelaria tribuloides. *A*: young, *B*: somewhat older, *C*: mature propagule. In *B* further a sterigma from a shed propagule is seen, in *B* and *C* in addition an old hair. *D-E*: germinating propagules. — The northern Kattegat: Hulsig Stene, Aalbæk Bugt. ×230.

somewhat in length. Seen in surface view the secondary segments contain 1—2—3 longitudinal walls, whereas they lack transverse walls. In a very few exceptional cases, however, as in *S. Plumula*, a transverse wall was observed, although only in the lower part of the erect filaments.

Hairs occurring singly are common, both near the apices of the shoots and at rather a long distance down the filaments (fig. 8 *B—C*). In some cases terminal hairs were observed as in SAUVAGEAU's fig. 29 C. This position of the hairs is due either to the formation of the hair cell in the middle of the uppermost part of the apical

cell or to the fact that the apical cell did not continue its growth after the formation of the hair cell.

The propagules are found laterally on the filaments, being found comparatively frequently below a hair (fig. 8 *C*). They issue from an upper secondary segment fastened to a sterigma. In several cases sterigmata were observed, which had borne propagules now fallen off; they are characterized by their collar (fig. 8 *B*). The sterigmata occurred singly or two consecutively. The young propagules are club-shaped (fig. 8 *A*—*B*), the mature ones wedge-shaped with 3 small horns (fig. 8 *C*). REINKE, (l. c. p. 9) proposes the designation cordate for them in contradistinction to radiated propagules in e. g. *S. cirrosa*. As to the mature propagules the length without the sterigma, was between 120 and 156 μ, the breadth between 94 and 127 μ.

Propagules, fallen off and germinating, were observed in a good number of cases; they occurred between the erect filaments. In some cases one of the lateral horns (fig. 8 *E*), in other cases the lowest cell of the propagule, or both one of the lateral horns and the bottom cell (fig. 8 *D*) had grown out into a monosiphonous filament. In other cases, again, both the lateral horns and the bottom cell could each of them have grown out into a monosiphonous filament. In some of these filaments longitudinal walls, too, were observed. In no case, however, the filaments had spread to become disk-shaped.

Both unilocular and plurilocular sporangia are known; but neither has been observed on the Danish plants; they are said to be rare. The former were found on specimens collected by KUCKUCK at Rovigno and depicted from here by SAUVAGEAU (l. c. fig. 47). When young they are somewhat elongate, cylindrical, when mature spherical, 65—80 μ in diameter. They are borne on a unicellular stalk and are scattered or unilateral, often placed above one another. They occurred on the same plants which bore plurilocular sporangia, at times on the same branches.

The plurilocular sporangia were first described by HAUCK from the Adriatic (1878 p. 291, pl. 3 fig. 16). Later they were found e. g. on plants from Rovigno by KUCKUCK and depicted from here by SAUVAGEAU (Remarques fig. 29 L). They are cylindrical, 60—80 $\mu \times 50$—55 μ, short-stalked, often unilateral. They were found on the lower part of filaments which bore propagules on the upper part.

Localities. **Kn:** Hulsig Stene, Aalbæk Bugt, July 25th 1933.

9. **Sphacelaria Plumula** Zanard.

ZANARDINI, Iconographia Phycologica Adriatica, Volume I, 1860, p. 139, pl. 33; REINKE, Atlas, H. 2, 1892, pl. 48; Sphacelariaceen, 1891, p. 10; SAUVAGEAU, Remarques, p. 78 (1901, p. 94), figs. 18—20.

Sph. pseudoplumosa CROUAN, Florule du Finistère, 1867, pl. 25 fig. 161 1-3.

Of this easily recognizable species I have in the Danish material seen only some small plants from a locality in the Skagerak, growing together with *S. cæspitula* on a shell of *Buccinum*, as also a single specimen from the northern Kattegat growing

on a small stone. The former, which were collected in August, attained a height of up to 0.8 cm, while the latter, deriving from July, was no more than 0.5 cm high.

The basal part in both cases was much reduced, only consisting of a few irregular, creeping threads, which did not form a disk, but locally were able to spread a little in a lateral direction. In the specimen from the Kattegat it was certainly slightly thickened. The erect thallus consisted of distinct, pinnate main axes with opposite branches (pinnæ) issuing from practically every upper secondary segment. In the lower part of the axes the upper secondary segments, however, were not fertile, or they sent out only one branch. The diameter of the axes amounted to 53—74 μ. In the specimen from Kattegat an apical cell was 86 μ in diameter. In the lowermost part the axes were thinner, the diameter here amounting only to 40—50 μ. Descendent rhizoids have not been noticed.

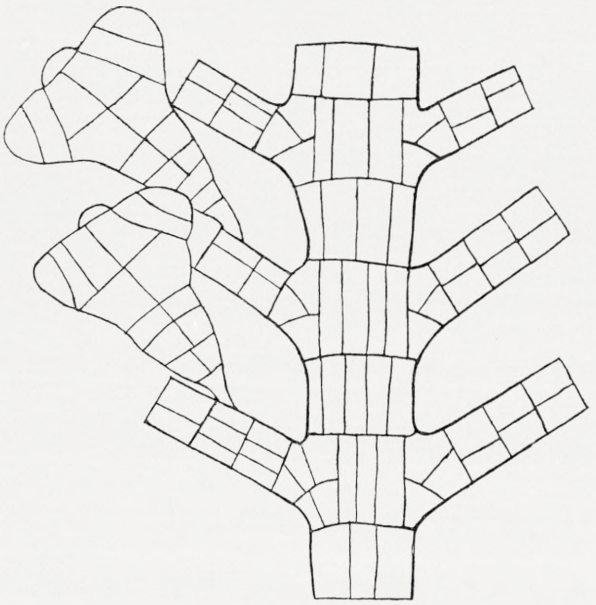

Fig. 9.
Sphacelaria Plumula. Part of a plant, two primary branches (pinnæ) of which each issue a propagule from its upper secondary segment No. 2. — The Skagerak: Mellemgrund off Lønstrup, 8—10 m, on *Buccinum*. ×230

The height of the secondary segments of the axes varies between half the breadth and a little more than the whole breadth. In most cases the secondary segments were hardly as high as the breadth. High secondary segments chiefly occur in the lower part of the axes. The secondary segments were always lacking transverse walls, but in the lower part of the axes a few secondary segments might quite exceptionally have a transverse wall. Seen in surface view they usually possessed (1—)2—4 longitudinal walls, separating (2—) 3—5 cells.

The pinnæ gradually become shorter towards the apex of the axis. The whole course of the uppermost, short pinnæ is nearly equal in diameter; the others tapering towards the apex. Their basal part is partly immersed in the axis, and the lowermost, inferior secondary segment when considered superficially seems to belong to the axis. The pinnæ are simple or in some cases branched. From both localities some of the branches possessed reduced hairs near the apex, in some cases certainly also terminally.

In the plant from the Kattegat some of the pinnæ bore propagules, which as a rule were rather young and club-shaped. However, a single one was mature and of the typical, wedge-shaped (tribuliform) form with three small horns as in *S.*

tribuloides. It measured about 140 μ in length and 110 μ in breadth and was fastened to a unicellular sterigma.

Also in the plants from Skagerak typical, mature, tribuliform propagules occurred (fig. 9). They measured 115—131 μ in length and about 103—131 μ in breadth. In addition many young propagules were found, including quite young ones, too. Finally in numerous cases sterigmata were found, which have born propagules now shed. These sterigmata left were chiefly found on the upper secondary segments Nos. 2 and 3 of the pinnæ (cf. SAUVAGEAU, l. c. pp. 86 and 88 (1901 p. 104)). Propagules were observed not only on the pinnæ, but also on the secondary ramuli, just as in a single case I noticed a propagule issuing direct from the axis opposite a pinna.

Unilocular sporangia were neither seen in the material from the Skagerak nor in that from the Kattegat.

S. Plumula has especially been studied by ZANARDINI, REINKE, and SAUVAGEAU. The last-mentioned author among other subjects offered a thorough mention of the branching, the hairs, the development of the propagules and finally described unilocular sporangia, which were not previously known. He also pointed out that the distinct contrast, emphasized by REINKE (1891), between long shoots and ramuli is more apparent than real, since any primary ramulus under certain conditions—after a truncation or the death of the apical cell—may become an axis.

The unilocular sporangia were by SAUVAGEAU found on individuals also bearing propagules, or on distinct plants. They are spherical, 55—80 μ in diameter and borne on a short, usually unicellular stalk. Like the propagules the first sporangia are frequently produced on the 2nd and 3rd upper secondary segments of the pinnæ, while the following sporangia occur more irregularly. In some cases a sporangium may rise from the apical cell of a branch, or two sporangia may issue from the secondary segment below the apical cell. Finally sporangia borne on a shorter or longer stalk may issue from truncated branches.

Plurilocular sporangia are not known.

Localities. **Sk:** ZK°, Mellemgrund off Lønstrup, 1.5 miles from land, 8—10 m, on *Buccinum*. — **Kn:** SW of the double broom at Nordre Rønner, 11—14 m, on stones.

10. **Sphacelaria racemosa** Grev. dilatus Rke.

REINKE, Algenflora westl. Ostsee, 1889, p. 40; Sphacelariaceen, 1891, p. 11.

F. **typica** RKE, Atlas, H. 2, 1892, p. 66; SAUVAGEAU, Remarques, p. 245 (1903, p. 74), fig. 14 C—D.

Sph. racemosa GREVILLE, Scottish Cryptogamic Flora, II, 1824, pl. 96; HARVEY, Phycol. Brit., III, 1851, pl. 349; SAUVAGEAU, Remarques, p. 99 (1901, p. 137) p.p.; WÆRN, Remarks on some Swedish Sphacelariaceae, 1945, p. 410, fig. 1.

F. **arctica** (HARV.) REINKE, Algenfl. westl. Ostsee, p. 40; Atlas, p. 66, plates 44, 45 figs. 1—10; SAUVAGEAU, Remarques, p. 246 (1903, p. 76); LAKOWITZ, Algenfl. Danziger Bucht, 1907, p. 28, fig. 17; SKUJA, Algenfl. Rigaschen Meerbusens, 1924, p. 349, figs. 1—2; LEVRING, Algenveg. v. Blekinge, 1940, p. 44.

Sph. arctica HARVEY, Nereis Bor.-Americana, III, Chlorospermeae, 1858, p. 124; KJELLMAN, Spetsbergens thallophyter, II, 1877, p. 34, pl. 2 figs. 4—6; WÆRN, l. c. p. 409, fig. 2.

Sph. racemosa GREV.; REINKE, Sphacelariaceen, p. 11 p.p.; SAUVAGEAU, Remarques, p. 99 (1901, p. 137) p.p., fig. 23.

Sph. racemosa GREV. f. *notata* C. AG., SVEDELIUS, Östersjöns hafsalgflora, 1901, p. 98.

Sph. notata (C. AG.) KJELLMAN, Handbok, 1890, p. 67.

Sph. olivacea REINKE, Atlas, H. 2, 1892, pl. 46.

S. racemosa [s. s.] was described and illustrated by GREVILLE in the "Scottish Cryptogamic Flora" in 1824 on the basis of a specimen from Firth of Forth in Scotland. The description was later entered in the "Phycologia Britannica" by HARVEY (1851), who here gave a similar illustration drawn after GREVILLE's original material. What particularly characterizes the species is the unilocular sporangia occurring in bunches on racemose stalks.

In 1858 HARVEY established a species of *Sphacelaria*, *S. arctica*, from Disko in West Greenland, on the basis of sterile material and without giving any figures. To this species KJELLMAN (1877) refers his material of *Sphacelaria* from Spitzbergen, comprising plants with unilocular and plants with plurilocular sporangia. Besides mentioning the two kinds of sporangia in more detail, KJELLMAN depicts them. Both types are stalked, but whereas the unilocular sporangia usually occur singly the plurilocular ones are placed one to several together on the same stalk.

Near Kiel in the western Baltic REINKE (1889) found plants with unilocular sporangia on branched stalks forming small racemes; these plants in all essentials showed accordance with HARVEY's picture of *S. racemosa* as also with English plants of this species that had been sent him by BATTERS. In addition he found near Kiel plants belonging to the same species with plurilocular sporangia on simple or branched stalks, agreeing well with KJELLMAN's figures. Hence REINKE supposes that *S. racemosa* and *S. arctica* belong to the same species, a view which he later (1891) seems to see further confirmed. He therefore unites the previous two species into one, *S. racemosa*, under which the former *S. arctica*, however, is entered as a variety (1889).

Actually several differences occur between var. *arctica* and *S. racemosa* s. s. = f. *typica*. Thus var. *arctica* is generally more robust, becoming higher than f. *typica*; the branching is more abundant, frequently distichous, just as rhizoids are common, especially on the lower part of the more vigorous axes, where they form thin coats of cortex. Finally the racemes formed by the unilocular sporangia are longer and more open, usually containing a fewer number of sporangia, even down to two, or the sporangia occur singly as was the case in KJELLMAN's plants from Spitzbergen and as is very often the case in REINKE's *S. olivacea* from the Baltic, which is identical with var. *arctica*.

REINKE's method has since usually been followed. However, SAUVAGEAU (p. 246 (1903 p. 76)) suggests that var. *arctica* perhaps deserves to be considered a distinct species, just as WÆRN (1945) maintains the original taxonomy, among other things

referring to his figures of *S. racemosa* from Firth of Clyde in West Scotland and *S. arctica* from Gottland in the Baltic.

I myself have not yet made up my mind regarding the problem. Partly I have not had an opportunity to examine British plants of *S. racemosa*, partly ROSENVINGE's posthumous Danish material, collected in the months of May—August, being sterile, practically exclusively consists of plants of the *S. arctica*-type. Only some small specimens, about 1 cm high, collected in Aalborg Bugt in the middle of the Kattegat in July 1892 are most closely related to f. *typica* (cf. SAUVAGEAU p. 246 (1903 p. 75)), but these plants were not very applicable, as they were sterile, possessing only some remaining fructiferous branches.—For the present I intend to follow the view of REINKE—using, however, the designation *forma* instead of *varietas*—thus calling the Danish plants, with the exception of those just mentioned, *S. racemosa* f. *arctica*.

F. *arctica* has been studied by KJELLMAN, REINKE, SAUVAGEAU, SVEDELIUS, WÆRN, and others. It forms dense, somewhat irregular, often penicillate tufts, which in the Danish waters generally are 1 to about 4 cm high. The basal part of the frond according to REINKE is spread out in disk-shape and may issue stolons that may cause a formation of new disks. In case the basal disk is only slightly developed the plant is fastened chiefly by means of the numerous descendent rhizoids issuing from the more vigorous shoots.

The erect frond is differentiated into main axes and branches. The latter are frequently distichous, now opposite for a stretch, now unilateral on one side or the other. The secondary segments, which usually are divided by one series of transverse walls, more rarely undivided (cf. fig. 10 *A*), are of the same height as the breadth or the height is greater than the breadth. Besides descendent rhizoids divaricate rhizoids also occur.

Hairs have been described by REINKE and SAUVAGEAU. REINKE (1891, 1892) found hairs issuing laterally, singly or in small bundles of 2—4. They are formed through the growing out of a pericentral cell. When several occur together, one is said to be formed first after which another may develop at the base of the first and so on. SAUVAGEAU found similar hairs, though none in bundles; however, he emphasized that they are endogenous, corresponding to secondary branches. Moreover SAUVAGEAU mentions sympodial hairs occurring in pairs formed by the apical cell.

Unilocular sporangia are the only fructification organs known for the Danish waters. They were found on a specimen, about 3.5 cm high, growing on *Cladophora rupestris*, which was collected near common water-mark at Saltholm in the Sound at the end of February by the author. They occur either in small racemes (fig. 10 *B*) or singly (fig. 10 *A*); in the latter case on a short, monosiphonous stalk, more rarely on a long and partly disiphonous one. Usually the racemes and the sporangia occurring singly issue laterally from the main axes and the longer branches of the first order, more rarely from the longer branches of the second order. However, I have also seen a raceme issuing terminally from rather a long branch just as sporangia on the rhizoids are not rarely found, the divaricate rhizoids as well as the descendent

ones. In several cases a raceme of sporangia rises from a descendent rhizoid nearly at the insertion of the rhizoid (cp. the erect shoot in SAUVAGEAU fig. 14 C).

The number of sporangia of the racemes is small, probably 3—4 as a rule; only in a few cases I have noticed up to 6 sporangia in the same raceme. Not rarely one (or more) of the sporangia of a raceme is (are) sessile. The sporangia are most frequently ovoid, in other cases oval or spherical, rather varying as to dimensions. In material kept in alcohol the length amounted to (41—)45—53(—62) μ whereas the diameter was (37—)45—49 (—57) μ.

In ROSENVINGE's material remaining sporangium-stalks were found on a very few specimens collected in July. The sporangia, however, were practically all thrown off; very few unilocular sporangia, emptied long ago, were still left.

Propagules are not known. Old, detached fragments are, however, frequently found, which in the lowermost part are provided with a large number of long rhizoids. I consider it probable that such fragments of the frond may cause the formation of new plants.

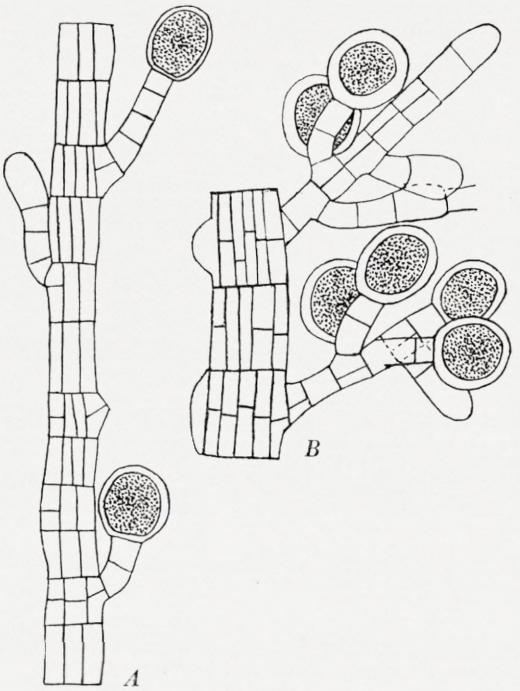

Fig. 10.
Sphacelaria racemosa f. *arctica*. *A*: lower part of branch of the first order with unilocular sporangia, occurring singly. In most of the secondary segments transverse walls are lacking. B: Fragment of a main axis of the same plant with racemes of unilocular sporangia. — Saltholm near Copenhagen, on *Cladophora rupestris* near common water-mark, 22-II-1934 (S. L.). ×230.

F. *arctica* in the Danish waters is distributed from the northern Kattegat to the Baltic at Bornholm. However, it seems to be very rare in the Kattegat, whereas it seems to be common at Bornholm. Its vertical distribution reaches from common water-mark down to a depth of 38 m. It is, however, usually found in relatively deep water; in the Bornholm area it has thus most frequently been collected at depths between 17 and about 30 m. When it occurs at such a great depth the tufts are generally very meager and open as well as lengthened. It is found chiefly on stones and shells, more rarely on other algae (*Polyides, Cladophora rupestris*). In some of the localities within the Bornholm area it was apparently detached, occurring together with loose specimens of the Baltic form of *S. plumigera*, which has been described as *S. racemosa* var. *arctica* f. *pinnata* Rke.

Localities. **Kn:** Nordøst Revet at Hirsholm. — **Ke:** XA, Kobbergrunden lightship N to W $^1/_2$ W a good $6^1/_2$ miles, 13 m(?). — **Km:** FL, Aalborg Bugt, 9 m (f. *typica*, det. C. Sauvageau, cf. Remarques p. 246 (1903, p. 75)). — **Lb:** Off Stenderup Skov; Sønderballehoved, on *Polyides*. — **Sf:** Ærø (Kiærbølling).

— **Sb:** Off Stavreshoved, 7 m; UF, Hov Sand, 9 m. — **Su:** PX, almost abeam Tibberup, 8 m; Taarbæk Rev, 12 m; Barakkebro, Saltholm, on *Cladoph. rup.* (w. uniloc. sporang. in February) and stones (January, 1 cm high, sterile) (S. L.); ibid. April, 3 cm high (sterile) (S. L.); eastern side of Saltholms Flak, 6 m. — **Bm:** SD, Stevns lighthouse N to W $^1/_4$ W hardly 13 miles, 24 m; QS, Møens Klint SSW 7 miles, 21 m, with numerous, remaining sporangial branches and a few emptied, old sporangia, July 25th; VG, north of Møens Klint, abeam Hellehavns Nakke, $^3/_4$ mile off the land, 17 m. — **Bb:** XZ[1], Davids Banke, 29 m; SV, Nordvestgrund at Christiansø, 30—32 m; SL, off Allinge, 6—11 m; Allinge, on vertical rocky walls in sheltered crack, 1—2 m; SP, off Svaneke, 28 m, entangled with *Phycodrys rubens* and *S. plumig.* f. *pinn.*; 3 miles SSE of Neksø harbour, 21 m, in company with *S. plumig.* f. *pinn.* (C. A. Jørgensen); YD, the double broom at Salthammer Rev V $^1/_4$ S hardly 1 mile, 19 m, a few old, emptied uniloc. sporang., July 6th, together with *S. plumig.* f. *pinn.*; YA, Dueodde lighthouse in W $5^3/_4$ miles, 38 m; 8 miles S $^1/_2$ E of Rønne Havn, 11—19 m (C. A. J.); SS, west border of Rønne Banke, 19 m; ST, western side of Rønne Banke, 18 m.

11. **Sphacelaria plumigera** Holmes.

Holmes, New British Mar. Algæ, 1883, p. 141; Batters, Mar. Alg. of Berwick-on-Tweed, 1889, p. 63, pl. 10 figs. 1—3 (referred to the subgenus *Pseudochætopteris*); Reinke, Sphacelariaceen, 1891, p. 12; Atlas, H. 2, 1892, pl. 47; Sauvageau, Remarques, p. 94 (1901, p. 111), fig. 22; Taylor in Lewis & Taylor, Notes from the Woods Hole Laboratory, 1933, p. 151, pl. 274 figs. 1, 4; Wærn, Remarks on Some Swedish Sphacelariaceae, 1945, p. 405, fig. 6; Kylin, Phaeophyceen schw. Westküste, 1947, p. 30, pl. 2 fig. 6 (= Wærn's fig. 6).

Sph. plumosa in Harvey, Phycol. Brit., I, 1846, pl. 87.

Conferva pennata in Engl. Bot., Vol. 33, 1812, pl. 2330 (figura media).

f. **typica.**

f. **pinnata** (Reinke); Sauvageau, Remarques, p. 102 (1901, p. 140); Wærn, l. c. p. 407, fig. 5.

Sph. racemosa f. *pinnata* Reinke, Sphacelariaceen, p. 12; Atlas, H. 2, pl. 45 figs. 11—12; Svedelius, Östersjöns hafsalgflora, 1901, p. 99; Levring, Algenveg. v. Blekinge, 1940, p. 44.

f. **patentissima** Sauvageau, Remarques, p. 233 (1903, p. 50).

This alga bears great resemblance to *Chaetopteris plumosa*, with which it has often been confounded. To the naked eye, however, it appears that the primary ramuli (pinnæ) of the axes here are of nearly equal length, usually occurring almost right down to the basal part of the latter (cf. Harvey's and Batters' figures). Moreover its pinnæ are shorter than those of *Chaetopteris*. A secure distinction between on the one hand sterile plants of *Chaetopteris* and on the other sterile and fertile plants of *S. plumigera* can only be made by means of the microscope, where the rhizoids in the former appear to rise without any order, whereas in the latter they issue in the plane of branching. A further difference between the two species is that the unilocular sporangia in *S. plumigera*, which are the only known sporangia in this species, occur singly or a few together on simple or branched stalks, or in racemes, on the pinnæ, whereas the unilocular and plurilocular sporangia in *Chaetopteris* are placed on special shoots issuing from the rhizoidal cortex of the axes. The latter phenomenon entails that fertile plants of *Chaetopteris* are easily determined macroscopically.

The species was first recognized by Holmes, who called attention to the different

position of the sporangia in the two algae. Later it was depicted by BATTERS, who referred it to the subgenus *Pseudochaetopteris*, and KUCKUCK in REINKE's Atlas. Finally it was made the object of a thorough examination by SAUVAGEAU, who detected the mentioned very important character concerning the rhizoids. For his examination besides plants from other localities he used material from the northern Kattegat and his fig. 22 was drawn from plants from here.

The basal part is disk-shaped, formed by radiating, coalescent filaments, which, seen from below at any rate, show a flabellate arrangement. On the upper side of the disk the descendent rhizoids issuing from the main axes spread, forming a felted thickening. The thickness of the disk is comparatively small, but at vertical sections it appears to consist of several layers of cells. The vertical filaments of the disk seem always to be simple.

The erect thallus consists of regularly pinnate main axes, which from practically every upper secondary segment gives out two opposite pinnæ. Some of these lengthen to be axes of the second order, which in their turn ramify pinnately with opposite ramuli. The axes of the second (or possibly higher) order occur irregularly or subdichotomously. The secondary segments are a little lower than broad or the height almost corresponds to the breadth. They are provided with one or more series of transverse walls. In the uppermost part the main axes are naked, but from a certain distance from the apex descendent closely apposed rhizoids occur, which, as mentioned, rise in the plane of branching. These issue from the upper half of the lower secondary segments, gradually forming a dense, coherent investment.

The pinnæ are of almost equal length, generally simple, attenuating at the apex. In the secondary segments a large central cell, surrounded by the smaller pericentral cells, is found. The central cell contains tannin and in the dried material it is frequently of a yellowish brown or dark brown colour.

Hairs are at times present on some of the pinnæ. They are terminal or found near the apex, in the latter case possibly two together. In the Danish material I have among other specimens seen them in some plants from March where they mainly occurred two and two together at the apex of the relatively young pinnæ. In several cases the youngest, hair-bearing pinnæ bore the number 30, reckoned from the apex of the axis.

In the Danish waters the species seems to be rather widely distributed, as it has been collected from the northern Kattegat to the area of Bornholm in the Baltic. Attached, typical specimens, however, are with certainty found only in the northern Kattegat and the Little Belt. In the first place, where it forms tufts of the height of 2—11 cm, it was collected repeatedly on moles in harbours, but was also found at greater depths, down to about 25 m. In the Little Belt it was only found a single time, forming small tufts to a height of well over 1 cm. Besides it occurs in a loose, sterile state, more or less deviating, in the Samsø area, the Great Belt, and the Sound as well as in the Baltic, the latter place in deep water (19—38 m). The colour in the present, dried plants is usually greenish or brownish.

The period of fructification in Denmark lasts from the winter and spring until the beginning of June. Fructiferous material exists from three collections, which were all made in the northern Kattegat. In one case some plants up to 11 cm high, which were collected on January 3rd, 1895, at Frederikshavn by F. BØRGESEN, were involved, in the other some small individuals up to 2.5 cm collected in deep water off Frederikshavn on June 2nd, 1897, by C. H. OSTENFELD, in the third case some plants 5.5 cm high from the northern mole of Frederikshavn harbour, found March 18th, 1933, by the author.

The plants first mentioned no doubt belong to the collection from which SAUVAGEAU at one time borrowed material for investigation; their unilocular sporangia are stalked, issuing from the upper half of the secondary segments of the pinnæ, frequently at a wide angle. They are the more numerous in the upper part of the pinnæ. The sporangial stalks are generally simple, consisting of 2—5 (sometimes more) cells, more rarely branched and then bearing up to 3—4 sporangia. Usually they are scattered, more rarely opposite, certainly chiefly pinnately arranged. The sporangia are ovoid or rounded, in my preparations being 49—66 μ long and 45—57 μ in diameter. Most of them were not quite mature, but some had the spores differentiated, while others again were emptied.

On the plants from June the sporangia usually also occurred on short, simple or branched stalks. Unlike the plants from January the sporangial stalks, however, relatively rarely issued direct from the pinnæ (fig. 11 *A*); as a rule the sporangia were found in racemes, whose axes in their turn rose from the pinnæ (fig. 11 *B*). In some cases the axis of the raceme was rather short, the raceme therefore containing only a small number of sporangia; in other cases it was lengthened, and in spite of the fact that the uppermost part generally was broken off, it might contain some twenty secondary segments. In such cases the number of sporangia was considerably greater. In many racemes the axis bore a terminal sporangium.

The racemes were chiefly scattered, usually occurring in the middle and upper part of the pinnæ. In several cases they issued near the apex or even terminally from the full-grown pinnæ. The secondary segments of the more vigorous axes of the racemes as a rule were provided with longitudinal walls, sometimes with transverse walls, too. However, they had not like the secondary segments of the pinnæ a rather large central cell containing tannin; the axes of the racemes therefore were remarkably light as compared with the pinnæ.

The specimens seem to have nearly finished fructification, a number of sporangia being emptied, just as a great number of remnants of sporangial stalks were found. Still no few mature sporangia with differentiated spores were observed. They were usually ovoid, generally being somewhat more lengthy and often also somewhat thicker than those of the previous plants. They measured (57—)62—82(—86) μ in length and 41—66 μ in diameter. Moreover quite young sporangia and initials of sporangia were found.

The racemes of sporangia of *S. racemosa* var. *arctica* depicted by KUCKUCK in

REINKE's Atlas pl. 45 fig. 8 correspond completely to many of the racemes in the plants just mentioned. But while the racemes in the former are particularly found on the main axes and on the longer branches of the first (and second) order, they occur in the latter only on the primary branches (pinnæ), these plants for that matter being characterized by their rhizoids formed in the plane of branching.

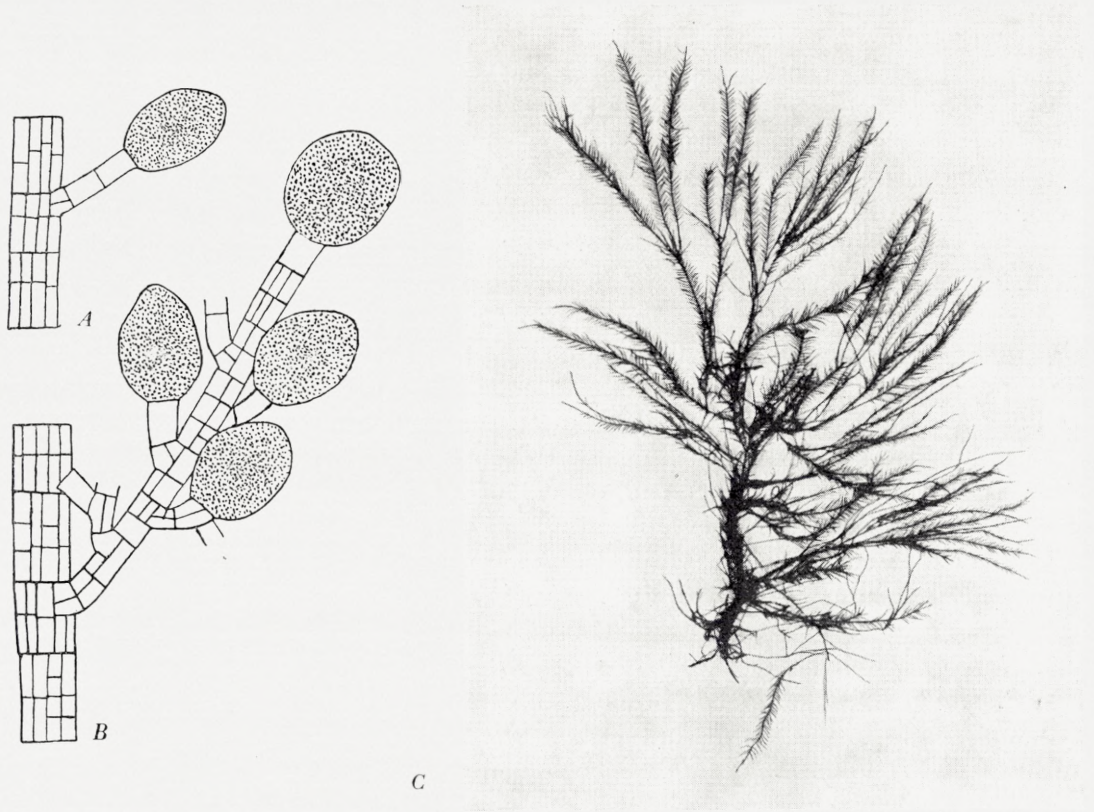

Fig. 11.
Sphacelaria plumigera. *A*: Pinna with a single unilocular sporangium. *B*: Pinna with a raceme of unilocular sporangia. Drawn from dried material. *A-B*: the northern Kattegat at Frederikshavn, 25 m, 2-VI-1897 (C. H. Ostenfeld). ×230. — *C*: f. *pinnata* from the Baltic east of Bornholm (*YC*, the double broom at Salthammer Rev NW. $^3/_4$ N. $1^1/_2$ miles, 24 m, 6-VII-1901). ×2.5.

On the plants from March, whose fructification was extremely rich and whose unilocular sporangia, measuring 62—70 $\mu \times 53$—57 μ, generally were mature with fully differentiated spores, the occurrence of the unilocular sporangia as a rule was like those of the plants from January; however, in some cases racemes were found corresponding to those of the plants from June. So far the plants from March thus are intermediate between those from January and those from June. For that matter it was remarkable that the apex of the full-grown pinnæ in numerous cases length-

ened direct into a simple or branched sporangial stalk. The apex of the pinnæ, slightly younger, often bore hairs.

The loose specimens of *S. plumigera* from the Danish waters—which like the attached ones all possess transverse walls in the secondary segments—are primarily characterized by the very great decline of the cortification. Moreover they are devoid of the attachment-disk and, as mentioned, sterile. Some are well developed, their habit only slightly deviating from that of the attached ones, as was the case in some specimens from the area of Samsø. Rhizoids were lacking in these plants in the greater part by far of the course of the main axes, and only in the lower part of the latter a more or less imperfect cortex might occur here and there.

More deviating, but in habit not very different from attached individuals, was a loose plant, about 5.5 cm high, from the Baltic north-east of Møen at a depth of 24 m. It was rather much reduced and slender, possessing rhizoids only on the lowermost part of the main axes, where the former could locally form a cortex. Owing to the habit I have referred this plant as well as the preceding ones to f. *typica*.

Most aberrant are f. *patentissima* Sauv. and f. *pinnata* Rke. (fig. 11 *C*), which both generally occur entangled with other loose algae. The former has divaricate, often rather long pinnæ, which issue almost rectangularly, whereas the pinnæ of the latter are shorter, rising at an acute angle. However, the characters are not distinct. In both forms rhizoids are practically lacking. In a fragment of f. *patentissima* I still observed partly a local incipient, typical formation of rhizoids occurring, however, on one side only, partly a local cortification. In f. *pinnata* a single, very long, descendent rhizoid occurs now and then, rarely a few long ones which at a short distance may incompletely surround the main axis. Wærn (l. c. p. 408) in f. *pinnata* found small parts with an incipient, typical formation of cortex by rhizoids. In fig. 11 *C* a fragment of f. *pinnata* is shown, prepared from a tuft containing also other loose algae.

F. *patentissima* has been collected at a depth of about 10 m in the Great Belt in January and in the Sound in April, in the latter place in the company of loose fragments of *S. cirrosa*. F. *pinnata* has been observed only within the area of Bornholm in the Baltic, where it has been collected several times in June—August at depths between 19 and 38 m, always in the company of *S. racemosa* f. *arctica*, occasionally also with *Delesseria sanguinea* and *Rhodomela*. Only this form has been observed in the area in question.

Localities. **Kn:** Skagen harbour, pier (J. Boye Petersen); 2 miles SE of Skagen harbour, 17—19 m, fragments (P. Kramp); fC, south of Skagen, 15 m; east of Nordøstrevet at Hirsholmene, 22—28 m; east of Marens Rev; near Frederikshavn, 25 m, June, with sporangia (C. H. Ostenfeld); Frederikshavn harbour, January, with sporangia (F. Børgesen); ibid. (L. K. R.); ibid., northern mole, March, with sporangia (S. L.); off Frederikshavn, 17—19 m (P. Kramp). — **Sa:** AQ, Kalø Vig, off Knebel Vig, 9 m, loose (det. C. Sauvageau); MV, Kirkegrund, 8—9 m, loose (det. C. Sauvageau). — **Lb:** Lyngsodde, numerous plants slightly more than 1 cm high. — **Sb:** NU, off Strandskoven at Bovense, 11 m, loose, f. *patentissima*, entangled with *Polysiphonia* and *Stypocaulon scop.* f. *spinulosum*. — **Su:** OH, north of Lous' Flak, Vedbæk WSW $^1/_4$ S 1 mile, 10 m, loose, f. *patentissima* (cf. Sauvageau, Remarques p. 233 (1903 p. 50)); northern end of Lous' Flak off Rungsted, 9 m, loose, f. *patentissima*; OG^1, between Trekroner and Middelgrunden, loose, f. *patentissima*. — **Bm:** SD, Stevns lighthouse N to W $^1/_4$ W, hardly 13 miles, 24 m, loose (det. C. Sauvageau). — **Bb:** All

specimens from the Bornholm area belong to f. *pinnata*; they were all loose, being entangled in other loose algae, especially *S. racemosa* f. *arctica*. — SP, off Svaneke, 28 m; YC, the double broom at Salthammer Rev NW $^3/_4$ N $1^1/_2$ miles, 25 m; YD, the double broom at Salthammer Rev W $^1/_4$ S hardly 1 mile, 19 m; YA, Dueodde lighthouse W $5^3/_4$ miles, 38 m; 3 miles SSE of Neksø harbour, 21 m (C. A. Jørgensen).

Chaetopteris Kütz.

1. **Chaetopteris plumosa** (Lyngb.) Kütz.

Kützing, Phycol. generalis, 1843, p. 293; Tab. phycol., VI, 1856, tab. 6 I; J. G. Agardh, Spec. Algarum, I, 1848, p. 41; Geyler, Zur Kenntniss d. Sphacelarieen, 1866, p. 511, Taf. 36 figs. 1—5; Magnus, Z. Morph. d. Sphacelarieen, 1873, p. 133, Taf. 1 figs. 15—20, Taf. 2 figs. 33—37; Areschoug, Observat. phycol., III, 1875, p. 20, pl. 2 fig. 4; Kjellman, Spetsbergens thallophyter, II, 1877, p. 32, pl. 2 figs. 2—3; Handbok, 1890, p. 65; Batters, Mar. Alg. Berwick-on-Tweed, 1889, p. 64, pl. 10 figs. 4—6; Reinke, Atlas, H. 2, 1892, Taf. 49—50; Sauvageau, Remarques, p. 106 (1901, p. 144), fig. 24; Kuckuck, Zur Fortpflanzung d. Phaeosporeen, 1912, p. 182, Taf. VIII (19) fig. 5; Oltmanns, Morph. u. Biol. d. Algen, 2. Aufl., II, 1922, p. 93; Printz, Algenveg. Trondhjemsfjordes, 1926, p. 165; Newton, Handbook, 1931, fig. 121; Schreiber, Üb. d. geschlechtliche Fortpflanzung der Sphacelariales, 1931, p. 236; Kylin, Phaeophyceen schw. Westküste, 1947, p. 31, Taf. 2 fig. 7.

Sphacelaria plumosa Lyngbye, Tentamen Hydr. Dan., 1819, p. 103, tab. 30 C; Wærn, Remarks on Some Swedish Sphacelariaceae, 1945, p. 404. — Not *S. plumosa* in Harvey, Phycol. Brit., I, 1846, pl. 87.

Ceramium pennatum in Flora Danica (Hornemann), 1813, tab. 1481.

This species has been studied by Geyler, Magnus, Batters, Reinke, Sauvageau, and others. In 1819 it was described by Lyngbye under the name of *S. plumosa*, but later it was referred by Kützing to a new genus, *Chaetopteris*, owing to the corticated main axes. As this character is also found in species of the genus *Sphacelaria*, Kützing's description was insufficient for the maintenance of the genus *Chaetopteris*. Nor is the latter sufficiently defined after Batters had emphasized the existence of the rhizoidal fructiferous branches as the most important character, for in *Sphacelaria*, too, rhizoidal sporangia are found. A true distinction between the two genera actually does not exist, and Wærn with perfect justice consistently interprets the species in the same way as Lyngbye.—When nevertheless I use the name of *Chaetopteris*, it is done with reference to the constant occurrence of the sporangia on the rhizoidal fructiferous branches, a character which Sauvageau (Remarques p. 112 (1901 p. 149)), too, thinks might justify the maintenance of the genus as also the time-honoured use of the name.

The basal part of the thallus consists of a well developed and well-defined, thick, perennial disk, with marginal growth, formed by radiating, coalescent filaments. Seen from below the disk very much resembles a *Myrionema*, seen from above it consists of smaller, more thick-walled cells arranged more irregularly. In radial sections the cells are arranged in vertical rows. Gradually the disk is strengthened by the downwards growing rhizoids from the axes spreading over the former. Sometimes the disk is overgrown by new disks belonging to other individuals, or another

disk may be formed by the growing out of surface-cells from the old one broadening over the latter as a new disk.

The erect thallus rises as prolongations of vertical threads of the basal disk. It consists of one—more(—many) main axes, which in the young plant are regularly pinnate with opposite primary ramuli right down to the base. Some of the latter will develop into axes of the second order, branching in the same way, etc. At a more advanced stage the plant is provided with a number of axes of second and higher order, occurring irregularly or subdichotomously, which above are regularly pinnate with opposite pinnæ, while the lower part of the plant is usually naked, the pinnæ here being thrown off. The axes are up to about 0.5 mm thick and dark coloured, while the pinnate sections, which usually are of an ovate—lanceolate outline, are of an olive green or olive brown colour. The pinnæ generally issue only from the upper secondary segments, but in plants from Spitzbergen and Haugesund in the south-west of Norway SAUVAGEAU found that the lower secondary segments were also fertile. At a certain distance from the apex of the axes numerous, branched, obliquely downwards growing rhizoids are given out. They issue from cells all around the axes and quickly form a thick, pseudoparenchymatous cortex.

The pinnæ are rather long, simple or branched; they may possess hairs terminally or near the apex. On the pinnulæ the hairs, however, are more common.—I have not systematically investigated the existence of hairs in Danish plants, but in a specimen collected in the Sound on April 16th which I casually examined they were very common.

Towards the end of the period of vegetation the pinnæ usually are thrown off, while short fructiferous branches in great number issue from the rhizoidal cortex covering as a dense felt the greater part of the axes. Both unilocular and plurilocular sporangia are known; both are short-stalked, the former spherical, the latter short-cylindrical. The two sorts of sporangia always occur on different plants.

KUCKUCK depicted the swarmers both from unilocular and plurilocular sporangia in material from Heligoland. The swarmers from the former are larger than those from the latter. Later SCHREIBER at Heligoland attempted making the supposed gametes from the plurilocular sporangia copulate; he did not succeed, however, nor when the swarmers derived from different plants. In spite of this it must be assumed that in nature an alternation of generations exists between two morphologically identical generations, meiosis taking place in the unilocular sporangia.

In the present material from the Danish waters the unilocular sporangia were rarer than the plurilocular ones, as they were only found on plants from two collections, both from the northern Kattegat, from December 8th and March 4th, respectively. In the former case the sporangia were chiefly young, in the latter mature or empty; the emptied ones had frequently been proliferated, enveloping new, mature sporangia.

Plurilocular sporangia (both young and nearly mature) have been found on November 19th on plants from the Great Belt, on January 5th on plants from the northern Kattegat (chiefly young ones), and on January 25th on plants from the

Great Belt (mature and partly falling ones). Moreover plants are available from various areas from February, April, May as also as late as August 7th (a single plant) with a few remaining, emptied plurilocular sporangia besides remnants of sporangial stalks.

After the cessation of fructification the fructiferous branches are frequently preserved long, and through the summer, indeed even quite until the end of October, a few plants may be found, which still are slightly felted owing to old fructiferous branches. On the other hand individuals have been observed which possess fresh fructiferous branches as early as August 10th, September 26th, October 6th, 19th, and 27th. On one and the same individual, collected on October 27th in the Great Belt, both old and new fructiferous branches occurred, the former on the older parts of the main axes, the latter on the younger parts which still bore pinnæ.

In the Danish waters the vegetative growth is resumed early in the year, partly while the fructification is still in progress. The present material includes four collections from January, 1 from February, 3 from March, a great number from the months of April to October, 2 from November, and 1 from December. In this material some small plants, up to 2 cm high, which were collected on January 5th, had already young pinnæ at the apex; they bore chiefly young plurilocular sporangia. The other plants from January, however, had not yet resumed growth (in one from January 25th with mature and falling plurilocular sporangia the old pinnæ were still preserved at the apices of the shoots). In the plant from February, collected on the 14th, and those from March, collected on the 4th, 6th, and 22th, young pinnæ, partly comparatively well developed, occurred at the apex. In April pinnæ mostly were well developed, even if a much felted plant, 5 cm high, had hardly begun shooting; it had been collected on April 19th at a depth of 24 m in the area of Samsø. From May—August and partly in September the species mostly wears its summer-habit, even if, as mentioned, a few plants may still bear a little felt caused by old fructiferous branches. In the material from September and October some of the pinnæ are often broken off; in October, at any rate, the main axes usually begin being felted. In one collection from November both pinnæ and felt from new-formed sterile fructiferous branches were found, in the other, in which the plants were much felted and bore numerous fructiferous branches with plurilocular sporangia, hardly any pinnæ occurred. The plants from December lacked pinnæ, but they were much felted and provided with unilocular sporangia. The habit completely corresponds to Areschoug, Alg. scand. exsicc., No. 408.

Chaetopteris plumosa in Denmark generally reaches a height of 4—10 cm, a single specimen, however, was 12.5 cm high. It is widely distributed in the Danish waters from the North Sea to the western Baltic. Also from the area of the Baltic round Møen a probably loose, not intact, specimen, 4 cm high, from a depth of 21 m is at hand. However, the species is absent in the Limfjord and the fiords proper. In Vejle Fjord I collected it in the outmost part near Rosenvold. It occurs, as a rule, at somewhat deeper water, reaching a depth of 30 m. In some cases it is found in shallow water

on harbour moles. It usually grows on stones and shells, e. g. those of *Cyprina* and *Balanus*. A frequent habitat is among the haptera of the *Laminarias*. Finally it has been noticed on the stipe of *Laminaria digitata*, the lower, stalk-like part of *Fucus serratus*, and the basal disk of *Halidrys*.

Localities. **Ns:** ZQ, Jyske Rev, Lodbjerg lighthouse E by S $26^1/_2$ miles, 24 m; aF, Thyborøn beacon SE $^1/_2$ E $14^1/_2$ miles, 31 m; eR, 9 miles NW $^1/_2$ N of Lodbjerg lighthouse, 27 m. — **Sk:** 6 localities at depths between 9 and 23 m at the stretch off Hanstholm—Hirtshals. — **Kn:** 35 localities near Hirsholmene, Frederikshavn, Nordre Rønner, Trindelen, and Tønneberg Banke. On harbour moles and at depths between 5 and 19 m. — **Ke:** several localities at depths of 10—30 m at Fladen; Groves Flak; Store Middelgrund. Further at Gilleleje and Nakke (Lyngbye). — **Ks:** Grenaa harbour; further 6 localities from 8—19 m. — **Sa:** Hofmansgave (Hofm. Bg., Carol. Rosenb. and others); further 21 localities mainly between 4 and 10 m, a few, however, at 23—24 m's depth. — **Lb:** Aarøsund pier and 12 localities from 4—19 m's depth. — — **Sf:** 4 localities, 7—15 m. — **Sb:** 18 localities, mostly 4—11 m, a single one, 19 m. — **Su:** 8 localities from Helsingør—Copenhagen, 6—13 m. — **Bw:** 5 localities S and SW of Als, 5—13 m; Aabenraa Fjord (P. Magnus); 2 localities at the south end of Langeland, 11 m. — **Bm:** QS, Møens Klint SSW, 7 miles, 21 m (loose?).

Holoblasteae.

Stypocaulon Kütz.

Kützing, Phycol. generalis, 1843, p. 293.

1. **Stypocaulon scoparium** (L.) Kütz.

Kützing, l. c., pl. 18 II; Tab. phycol., V, 1855, tab. 96; Geyler, Zur Kenntniss d. Sphacelarieen, 1866, p. 481, pl. 34 figs. 1—13; Magnus, Zur Morph. d. Sphacelarieen, 1873, p. 139, pl. 2 figs. 38—41; Kjellman, Handbok, 1890, p. 66; Reinke, Sphacelariaceen, 1891, p. 24, pl. 7 figs. 1—5; Oltmanns, Morph. u. Biol. d. Algen, II, 1922, p. 98; Newton, Handbook, 1931, fig. 124; Higgins, A Cytological Investig. of Stypocaulon scop. ..., 1931, p. 345.

Conferva scoparia Linné, Spec. pl., II, 1753, p. 1165; Dillwyn, British Confervæ, 1809, pl. 52.

Sphacelaria scoparia Lyngbye, Tent. Hydr. Dan., 1819, p. 104, tab. 31 B; Meneghini, Alghe Italiane e Dalmatiche, 1842, p. 344; Harvey, Phycol. Brit., I, 1846, pl. 37; Hauck, Meeresalgen, 1885, p. 347.

Halopteris scoparia (L.) Sauvageau, Remarques, p. 349, figs. 69—73; Sur la sexualité de l'Halopt. scop., 1907, p. 506; Sur le développement de l'Halopt. scop., 1908, p. 162; Sur le développement échelonné de l'Halopt. scop. ..., 1909, p. 44, figs. 1—10; Wærn, Remarks on Some Swedish Sphacelariaceae, 1945, p. 412, figs. 3—4.

Sphacelaria disticha Lyngb., l. c. p. 104, tab. 31 A.

f. **typicum**. Kjellm. l. c.

f. **patentissimum** Sauv., Remarques, p. 372, fig. 73; *Sphacelaria scoparioides* Lyngb., l. c. p. 107, tab. 32 C; Flora Danica, tab. 1953, fig. 1, 1829 (Hornemann).

f. **spinulosum** (Lyngb.) Kjellman, l. c.; Reinke, Atlas, H. 2, 1892, Taf. 48 figs. 8—14; *Sphacelaria spinulosa* Lyngb., l. c. p. 106, tab. 32 B; *Halopteris spinulosa* (Lyngb.) Sauv. var. *patentissima* Sauv., Remarques, p. 379, figs. 74—75.

Investigations on this species have been carried out by Geyler, Magnus, Reinke, Sauvageau, Higgins, and others. As shown by Sauvageau on material from Banyuls-

sur-Mer on the French Mediterranean coast, the plant commences—with the starting point in the germination of the swarmers from the unilocular sporangia—its development by the formation of a many-celled, small basal disk from which an erect, short shoot issues. At the base of the shoot a new, erect short shoot of the second generation develops which is considerably more robust. This shoot in its lower part differentiates pericysts and from one of these a long shoot is issued. However, the rise of the latter may be delayed through the formation of another one or two erect, short shoots.

The long shoot develops into a vigorous main axis bearing alternating, distichous pinnæ, which in their turn bear alternating pinnulæ. Some of the pinnæ and pinnulæ are lengthened, likewise becoming axes, and so on. From the axes substitute shoots issue and short shoots developed from pericysts, and the mature plant forms densely branched, compact, lobed tufts, usually of a dark brown colour. The pinnæ are supported on each or every second primary wall of the axes. The axes in the lower part are covered by descendent, closely apposed, branched, corticating rhizoids. The investment is especially vigorous on the main axis, the lower part of which is thickened and tomentose. At the base the rhizoids form a spongy attaching-system.

The rhizoids develop from pericysts, which occur both in the upper and the lower secondary segments. According to Geyler and Reinke the rhizoids rise from the lower secondary segments, but Sauvageau emphasizes that he found the pericysts to occur most constantly in the upper secondary segments. The pericysts are found to a number of 4—or fewer—in each secondary segment; they are found only in the axes, while they are lacking in the pinnæ. Besides developing into rhizoids they may, as appears from the preceding passage, give rise to erect short shoots—the latter thus being hemiblastic in origin—or, through a formation of septa, be transformed into corticate cells.

The habit of the plant is varying, and with J. G. Agardh (1848 p. 36) it is possible to distinguish a f. *æstivalis* and a f. *hiemalis*, with transition stages between them. The former is tufted with lengthened, somewhat apposed, fastigiate, not distinctly distichous pinnæ, which are compacted to dense, almost obconical clusters; the pinnæ bear short spinuliform pinnulæ. The latter is feathery with shorter, divaricate pinnæ with longer, branched, divaricate pinnulæ (cf. the pictures in Harvey and Kützing (Tab. phycol.)). However, the habit of the two forms may scarcely be regarded as connected with the seasons, but corresponds to the stages in the development of the plant (Sauvageau).

Hairs occur in varying number in bundles in the axils of sterile branches. They develop through repeated divisions of the axillary apical cell and later they are shed, breaking off at the base.

The reproduction takes place by swarmers from unilocular sporangia. The latter are short-stalked, spherical or oval, occurring in bundles in the axils of special short shoots, where they develop from a placenta formed by the axillary apical cell. Thus they are of the same origin as the hairs. The fertile shoots are clustered, occurring in 4 rows at the apex of the pinnæ, by which arrangement spikelets are formed.

Later on the apex of the fertile axes, too, may develop into a spikelet. The unilocular sporangia were first described by MENEGHINI.

Cytologically the unilocular sporangia have been made the object of examination by HIGGINS, who in material from Naples found that a meiosis takes place in them. Hence the swarmers become haploid.

SAUVAGEAU examined the swarmers from the unilocular sporangia. They are rather large, pyriform, and provided with 2 cilia, being said to germinate without any preceding copulation with the above result. On the other hand KNIGHT (1929 p. 317) states that they are able to copulate.

Fig. 12.
Stypocaulon scoparium from Trindelen in the northern Kattegat at a depth of 15 m. 13-VII-1892. Nat. size. — The plant is partly overgrown with *Ceramium* sp. and other epiphytes.

Provided a meiosis occurs regularly in the unilocular sporangia and the germination is direct, it is not obvious how the transition from the haploid to the diploid stage may take place. *A priori* one might imagine that an alternation of generations took place between the asexual generation and a sexual generation, a thought which is supported by the fact that SAUVAGEAU states having found a single plant with supposed antheridia and oogonia but without sporangia (in the Bay of Gascogne, washed ashore). Even if this plant really was a sexual plant—a view which is doubted by HIGGINS, who thinks that the supposed sexual organs may have been abnormal unilocular sporangia—a regular alternation of generations, however, owing to the rarity of the sexual generation, cannot be imagined to take place.

It is not excluded, however, that in the species originally an alternation of generations existed, but that now it has completely or nearly vanished, so that *Stypocaulon scoparium* is perfectly or mainly maintained by the sporophyte, whose unilocular sporangia perhaps normally in nature is not submitted to a meiosis. The phenomenon might be imagined to correspond to the life-history of *Cutleria multifida* in places where the gametophyte is rare and this species therefore chiefly is maintained by *Aglaozonia*. The latter then must be supposed normally to reproduce itself by diploid swarmers from the unilocular sporangia, but now and then the unilocular

sporangia undergo a meiosis, so that haploid swarmers are produced which give rise to a generation of gametophytes.

Besides by the swarmers from the unilocular sporangia the species can also reproduce by means of detached parts, the latter being capable of growing out into new plants.

In the Danish waters the species has only been found in the attached state a single time, viz. in the northern Kattegat, where ROSENVINGE in 1892 found a typical specimen (fig. 12). It was intact and hardly measured 9 cm in length, partly hair-bearing and belonging to the *æstivalis* state.

On the other hand, in several places in the inner waters it has been found in the loose, sterile state, partly as f. *patentissimum* SAUV., partly as f. *spinulosum* (LYNGB.) KJELLM., which both are characteristic by not being caulescent and by having divaricate branches. The former is characterized particularly by the pinnæ being branched and the axillary apical cell usually developing into a bundle of hairs, very rarely into a simple branch. In the latter the pinnæ are spinuliform and often simple, while the axillary apical cell frequently produces 1—2 branches, but no hairs. Moreover the pinnæ are more irregularly separated and irregularly distichous. Both forms occur together with other loose algae and *Zostera*.

SAUVAGEAU has given a description of f. *spinulosum* on the basis of Danish plants, arriving at the result that it ought to be interpreted as var. *patentissima* of a distinct species, *Halopteris spinulosa*, whose main form, however, is unknown. In support of the segregation of f. *spinulosum* from *Halopteris* (*Stypocaulon*) *scoparium* SAUVAGEAU refers to the behaviour of its branches and axillary shoots.

Localities. **Lf:** Off Refshammer near Nykøbing Mors, near land, 2 m (f. *patentissimum*). — **Kn:** FF, Trindelen, the double broom S to W $^1/_2$ W $^1/_2$ mile, 15 m (f. *typicum*). — **Sa:** PK, Norsminde Flak, 6 m (f. *spinulosum*, cf. Sauvageau, Remarques, p. 380 et seq., fig. 74), entangled between *Chætopteris* and *Ahnfeltia*; aZ, Fyens Hoved east $^3/_4$ N $5^1/_2$ miles, 4—6 m (f. *spinul.*); Hofmansgave (f. *spinul.* and f. *patent.* (Lyngb., C. Rosenb.)). — **Lb:** dE, Holsts Banke north of Als, 8—13 m (f. *spinul.*).

Polyblasteae Sauv.

SAUVAGEAU, Sur les pousses indéfinies du Cladostephus verticillatus, 1906, p. 94.

Cladostephus C. Ag.

C. AGARDH, Synopsis Alg. scand., 1817, p. XXV.

Key to the Danish species.

Whorls of ramuli closely approached to one another, difficult to distinguish from one another; whorls containing about 24 ramuli; microblastic shoots during winter till late in the spring with unilocular or plurilocular sporangia; plant attached ..... 1. *Cl. spongiosus.*

Whorls of ramuli distinctly separated; whorls containing 8—12 ramuli; microblastic shoots sterile; plant loose ..... 2. *Cl. verticillatus* f. *patentissimus.*

1. **Cladostephus spongiosus** (Huds.) C. Ag.

C. AGARDH, l. c.; HARVEY, Phycol. Brit., II, 1849, pl. 138; KÜTZING, Tab. phycol., VI, 1856, tab. 7 fig. 2; GEYLER, Zur Kenntniss d. Sphacelarieen, 1866, p. 523, pl. 36 figs. 30—33; MAGNUS, Z. Morph. d. Sphacelarieen, 1873, p. 135, pl. 2 figs. 21—32; KJELLMAN, Handbok, 1890, p. 64; SAUVAGEAU, Remarques, p. 581, figs. 126—28; SCHREIBER, Üb. d. geschlechtliche Fortpflanzung d. Sphacelariales, 1931, p. 235; KYLIN, Phaeophyceen schw. Westküste, 1947, Taf. 1 fig. 5.

Conferva spongiosa HUDSON, Fl. Anglica, 1762, p. 480; DILLWYN, British Confervæ, 1809, pl. 42; Engl. Bot., Vol. 34, 1812, pl. 2427.

Cladostephus laxus in Flora Danica (HORNEMANN), Fasc. 33, tab. 1955 fig. 3, 1829.

Cl. densus KÜTZING, l. c. tab. 7 fig. 1.

From a leathery, disk-shaped basal part one—several, terete, long shoots issue, irregularly dichotomizing, about 0.5 mm thick, besides inconspicuous short shoots. The long shoots are densely covered by numerous, clustered, indistinct whorls of ramuli, the latter giving the plant a *Lycopodium*-like habit. The colour is darkish brown. In summer, when the growth is vigorous, the upper part of the long shoots, however, is of a somewhat lighter colour just as the verticillation of the ramuli in this part may be comparatively distinct.

As to anatomy the species has been studied by GEYLER, MAGNUS, SAUVAGEAU and others. I shall not go into detail on this point, but content myself with referring to the mention of formation of branches, cortex, and rhizoids on pp. 7—8. The period of growth of the species is from spring to autumn, the most intense growing being in summer; the fructification chiefly takes place during winter. The verticillate ramuli are 1—3 mm long, divaricate, frequently somewhat falcate, attenuating at the base, pointed at the apex. Those from the first and last part of the period of growth are usually simple, whereas those from the summer-time generally bear one—a few short, holoblastic spiny shoots as also hairs, placed in pairs, on the abaxial side, the latter rising from the axillary apical cells. The whorls contain about 24 ramuli. The ramuli are shed during autumn and winter.

The microblastic shoots, possibly together with whorled ramuli still preserved or partly broken off, form dense coats at long stretches of the long shoots. They bear oval unilocular or irregularly cylindrical plurilocular sporangia, both types being short-stalked. The two kinds of sporangia always occur on distinct, but morphologically identical plants.

Cultivation experiments with swarmers from the plurilocular sporangia were carried out by SCHREIBER at Heligoland. This author succeeded in demonstrating that they are of a sexual nature since they copulate. The two kinds of gametes are morphologically identical, but physiologically different. Fertilization takes place after the female gamete has become attached. However, the experiment was not successful when only gametes from the same plant were employed, from which it appears that the sexual plants are dioecious. Probably an alternation of generations within the species between a sexual generation bearing plurilocular sporangia and a sporophyte bearing unilocular sporangia occurs in nature.

The germination of the swarmers from the unilocular sporangia and the fertilized

gametes has not been followed, but must be supposed to take place in the same way as in *Cl. verticillatus*. In this species, according to SAUVAGEAU (Sur la germination et les affinités des Cladostephus, 1907, p. 921; Nouvelles observations sur la germination du Cl. verticillatus, 1908, p. 695; Remarques p. 563), the swarmers from the unilocular and plurilocular sporangia (the gametic nature of the swarmers from the latter has not yet been demonstrated, but will of course be confirmed) produce a small disk, which first issues a long, endogenous hair and then one or more short shoots, which at the beginning are monosiphonous, but later become polysiphonous, with a marked apical cell and bearing hairs, single or geminate. Then the disk sends out one or more holoblastic short shoots and finally from its centre a long shoot. From the disk stolons develop, which partly issue short and long shoots, partly spread laterally, hereby uniting.

In the Danish waters *Cl. spongiosus* has only been observed in two localities, one in the southern and one in the northern Kattegat. At the first place it was collected July 10th, 1826, "in sinu Gjerrild ad radicem *Fuci serrati*" by LYNGBYE, who referred his plants to *Cladostephus laxus*. The larger individual from here is 2.5 cm high; it is depicted in Flora Danica (l. c.). The smaller one is provided with a basal disk.

In the locality in the northern Kattegat, Hirsholm harbour (near Frederikshavn), it was found by ROSENVINGE on July 14th, 1892, on large stones at a depth of 1—2 m. In the herbarium two specimens from here exist. The larger one, which is 3 cm high, on its lower part has a dense felt formed by microblastic shoots, still bearing unilocular sporangia. Both of these plants as well as LYNGBYE's mentioned above have been mentioned by SAUVAGEAU (Recherche de la paternité du Cl. verticillatus, 1906, p. 23ff.).

In the years down to 1934 the species has been collected again at Hirsholmene several times, partly by ROSENVINGE, partly by others, each time in July (except once in August). Several of these plants, collected later, were remarkably larger than those found first; the largest specimen thus measured no less than 10 cm in height. They were certainly all sterile.

Cl. spongiosus is closely allied to *Cl. verticillatus*, which is particularly characterized by having the whorls of ramuli more conspicuously separated. However, neither this nor other distinguishing characters are distinct. Generally the two species have been separated, even if some authors merge them into one, e. g. TAYLOR (Mar. Alg. Northeastern Coast of N. Am., 1937, p. 135). This author (like FARLOW 1881 p. 78) uses *verticillatus* as the specific name. As the name of *spongiosus*, however, is the older one (cf. SAUVAGEAU, Recherche de la paternité du Cl. verticillatus, 1906, pp. 9—11), it ought to have been used.

Localities. **Kn:** Hirsholm harbour (L. K. R.; J. Boye Petersen; C. A. Jørgensen). — **Ks:** Gjerrild (Lyngbye).

2. **Cladostephus verticillatus** Lyngb.

F. **patentissimus** SAUVAGEAU, Recherche de la paternité du Cl. verticillatus, 1906, pp. 29, 31; Remarques, pp. 579, 602.

Cladostephus verticillatus LYNGBYE, Tentamen Hydr. Dan., 1819, p. 102, tab. 30 B; KYLIN, Phaeophyceen schw. Westküste, 1947, Taf. 1 fig. 4.

Cl. laxus C. AGARDH, Systema Alg., 1824, p. 169.

Cl. spongiosus β laxus C. AGARDH, Spec. Alg., II, 1828, p. 13; ARESCHOUG, Phyceæ Scand. mar., 1850, p. 162.

In the inner Danish waters a loose form of *Cladostephus* is found in several places which among other things is characterized by possessing whorls of ramuli more conspicuously separated than in the previous species. It was originally described by LYNGBYE from Hofmansgave on the north coast of Funen, but later investigated by SAUVAGEAU, who after a discussion of its identity chose to refer it to *Cl. verticillatus* as var. *patentissima*.

According to SAUVAGEAU it is more slender and supple than the main form of *Cl. verticillatus*, just as it, among other things, deviates from the latter by the whorls containing only 8—12 ramuli. Moreover it is characteristic by the ramuli being longer, less divaricate and less falcate. The microblastic shoots, which always are sterile—possibly together with the still more or less well-preserved ramuli—form short cushions. And whereas the apex of the long shoots in the main form of *Cl. verticillatus* and in *Cl. spongiosus*, owing to the young fastigiate ramuli, are cylindrically penicillate, the apex here is more conical, the ramuli being more separated already from the beginning, these lengthening more slowly.

The plant in the Danish waters has been collected in the months of April and July—December. It occurs especially on sandy bottom with vegetation of *Zostera* together with other loose algae (*Phyllophora Bangii, Ahnfeltia plicata divaricata* . . .). It has been found down to a depth of 10 m.

On the Swedish west coast *Cl. verticillatus* has been found only in a few localities, viz. by ARESCHOUG on the coast of the Skagerak. According to SAUVAGEAU these plants belong to var. *patentissima*. KYLIN (1947 p. 31) does not seem to agree in this, since he does not mention this form at all, just as the diagnosis given refers to the main form of the species.

Localities. **Lf:** Livø Bredning off Feggesund (Th. Mortensen). — **Sa:** Norsminde Flak, Aarhus Bugt, 6 m; aY, Fyens Hoved E $^3/_4$ N $4^3/_4$ miles, 9—10 m; Hofmansgave, numerous specimens (Lyngb., Hofm. Bg., Carol. Rosenb.).

Dichoblasteae.

Disphacella Sauv.

SAUVAGEAU, Remarques, pp. 272—73, 280 (1903, pp. 338, 345).

1. **Disphacella reticulata** Sauv.

SAUVAGEAU, l. c. p. 275 (1903 p. 340), figs. 52—53.

Sphacelaria reticulata LYNGBYE in Flora Danica, 1818, tab. 1600; Tentamen Hydr. Dan., 1819, p. 106; J. AGARDH, Species Alg., I, 1848, p. 33.

Sph. cirrhosa δ Reticulata C. AGARDH, Species Alg., II, 1828, p. 28.

Sph. cirrhosa REINKE, Atlas, H. 2, 1892, p. 65 p.p.

This species, which is only known in the loose state and from a single locality, Hofmansgave on the north coast of Funen, was originally described by LYNGBYE as *Sphacelaria reticulata*. Having later been mentioned by C. AGARDH, J. AGARDH, and REINKE it was on the basis of the material kept in the Botanical Museum of Copenhagen investigated by SAUVAGEAU, who refers it to a new genus *Disphacella*, representing a new group, *Dichoblasteae*. OLTMANNS (Morph. u. Biol. d. Algen, II, 1922, p. 90) refers it to *Hemiblasteae*, at the same time, however, indicating the possibility that the species may be abnormal. Referring to SAUVAGEAU's description I shall content myself with giving a short summary from the latter.

The largest specimens examined were less than 1 cm high. They consisted of 1—3 mm long and up to 40—50 μ thick, simple, straight or curved filaments developed by dichotomy, which suddenly pass into a portion, much branched by dichotomy, consisting of thinner shoots, up to 22—30 μ in diameter. The dichotomous branching takes place by a longitudinal division of the apical cell, by which two new apical cells are formed. The secondary segments are divided both by longitudinal and transverse walls and in the thicker filaments a pericyst is usually found in the upper secondary segments. The pericysts may grow out into branches. The structure and diameter of the shoots are said to remind of *S. olivacea* (which is, indeed, identical with *S. cæspitula*, cf. pp. 16—17 in the present work), and SAUVAGEAU indicates that there is perhaps a possibility of a certain relationship to the latter (cf. Remarques, p. 384, footnote). Reproductive organs were not observed, but LYNGBYE mentions and depicts assumed sporangia.

Localities. **Sa:** Hofmansgave, entangled between *Stypocaulon scoparium* f. *spinulosum* and other loose algae (Lyngbye, C. Rosenb.). — OLTMANNS (l. c.) erroneously refers the locality to Greenland.

Cutleriales.

Cutleriaceæ.

Cutleria Grev.

GREVILLE, Alg. Brit., 1830 p. 59.

1. **Cutleria multifida** (Smith) Grev.

GREVILLE, p. 60, pl. 10; HARVEY, Phycol. Brit., I, 1846, pl. 75; THURET, Recherches sur les zoospores d. Algues et les anthéridies d. Cryptogames, 1850, p. 241, pl. 31; 1851, p. 12, pl. 1; KÜTZING, Tab. phycol., IX, 1859, pl. 45 I; JANCZEWSKI, Observ. sur l'accroissement du thalle d. Phéosporées, 1875, p. 108; THURET & BORNET, Études phycol., 1878, p. 21, pl. 9—10; REINKE, Entwicklungsg. Unters. üb. die Cutleriaceen d. Golfs v. Neapel, 1878, p. 59, pl. 1 (VIII), pl. 2 (IX) figs. 1—6; FALKENBERG, Die Befruchtung u. der Generationswechsel v. Cutleria, 1879, p. 420, pl. 13; HAUCK, Meeresalgen, 1885, p. 404; KJELLMAN, Handbok, 1890, p. 15; KUCKUCK, Bemerkungen, [I], 1894, p. 251, fig. 20; id., Üb. d. Generationswechsel v. Cutleria multifida, 1899, p. 61, pl. VIII (14); id., Monographie, 1929, p. 15, figs. 5—7; SAUVAGEAU, Les Cutlériacées ..., 1899, pp. 307 and 347, figs. 9, 25, pl. 9 (= fig. 26); CHURCH, Polymorphy of Cutleria multifida, 1898, p. 75, plates 7—9; YAMANOUCHI, Life History of Cutleria, 1912, p. 441, figs. 1—15, plates 26—35; NEWTON, Handbook, 1931, fig. 125; HAMEL,

Phéophycées de France, Fasc. IV, 1938, p. 321; KYLIN, Phaeophyceen schw. Westküste, 1947, p. 33, pl. 3 fig. 8.

Ulva multifida SMITH in Engl. Bot., Vol. 27, 1808, pl. 1913.

Zonaria multifida AGARDH, Sp. Algarum, I, 1821, p. 135.

Aglaozonia parvula (GREV.) ZANARDINI, Saggio di classificazione nat. delle Ficee, 1843, p. 38 (not seen); JANCZEWSKI, l. c. p. 103; KUCKUCK, 1899, p. 66, pl. VII (13); HAMEL, l. c. p. 327.

Zonaria parvula GREVILLE, Scottish Cryptogamic Flora, Vol. VI, 1828, pl. 360; HARVEY, Phycol. Brit., III, 1851, pl. 341.

Aglaozonia reptans (CROUAN) KÜTZING, Spec. Algarum, 1849, p. 566; CROUAN, Florule du Finistère, 1867, p. 169, pl. 29 fig. 182; REINKE, l. c. p. 81, pl. 11 figs. 13—27; HAUCK, l. c. p. 408.

The thallus of the *gametophyte* is annual, erect, membranaceous, fan-shaped, repeatedly and irregularly dichotomously branched into segments gradually narrower, at the apices of the shoots tapering into a fringe, formed by free, monosiphonous filaments, whose cells contain chromatophores. The attaching part is somewhat felted, formed by numerous rhizoids, and disk-shaped expanded. The segments are ribbon-shaped; the broadest ones of the present material are up to 3—5 mm in breadth. Usually the individual segment is of fairly equal breadth in its whole length. The colour in the dried state is olive green to olive brown. The length in Danish plants is generally short, from 0.5—5 cm. Only a single, male individual, abundantly fructiferous, was 10 cm long and well developed (fig. 13).

Investigations on the structure and growth have especially been carried out by REINKE, as to the sexual organs besides by THURET. Anatomically the thallus usually consists of 6 cell-layers the outmost one of which on each side consists of small cortical cells with a number of disk-shaped chromatophores. The subcortical layer is formed by somewhat larger cells, which contain less abundant chromatophores. The innermost layer consists of large, colourless cells, which are stretched in the longitudinal direction of the thallus.

In surface view the cortical cells of the segments are arranged in longitudinal rows—distinct at any rate in the upper part—which at the upmost margin of the segments pass into free filaments. A detailed examination shows that one free filament corresponds to two rows of surface cells of the segment, moreover that the free filaments are not found at the same level. In *C. adspersa*, which regarding growth is said completely to correspond to *C. multifida*, REINKE found that the free filaments were placed in 3 floors so that each free filament will correspond simultaneously to 2 of the 6 cell layers of the thallus.

The growth is intercalary, taking place near the base of the free filaments, where a very long, meristematic zone is found, whose cells undergo a transverse division. The cells formed below the meristems stretch, dividing longitudinally and transversally and touching one another; hereby a pressure is exercised and coalescence takes place. Through divisions into various planes in the individual cells the segment gradually appears differentiated as described.

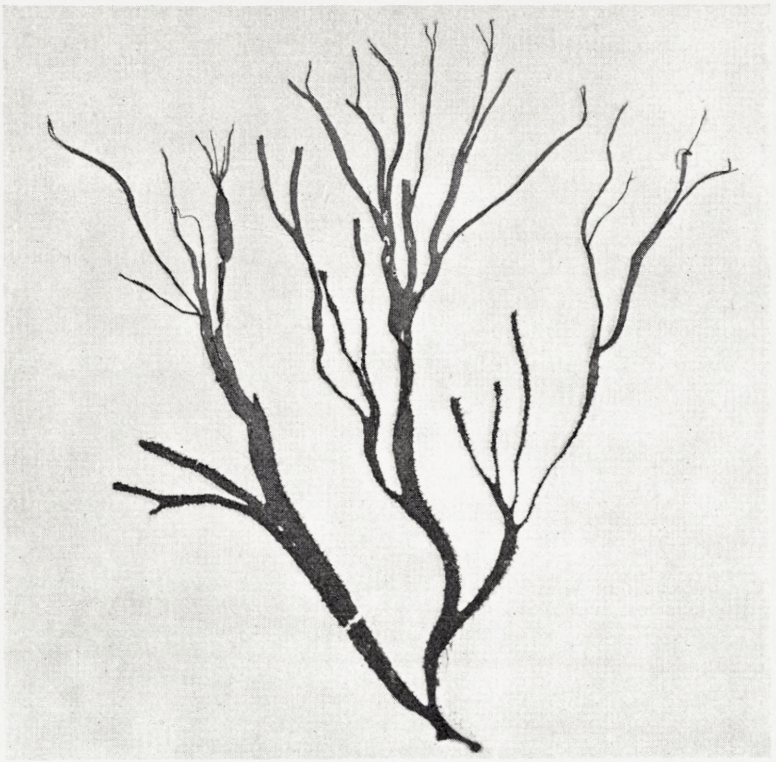

Fig. 13.
Cutleria multifida. Male gametophyte from the northern Kattegat (Chr. Thomsens Rev, 6—9 m, 9-VIII-1934, leg. Henn. E. Petersen). The plant preserved in alcohol, but photographed in the dried state after previous soaking. The sori are partly visible in the lower half of the plant. — Nat. size.

The growth in breadth of the young shoots results from the branching of the free filaments in the meristematic and hypomeristematic zone. Gradually, as the hypomeristematic parts of the free filaments coalesce, the basal part of the branch, too, will be involved in this tissue, and the direction of the branch will now be the same as that of the free filaments, soon presenting a divisional zone like the latter.

The branching of the thallus takes place by the fact that the lateral fusion of the hypomeristematic parts of the free filaments fails to appear. Correspondingly holes and splits of the thallus are due to a local failing coalescence owing to the transient, diverging direction of the filaments.

Hairs occur in groups on both sides of the thallus. On the young, sterile parts of the frond they may be found singly or very few together. In such cases they have a basal growing zone. On fructifying parts, on the other hand, the growing zone is usually found at a certain distance above their base, several somewhat lengthened cells often existing below (fig. 14 *A*).

Antheridia and oogonia are always found on distinct plants. However, Kuckuck (1929) states having observed two small, monoecious specimens at Rovigno in the

Adriatic. Both kinds of sexual organs are found together with the hairs in roundish sori on both surfaces of the thallus. In the living state the male plants may be distinguished from the female ones by the much brighter tinge of the sori; for the antheridia are bright yellow, whereas the oogonia are dark-brown.

The antheridia chiefly occur laterally on simple or branched, uniseriate threads, somewhat arched. They are cylindrical, frequently somewhat curved, generally sessile and to a great extent secund on the inner side of these threads (fig. 14 *A*—*C*); particularly above the point of insertion of the upmost antheridia the threads generally are much curved. Other antheridia may occur terminally (and laterally) on short pedicels issuing direct from the surface of the thallus (fig. 14 *A*). The thread bearing antheridia, in numerous cases, above the fertile portion, develops into a terminal hair with a nearly basal growing zone (fig. 14 *C*).

Only one male plant has been observed in the Danish waters, viz. the above-mentioned, well developed specimen, 10 cm high, which was collected in the northern Kattegat on August 9th, 1934. The antheridia of this plant were exceedingly numerous, mostly emptied, most frequently 57—62 μ long (49—64 μ) and 10 μ (9—12 μ) in diameter.

According to Reinke the antheridia contain up to 16 floors and such was frequently the case, too, in my preparations. In material from Naples Yamanouchi found antheridia possessing up to more than 22 tiers. After the young antheridium is divided into floors, each of these is provided with a longitudinal wall; later on each half through radial divisions is gradually divided into 4 cells. Each floor thus will contain 8 cells, each producing a spermatozoid. The latter are liberated separately from each loculus through a lateral aperture and are provided with 2 cilia.

The oogonia are short-cylindrical; like the antheridia they occur either laterally on uniseriate filaments or terminally on short pedicels. The uniseriate threads are simple or little branched; in addition to oogonia they may issue a hair. In the Danish material they are only observed in two small, not intact plants, collected in the northern Kattegat in August and October, respectively. In both cases all the oogonia were terminal on short pedicels (fig. 14 *D*), as a rule of the same length as the antheridia: 57—62 μ (49—62 μ). The diameter usually amounted to 31 μ (27—37 μ).

The oogonia consist of 4—8 floors, in the two Danish plants as a rule of 4, more rarely 5, each containing 4 cells (according to Yamanouchi 4—7 tiers each consisting of 4 or 8 cells). The swarmers (ova) are evacuated separately, each compartment getting a lateral aperture. Like the spermatozoids the ova are provided with two cilia, but they are much larger than the former. In Kuckuck's measurements (1929) the length amounted to 21.6—29.5 μ, the diameter to 12—18 μ.

The frequency of occurrence of the two sexes in proportion to one another according to the literature is different at various places. At Naples Reinke found 50 per cent. more male plants than female ones, whereas Falkenberg states that the two sexes are nearly equally frequent. At Rovigno in the Adriatic according to Kuckuck (1929) male and female plants were present almost in the proportion 1:1. On the

Fig. 14.
Cutleria multifida from the northern Kattegat. *A-C*: Antheridia from the plant depicted in fig. 13, chiefly emptied. In *A* and *C* besides a hair is seen. — *D*: Sorus of oogonia with a hair. East of Deget, 11 m, 4-VIII-1932 (H. E. P.). — *A-D*: ×397.

Channel coast THURET and CHURCH found, at St. Vaast and Plymouth, respectively, considerably more female plants than male ones. On the coast of Heligoland, finally, according to KUCKUCK (1899) only female plants were found.

How the proportion is in the Danish waters cannot be decided from the 9 collections in all which are available, for only the plants in the 3 cases mentioned bore sexual organs (1 male and 2 female), while the remainder was sterile.

The gametophyte, for that matter, seems to be rare in the Danish waters, where it has been noticed in the Skagerak and the northern Kattegat only. It has been found at depths from 6—9 m down to 20—23 m and has only been collected in July, August, and October.

In the *sporophyte*, which was formerly described as a special species particularly known under the names of *Aglaozonia parvula* and *Agl. reptans*, the thallus is creeping, membranaceous, lobate. In the Danish waters it measures at least 5 cm. From the under side few-celled, simple or branched rhizoids issue, attaching the plant to the substratum rather loosely. The colour in the dried state is light brown; still the young lobes may be olive greenish, while the older parts of the thallus are often intensely dark brown.

The structure and development have especially been studied by REINKE, FALKENBERG, and KUCKUCK (1899). In transverse sections of mature plants a two-celled corticate layer is found uppermost, consisting of small cells with numerous disk-shaped chromatophores. Below this two—several layers of larger, lighter, parenchyma-like cells follow, while the basal layer, again, consists of somewhat smaller, cortical cells. In surface view the cortical cells are arranged in rows after the longitudinal direction.

The growth takes place in the margin, where the thallus consists of one cell-layer only. The longitudinal growth is effected by the meristematic cells at the back cutting off narrow cells; to begin with, these stretch a little, afterwards undergoing various divisions. The growth in breadth is due to an increase of the number of meristematic cells, some of the latter being divided longitudinally into two cells of equal size.

The growth in thickness starts from the upper cortical cells and takes place through the latter cutting off cells inwards, which form the inner parenchyma-like portion. During the further growth in thickness on the surface of the thallus a characteristic convexity appears, which is due to the fact that the recently formed parenchymatous cells are smaller and provided with more vertical walls than the older ones. When they attempt to stretch the older parenchymatous cells lying beneath are unable to keep step and the thallus will therefore become somewhat curved. The growth of the cortical cells is also influential in respect.

Scattered on the surface of the thallus bundles of hairs, with a basal growing zone, occur in small depressions. They are initiated at an early date, developing from cortical cells. To begin with they are quite superficial, but as the thallus becomes thicker through the cortical cells cutting off cells inwards, they appear somewhat sunk.

The fructification organs consist of cylindrical or prismatic unilocular sporangia, which occur in sori of a larger or smaller extent on the surface of the thallus. The sporangia are separated from the inner portion by two cell-layers, which is due to the fact that the sporangia-initials, arising through division of the cortical cells parallel to the surface of thallus, first cut off some low cells downwards. The discharge of the sporangia, which are much thickened at the apex, is made terminally. The swarmers are pyriform with two cilia.

The sporangia in the Danish waters have been found in July (immature, mature and emptied), September (emptied), and October (quite small sori). They have only been observed a few times in the material, rather comprehensive for that matter, which has been collected in January, April—May, and July—October, especially in July (and August—September). The material from April, collected on 29th, mainly consisted of old, hibernating specimens without a meristematic zone. Thus the plant is—or may be—a perennial.

The plant has only been found in the Skagerak and the northern and eastern parts of the area of Kattegat, where it has been collected at depths from 7 to 24 m. It seems to be rather common in the northern Kattegat. The largest quantity was found at Herthas Flak and near Trindelen lighthouse on stony or gravelly bottom at a depth of about 20 m. It has particularly been found on stones and on *Laminaria saccharina, L. digitata,* and *L. hyperborea.* On *Laminaria* it has mostly been found on the lamina, but it may also occur on the haptera. Moreover it has been noticed on *Fucus serratus, Delesseria sanguinea, Phyllophora membranifolia,* and *Lithothamnion polymorphum,* on *Serpula*-tubes as also on dead shells of *Cyprina* and *Buccinum.*

Culture experiments with the gametes of the gametophyte and the swarmers of the sporophyte have been carried out by several investigators. The former were especially cultivated by THURET, REINKE, FALKENBERG, CHURCH, KUCKUCK (1929), and YAMANOUCHI, while the latter were cultivated by REINKE, CHURCH, KUCKUCK (1899), and YAMANOUCHI. In the following survey the designations *Cutleria* and *Aglaozonia* are used for the gametophyte and the sporophyte, respectively. The experiments with the gametes of the gametophyte will be mentioned first.

THURET made his experiments at St. Vaast on the French coast of the Channel, where, as mentioned above, female plants are in considerable excess. He found that the ova germinated without fertilization, growing into an erect, monosiphonous filament, attached at the base by rhizoids. Through intercalary divisions the filament grew in length and from the lower part it issued branches, which behaved like the main shoot.—This product of germination, which represents young *Cutleria* plants, at SAUVAGEAU's suggestion (1899) is generally known in the literature as "forma THURET".

In contradistinction to THURET, REINKE and FALKENBERG at Naples found that the ova only germinated after fertilization. The zygote grew out into a monosiphonous thread with rhizoids at base. Through longitudinal and transverse divisions it developed

into a club-shaped body, the so-called column. In FALKENBERG's cultures, from the basal part of the column, a dorsiventral disk developed, which bore great resemblance to an *Aglaozonia*. This form is known as "forma FALKENBERG".

Near Plymouth on the English coast of the Channel CHURCH, in accordance with THURET, found that the ova always germinated without fertilization. However, they grew out into germlings with a column developing an *Aglaozonia* as in FALKENBERG's cultures.

KUCKUCK made his experiments at Rovigno in the northern part of the Adriatic in 1904 (KUCKUCK 1929). He found that the ova here developed equally easily whether a fertilization preceded or not. The unfertilized ova generally produced germlings with a column, later developing an *Aglaozonia*, accordingly "forma FALKENBERG". The zygotes, too, gave rise to an *Aglaozonia*, but a small percentage of them produced germlings, which represented an intermediate form between *Cutleria* and *Aglaozonia*, consisting of a column which above continued into monosiphonous *Cutleria* threads, while below an *Aglaozonia* developed.—This form, which was first observed by CHURCH in cultures from *Aglaozonia*-swarmers (see below), is usually designated as "forma CHURCH".

As to YAMANOUCHI's cultures, finally, they were like REINKE's and FALKENBERG's carried out at Naples. Correspondingly, as in these authors' experiments, the zygotes grew out into germlings with a column which, as in FALKENBERG's cultures, produced an *Aglaozonia* below; but unlike REINKE and FALKENBERG, YAMANOUCHI also succeeded in making the unfertilized ova grow out. It is true that the first cell division only tooke place later than in the fertilized ova, just as the growth of these germlings was much slower than of the normal ones. And whereas the zygotes produced normal *Aglaozonias*, those produced by the parthenospores were haploid.

One of the first to study the spores of the *sporophyte* was REINKE. He found that at the germination a monosiphonous, erect filament was formed, which below bore a rhizoidal cell. In 8 weeks these germlings consisted of 12—24 cells, but afterwards the contents of the cells came out as secondary spores. From the base of the emptied germlings creeping, plantiform ("sohlenförmige") filaments grew out.

In CHURCH's cultures some of the *Aglaozonia*-spores gave rise to monosiphonous filaments, which might produce antheridia. These germlings correspond to the variety of *Cutleria multifida*, var. *confervoides*, described by KUCKUCK (1894, p. 251) from Heligoland and to some of the germlings obtained by KUCKUCK in cultures from *Aglaozonia*-swarmers; later they have been designated in the literature as "forma KUCKUCK". Others of CHURCH's *Aglaozonia*-spores developed into germlings, which became polysiphonous in the lower part, here producing an *Aglaozonia*-disk ("forma CHURCH").

KUCKUCK (1899) made his experiments at Heligoland. He found here that the *Aglaozonia*-spores developed as "forma THURET". Gradually young, typical *Cutlerias* were produced, the hypomeristematic part of the primary, erect thread and the lateral shoots fusing and being submitted to longitudinal divisions. On some of these

plants oogonia occurred. Some of the germlings, however, did not develop farther than the monosiphonous, confervoid stage, even if some might have a few longitudinal walls below. Also in these plants ("forma KUCKUCK") oogonia might be found. Further KUCKUCK obtained germlings, developing an *Aglaozonia*-disk below and being able on the erect, confervoid part to develop oogonia ("forma CHURCH")—as also germlings which produced a large, lobed disk below, while the erect part soon was shed ("forma FALKENBERG"). The latter were sterile.

In YAMANOUCHI's cultures the *Aglaozonia*-spores grew out into young *Cutleria*, but fructification organs were not found in the time the experiments lasted.

That *Cutleria* and *Aglaozonia* are the gametophyte and the sporophyte of the same species was cytologically proved by YAMANOUCHI, who at Naples found that *Cutleria* contains only half the number of chromosomes of *Aglaozonia* and that meiosis takes place in the young sporangia of *Aglaozonia*. This phenomenon in connection with YAMANOUCHI's demonstration of an alternation of generations in cultures suggests that at Naples a regular alternation of generations takes place in nature, even if matters perhaps may be somewhat complicated through germination of unfertilized ova.

Judging from the present experimental results it is, however, just as certain that at any rate a regular alternation of generations does not occur on the French and English coasts of the Channel nor at Heligoland—and probably not near Rovigno on the Adriatic coast either. Thus the slight occurrence of male plants in nature in proportion to female plants near St. Vaast, Plymouth, and Heligoland (at this last place male plants, as mentioned above, have not been found at all) goes against this. Likewise the short period of occurrence of male plants as compared with that of female plants. On the coasts of the Channel female plants occur during the whole summer, male plants only in a rather short period. As the occurrence of the gametophyte in the northern periphery of the distribution of the species on the whole is much restricted as compared with that of the sporophyte, it must be supposed that the species there—among other places in the Danish waters—is chiefly maintained by *Aglaozonia*-plants which are able to reproduce themselves (cf. p. 60), although perhaps now and then with a gametophyte-generation as an intermediate link.

Localities[1]. **Sk:** ZK[12], Kongshøj Grund, abeam Maarup church, 1 mile, 8 m, August, the gametophyte (a sterile plant, 0.7 cm long); 1 mile NW of Hirtshals, about 15 m, Aug., the gametophyte (a sterile plant, 1.7 cm long); Folden, NW of Hirtshals, 13 m, on *Lithothamnion polym.* — **Kn:** XI, Herthas Flak, 20—23 m, July 29th, 1896, the gametophyte (3 sterile plants: 0.35, 0.4 and 1 cm long) + the sporophyte (with mature sporangia); FG, ibid., 19—22 m, July 3rd, 1892, on haptera of *Laminaria*, stones and shells of *Cyprina* (with sporangia); ibid. Sept. 1898, with emptied sporangia (F. Børgesen); TX, at broom N of Græsholm, 6—10 m, Oct. 2nd, 1894, the gametophyte (a ♀ plant w. oogonia, 3.8 cm long); at broom N of Græsholm, 9 m, January, on *Lamin. hyperb.*; at the double broom east of Hirsholmene, 10 m, on upper part of lamina of *Lamin. digit.*; between Hirsholm harbour and Kølpen, 8 m, on stones; Marens Rev, 8 m, on stones; Borrebjergs and Laurs Rev, on *Serpula*-tubes; Chr. Thomsens Rev, 6—9 m, Aug. 9th, 1934,

[1] In all localities where the gametophyte has been found, a note of this is made. If nothing special is stated, finds of the sporophyte are involved.

gametophyte (a ♂ plant, 10 cm long, w. large number of sori of antheridia, most antheridia emptied; Henn. E. Petersen; fig. 13); E of Deget, 11 m, July 30th, 1932, gametophyte + sporophyte, on *Lamin. sacch.*; ibid. Aug. 4th, 1932, gametophyte (a small, not intact, ♀ plant with mature, immature, and emptied oogonia; H. E. P.); near Frederikshavn, July 1934, gametophyte (a sterile plant, 5 cm long; J. Benth Hansen); broom of Nordre Rønner SE $^1/_2$ E about 500 m, 7 m, on *Buccinum*; at Nordre Rønner, near SW of the double broom, 11—14 m; 3 miles W of Læsø Trindel lightship, 15 m, on *Lamin. hyperb.*; TO, Tønneberg Banke, Trindelen lightship S $2^1/_2$ miles, 18 m, on *Phyll. membr.*; Tønneberg Banke, 16 m, on *Lamin. sacch.* (J. Boye Petersen); TQ, at Læsø Trindel lightship; TR, Trindelen lightship NW $1^1/_4$ mile, 24 m; dS, Læsø Trindel, halfway between lightship and broom, 16 m, on stones; dT^1, near broom at Trindelen, 11 m, on *Lamin. sacch.*, small sporophytes with young shoots of gametophyte ("forma Church"). — **Ke:** northern part of Groves Flak, April 1897 (F. B.); Groves Flak, 24 m (Hj. Ditlevsen); XA, Kobbergrunden lightship N to W $^1/_2$ W fully $6^1/_2$ miles, on *Fucus serr.* and *Serpula.*

Dictyotales.

Dictyotaceæ.

Dictyota Lamour.

Lamouroux, Exposition d. caractères du genre Dictyota..., 1809, p. 42 (not seen).

1. **Dictyota dichotoma** (Huds.) Lamour.

Lamouroux, l. c.; Greville, Algæ Britannicæ, 1830, p. 57, pl. 10; Harvey, Phycol. Brit., I, 1846, pl. 103; Nägeli, Die neuern Algensysteme, 1847, p. 184, pl. 5 figs. 10—21; Thuret, Recherches sur les anthéridies d. Algues, 1855, p. 8, pl. 2; Thuret & Bornet, Études phycol., 1878, p. 53, pls. 27—30; Cohn, Ueb. einige Algen v. Helgoland, 1865, p. 17, pls. 3—5; Crouan, Florule du Finistère, 1867, fig. 178; Reinke, Entwicklungsgesch. Unters. üb. die Dictyotaceen d. Golfs v. Neapel, 1878, p. 3, pls. 1—2; Hauck, Meeresalgen, 1885, p. 304; Mottier, Nuclear and cell division in Dictyota dich., 1900, p. 163; Williams, Studies in the Dictyotaceæ, 1904—05: I, p. 141, pls. 9—10; II, p. 183, pls. 12—14; III, p. 530; Hoyt, Alternation of generations and sexuality in Dictyota dich., 1910, p. 55; Newton, Handbook, 1931, fig. 134; Schreiber, Üb. Kultur u. Geschlechtsbest. v. Dictyota dichotoma, 1935, p. 266, figs. 1—4; Hamel, Phéophycées de France, Fasc. V, 1939, p. 347, fig. 57 VI; Lund, Om Dictyota dichotoma ... i Nissum Bredning, 1940, p. 180, fig. 1; Kylin, Phaeophyceen schw. Westküste, 1947, p. 35, pl. 3 fig. 9.

Ulva dichotoma Hudson, Flora Anglica, Ed. 2, II, 1778, p. 568; English Botany, Vol. XI, 1800, pl. 774; Lyngbye, Tent. Hydr. Dan., 1819, p. 31, pl. 6 C.

Zonaria dichotoma Agardh, Sp. Alg., I, 1821, p. 133.

Dichophyllium vulgare Kützing, Phycol. generalis, 1843, p. 337, pl. 22 II.

Dictyota vulgaris Kützing, Tab. phycol., IX, 1859, pl. 10.

D. attenuata Ktz., ibid. pl. 11.

D. elongata Ktz., ibid. pl. 11.

D. latifolia Ktz., ibid. pl. 12.

The thallus up to 26 cm long, membranaceous, ribbon-shaped, without a midrib, regularly dichotomously branched in one plane. The breadth of the segments of the broadest plants up to 5—6 mm (measured in dried material), generally, however, narrower. In a few plants the breadth is fairly equal from the basis up to the apices of branches, but as a rule the breadth decreases gradually in the upper part, some-

times to such a degree that the apices of the shoots become filiform (cf. LUND 1940 fig. 1). Most plants, by far, may without doubt be referred to var. *implexa* (DESF.) J. AG. The colour in the dried state is olive green to olive brown, usually considerably lighter above than below.

The lowest part of the plant generally consists of cylindrical shoots, from which issue a large number of many-celled rhizoids, serving the attachment. On the flat thallus, too, small tufts may be found of simple, possibly branched rhizoids, which now and then attach to new host plants. In the cylindrical lower shoots the branching is lateral, but also on the flat thallus numerous, short, lateral branches may be found, not least on injured shoots.

The species, which has been studied anatomically by NÄGELI, THURET, COHN, THURET & BORNET, REINKE, and others, grows by means of an apical cell at the apex of the segments, and the branching takes place in the way that this cell through a vertical wall is divided into two equal cells, each becoming a new apical cell. Anatomically the thallus shows 3 cell-layers, the middle of which consists of large, colourless cells; in the lateral walls of these, large pits may sometimes be observed. The layer of both surfaces forms a cortical layer and consists of small cells, which contain numerous disk-shaped chromatophores. The cells of the central layer may be recognized through the cortical layer by a magnifying-glass. The thickness of the thallus in Danish plants preserved in alcohol amounts to 100—125(—135) μ.

Colourless hairs with a basal growing zone are found in tufts on both surfaces of the thallus. They are shed during the period of fructification. In plants destitute of hairs, however, it is distinctly seen where the latter have been placed, for the sterigmata form small macroscopically visible spots. In longitudinal or transverse sections the sterigmata appear as cortical cells, having elongated rectangularly from the thallus. The length in my preparations amounts to about 30 μ or a little more. The sterigmata very much resemble immature antheridia; particularly striking was the resemblance to REINKE's picture of a section through a young, immature antheridia-sorus (l. c., pl. 2 fig. 3), although the elongate cortical cells in my preparations certainly were not so long as those in this figure.

Of reproduction organs sporangia, antheridia and oogonia occur in the species, each of them being found on distinct individuals, morphologically identical (at Plymouth WILLIAMS (1905 p. 552), however, found an individual which was provided both with antheridia and oogonia. Also HOLDEN (1913 p. 2) discovered abnormal specimens, mentioning male and female plants which in addition to sexual organs bore scattered sporangia). Between the sporangia-bearing individuals, representing the sporophyte, and the sexual plants an alternation of generations occurs (HOYT). Meiosis takes place in the young sporangium, which produces 4 spores, tetraspores (MOTTIER,WILLIAMS), 2 of which grow out into male plants, the other 2 into female plants (SCHREIBER). In some cases meiosis may fail to appear and the contents of the sporangia directly grow out into diploid germlings (REINKE l. c. p. 8 and other workers).

The sporangia occur on both surfaces of the thallus, though not right out to

the margin of the latter. They are found in large numbers, partly singly, partly a few together; in the mature state they are spherical, provided with a thick wall. The sporangium develops through transformation of a cortical cell, which below cuts off a basal cell, while the remainder turns into the sporangium.

The sporangia in Danish plants have been observed in July, August, and October. In the middle of July they were still comparatively young, but at the end of July and in August mature sporangia with differentiated tetraspores were present in large numbers. In the plants from October the majority were emptied, provided with a large discharging aperture, but some still held their contents. Strange to say, none of the latter showed symptoms of a division of the contents. In the mature state the sporangia measure about 120—125 μ in diameter.

Both the antheridia and the oogonia form oblong sori on both surfaces of the thallus. Both kinds of sexual organs develop like the sporangia (and the hairs) from cortical cells. The latter elongate rectangularly, cutting off a small basal cell below, while the remainder becomes an antheridium or an oogonium. The cells bordering on the antheridia also elongate, though remaining sterile; they form an involucrum round the antheridia and are preserved for some time after the evacuation of the latter. As the young antheridia grow in size, they are divided into a large number of small loculi, each producing a globular or ovate spermatozoid, possessing only one cilium. In each of the obovoid oogonia a naked, round egg cell is formed of the same appearance as the tetraspores; they are liberated at maturity, and the fertilization takes place in the water.

Of the two kinds of sexual organs only oogonia have been observed in Danish plants; they were found at the end of July and in August. The plants concerned in several cases were characteristic by their relatively small size and their comparatively broad thallus, which did not taper at the apex of the shoots.

Dictyota dichotoma is an annual. In the Danish waters it has been collected in the months of April, July—August, and October. The plants from April were small, up to 1.3 cm high, and sterile, but similar plants are available from July, too. The great majority from July, August, and October were well-developed. The species was found both in quite shallow water, a little below common water-mark, and at a depth of 5—6 m; it has been observed partly on other algae (*Fucus, Chylocladia kaliformis*), partly on shells and stones.

In Denmark the species has been found only in the western part of the Limfjord, where no doubt it has not arrived until quite recently, probably after 1920. It was found for the first time in October 1939 in numerous, well-developed specimens by the author at Rønnen in Nissum Bredning, where it was chiefly attached to rather young *Fucus* plants washed ashore (which in their turn were growing on small stones). Later it was found in other neighbouring places, but farther east. Thus at Ørding in Sallingsund, where Tyge Christensen, M. Sc., found it on July 30th, 1945. The sea-floor was here stony, and the vegetation nearest to the land consisted of *Enteromorpha*; after this a belt of *Chaetomorpha aerea-Linum* followed and not until outside

this—or partly together with *Chaetomorpha—Dictyota* occurred at a depth of 0.15 m. *Dictyota* formed large tufts, chiefly attached to *Mytilus*, which was lying as clumps together with pebbles, held on by byssus. At a depth of 0.70 m a single tuft was found, too. The following year on August 22nd Mr. TYGE CHRISTENSEN once more visited the locality, but this time most plants were loose, either lying on the bottom or washed up on the shore.

Localities. **Lf:** Rønnen at Lem Vig in Nissum Bredning, 18-X-39 (S. L.); outside the oyster-banks off Røjens Odde, 5—6 m, 20-IV-42 (S. L.); eastern part of Nissum Bredning, July 1940 (The Marine Biological Summer Course); SW coast of Jegindø, 15-VII-44 (Tyge Christensen); bay SSE of Ørding, Sallingsund, 30-VII-45 and 22-VIII-46 (T. Chr.).

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See also lists of literature in Parts I—III of the present work.

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