STUDIES ON THE SAPROPELIC FLORA OF THE LAKE FLYNDERSØ WITH SPECIAL REFERENCE TO THE OSCILLATORIACEAE

BY

TYGE W. BÖCHER

1. Introduction.

Foul mud at the bottom of the small brackish-water lagoon Flyndersø in N.W. Zealand has been examined. Among the large number of different organisms found in the mud particularly the *Oscillatoriaceae* attracted the writer's attention, among them some species that were yellowish green, thus of quite a different colour from other *Cyanophyceae*. Both LAUTERBORN (1915) and GEITLER (1932) mention the yellowish green forms and discuss their peculiarities.

The samples of foul mud were examined partly immediately after being collected, partly after standing over. The latter procedure proved to be profitable because after a prolonged standing over under suitable conditions it was possible to obtain a rapid growth and multiplication particularly of the blue-green algae. The *Oscillatoriae* might develop very vigorously and form a dense coating over the mud. The best culture conditions were obtained by filling long narrow glasses with foul mud, saturating the mud with water, stoppering the glasses, and placing them on a window-sill, or a little mud might be put into a tall narrow glass, which was filled up with water, and then a glass lid was put over its neck. It was evident that a good development of the blue-green algae was tantamount to putrefactive bacteria not developing. In some of the glasses these from the start got the upper hand and here there was only a scanty development of *Oscillatoriae* and the like. In the best cultures, which were examined at intervals for more than two years, the flora changed somewhat. In one of the glasses the yellowish-green *Oscillatoriaceae* at first were predominant, later the purple sulphur bacteria took the lead. The possibility of making prolonged observations under cover-glass was of great importance for the investigations. A number of organisms could live in a little mud stirred into water or simply in water under a large cover-glass closed at the edge, in the best

1*

way by means of paraffin oil. Several good preparations could
be used for 4—6 months, *Oscillatoriae*, *Flagellates*, and certain of
the bacteria being motile during the whole of this period. It was
tried without success to isolate and cultivate the species by transfer
to a sterile nutrient solution (Benecke solution with or without
the addition of sugar or peptone) or a sterilized diluted decoction
of the foul mud. Not either in the cases when these nutrient
media were used under anaerobic culture conditions it was
possible to make the plants grow and multiply.

2. Ecological Conditions in Flyndersø.

Flyndersø is an alkaline shallow brackish-water lake only
separated from the sea by a rather narrow isthmus covered with
vegetation. Sig. Olsen (1944, p. 20) states the pH of the water
to be 7.6 (7.2—8.6), total hardness 9.0 (German degrees) and the
contents of salt 590 mg chloride per litre. The lake in most places
is surrounded by a reed-swamp of *Phragmites*, *Scirpus Tabernae-
montani* or in some places of *Cladium mariscus*. Towards the land
the surrounding vegetation bears the character of a spring fen
with abundant *Juncus subnodulosus*. Many large stones rise above
the surface of the water. Below they are surrounded by a white
zone of chalk formed by the blue-green algae at a time when
the surface of the water in the lake was a little higher. At present
there is at and immediately below the water-level most frequently
a zone of *Dichothrix gelatinosa* vegetation with a heavy incrustation
of chalk (cf. Böcher 1946). There is no vegetation of plants with
floating leaves and the rooting vascular hydrophytes are very
scattered; but there are well developed communities of *Characeae*
(*Chara contraria*, *hispida*, *polyacantha* and *aspera*, and *Tolypella
glomerata* according to Sig. Olsen), particularly where the bottom
is softest. The eastern part of the lake is cut through by a dam.
Near this the soft layer of mud is particularly thick, viz. 15—30,
rarely 40 cm, and is here covered by 20—50 cm water. The lower
part of the mud contains comparatively much sand and less
organic matter, whereas the upper part is mainly of organic origin.
The mud is calciferous and effervesces at acid being added.
The contents of oxygen and hydrogen sulphide in the mud is

of great interest. In the mud gases are developed which fairly often rise to the surface as bubbles. These mainly consist of hydrogen sulphide. A quick bubbling may be started by thrusting a stick into the mud a few times. This is due to the fact that a
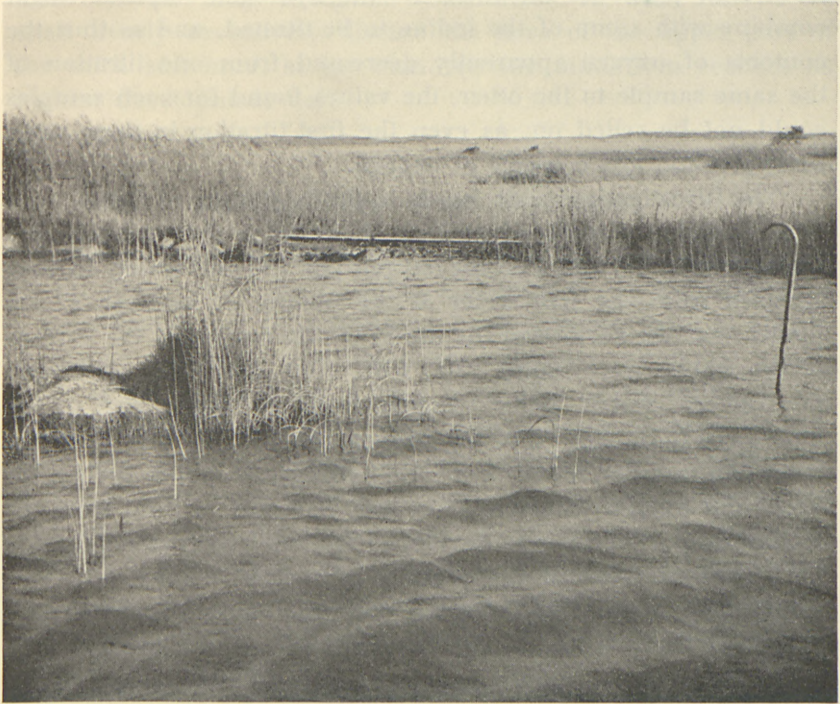

Fig. 1. The lake Flyndersø near Rørvig in Zealand. The stick on the right has been stuck through the mud on the firm sandy bottom. The lake is cut through by a narrow, low dam, part of which is seen. Near the dam on the left *Phragmites communis*. Beside the stone jutting out in the foreground *Scirpus Tabernaemontani*. T.W.B. phot. Oct. 1944.

rather dense surface layer is often formed which keeps back the air. The organisms living in the mud no doubt are exposed to the effect of hydrogen sulphide dissolved in the water. Under such conditions the contents of oxygen must be very low. In order to have this problem elucidated some analyses were made by means of WINKLER's oxygen titration.

Mud or water was sucked up in a tube and transfered to 3 bottles of 15 cm³ and with ground glass stoppers. Only the middle part of the contents of the tube, which had not been in

touch with the air, was used. Then, before closing, manganous chloride and caustic soda were added. During the titration the addition of hydrochloric acid in some of the samples caused a vigorous development of hydrogen sulphide, probably originating from iron pyrite in the mud. As the hydrogen sulphide might combine with some of the iodine to be titrated, and as thus the contents of oxygen apparently decreased from one titration of the same sample to the other, the values found for such samples could not be relied on, as even the first titration in these cases must give too low contents of oxygen.

The investigations were made in the beginning of October. In three samples of surface water (3—5 cm below the surface) were found 1.30, 1.29, and 1.18 mg oxygen per 100 cm³ water. In four samples from the free water at the bottom or between Chara plants near the surface of the mud (15—30 cm below the surface of the water) were found 1.09, 1.07, 1.00, and 0.68 mg oxygen per 100 cm³ water. Three samples from the upper part of the mud gave 0.31, 0.02, 0.00 mg oxygen per 100 cm³ water. In the latter two samples, however, a little hydrogen sulphide developed, hence the oxygen values are too low. Samples of mud from the lowermost part of the mud developed too much hydrogen sulphide for a determination of the quantity of oxygen. It may, however, simply be assumed that there are very small quantities of oxygen present in these layers, as the accumulation of iron pyrite is due to the activities of strictly anaerobic bacteria. At the prevailing temperature the surface water was saturated with oxygen. The decrease in the oxygen value with increasing depth is not even, as immediately above the surface of the mud there are values of about 1 mg, while there is only 0.3 mg or less in the upper part of the mud.

The vegetation in the lowermost part of the mud is very sparse. By microscopy one chiefly comes across bacteria, some animal flagellates, and very few diatoms and blue-green algae, but the uppermost part of the mud, which is in the light, there is a fairly rich flora. It is particularly rich where the layer of mud is very soft and thick. Sampling from different places in the lake, from the middle, where there is a thin layer of mud, and from the dense Chara sociations nearer to the shores or from reed-swamps or the surroundings of the dam, where there

is deep, soft mud, gives widely different results. In several samples from the middle no blue-green algae developed at all, only green and purple sulphur bacteria and a very large spirillum. No doubt the thin layer of mud is less rich in nutritious matter, and also contains more inorganic constituents. In what follows we shall nearly exclusively discuss the flora of the upper part of the thick soft mud, as the characteristic mud flora reaches its highest development here.

3. The Flora of the Foul Mud.

Introductorily it should be remarked that the following list of the flora cannot be considered exhaustive. In the first place I have found that by examining fresh samples there is always a chance of finding new organisms, secondly my expert know-ledge is not so great that I have been able to determine all the vegetable organisms I have come across. Some of these, in fact, were too sparse to permit a closer determination. I have par-ticularly taken pains to have the characteristic species determined and among them the *Oscillatoriae* are in an absolute majority. The list of bacteria is very defective, as nearly only the groups of sulphur bacteria and *Spirochaetales* have been considered. Mr. ERIK G. JØRGENSEN, M.Sc., has kindly examined the diatomaceous flora of a single sample.

Cyanophyta.

1. *Microcystis elabens* Kütz. Very common, in some places forms green coatings over the mud. Survives in the culture glasses and multiples quickly also in old cultures. No doubt indigenous to the mud.

2. *Microcystis marginata* (Menegh) Kütz. In a single sample, no doubt an accidental visitor to the mud vegetation.

3. *Microcystis parasitica* Kütz. A few small colonies in some of the samples. Also observed by HAYRÉN (1944) in Oscilla-torietum.

4. *Microcystis pulvera* (Wood) Forti. Small colonies in a single sample.

5. *Aphanocapsa pulchra* (Kütz) Rabenh. Several colonies in a single sample.

6. *Aphanocapsa* cp. *litoralis* var. *macrococca* Hansg. In one of the samples an *Aphanocapsa* was observed, which from its size and other qualities should, if anything, be referred to the variety mentioned. *A. litoralis* is a halophilous species. Among freshwater species with cells of about 8 μ like *A. lit. macrococca* hardly any but *A. Roeseana* may be considered, but this species has broadly oval, pale blue-green cells, whereas the species found
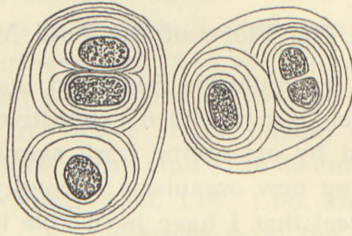

Fig. 2. *Gloeothece* cf. *rupestris* (Lyngbye) Bornet, probably a variety or form with small cells from sample of foul mud from Flyndersø $\times$ 800.

by me had spherical, deeply blue-green cells. *A. litoralis* was found in sapropelic vegetation by HAYRÉN (1944).

7. *Gloeocapsa granosa* (Berk) Kütz. In mucus among sulphur bacteria and *Chroococcus*. Observed a few times.

8. *Gloeocapsa dermochroa* Näg. This species is not indigenous to the foul mud. It preferably grows on the stones in the lake, but it was found in mucus among other *Chroococcaceae* from a sample taken near the stones in the dam across the lake. Undoubtedly an accidental visitor.

9. *Gloeothece* cf. *rupestris* (Lyngbye) Bornet. In mucus among other algae, perhaps also a fairly accidental visitor. It multiplied quickly in the surface of the mud in one of the old culture glasses. Obviously it cannot endure the strongly anaerobic conditions farther down in the mud. The cells were at most 9 μ in length and 5.5 μ in breadth, the contents of the cells were very granular and the integuments round the cells very distinct, cf. fig. 2. As the cells generally did not exceed 8.8 μ in length, I have referred it to *G. rupestris* with some hesitation. It may be a variety or a modification of *G. rupestris* with small cells. A referring to *G. membranacea* cannot, however, be excluded.

10. *Chroococcus turgidus* (Kütz.) Näg. in a form which without integuments is 10—14 μ in breadth with a very distinct formation of integuments as in *C. tenax*. Abundant in all samples. Undoubtedly indigenous to the surface of the mud. It was also abundant in old cultures.

11. *Chroococcus minutus* (Kütz.) Näg. A few single specimens in some samples. Also found in foul mud by HAYRÉN (1921).

12. *Chroococcus limneticus* Lemm. Plankton alga, which may be found accidentally, perhaps dying, in the surface of the mud.

13. *Gomphosphaeria aponina* Kütz. Abundant in fresh samples, particularly in the surface of the mud. Survives and multiplies in the culture glasses, also in two year old cultures. There can be no doubt that this species, which otherwise lives as a plankton organism, is indigenous to the mud.

14. *Eucapsis alpina* Clements & Shantz. A few colonies in one of the samples. Cells 5.5—6 μ in breadth. — var. *minor* was observed by HAYRÉN growing on bottom mud.

15. *Synechococcus Cedrorum* Sauvageau. In mucus among *Oscillatoriae* and *Pseudanabaena* there were in several samples some peculiar ellipsoidal cells, blue-green, but rather pale. Generally the cells stuck together by twos (fig. 3), but the bicellular groups were apt to form irregular lumps or coenobia (fig. 3 *g*) in the mucus. These coenobia had never any independent mucous integuments. Often the cells showed a clear division between centro- and chromoplasm (fig. 3 f). Movements were not observed with certainty, not even in cells detached from the mucus. But in some cases a polar formation of often very large gas vacuoles (fig. 3 *a*—*c*) was observed. The cells are 3—4 μ in breadth and 4—7 μ in length, which agrees with the description of *S. Cedrorum*, a species which has elsewhere been found i. a. in stagnant water. The similarity between the organism found and bicellular stages of species of *Pseudanabaena* is remarkable and will be mentioned below on p. 43.

16. *Synechocystis minuscula* Woron. In the same places as the preceding species a great many pale blue-green spherical cells were found, about 2—2.5 μ in diameter and with a thin, hyaline membrane. Sometimes they stuck together by twos, but they were generally more inclined to part after division (see fig. 3*h*) than was the case of *Synechococcus Cedrorum*. The size of the cell

corresponds to that of *S. minuscula* and the pale-green colour
may be due to the special environment. The species is otherwise
reported from a salt-spring in the Caucasus. In one of the pre-
parations in which this organism occurred, there were two cases
of chain-formation in which the cells stuck together. In one case
there were 17 cells in the chain (fig. 3*h*), in the other 24 cells.
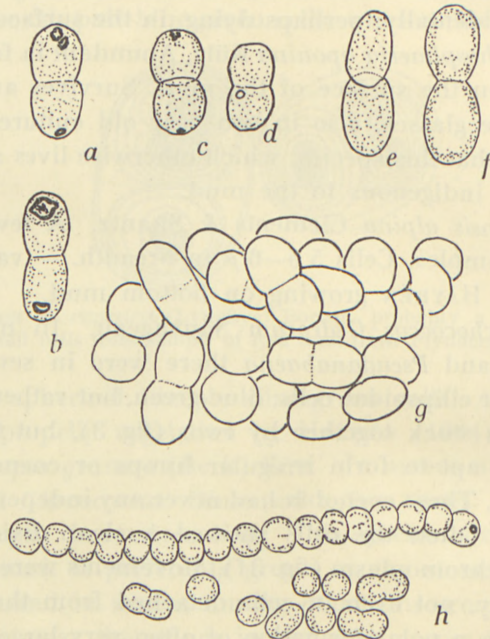One of the terminal cells in the chain with 17 had a gas vacuole.

Fig. 3. *a—g Synechococcus Cedrorum, a—c* individuals with gas vacuoles, *d—f*
without vacuoles, *g* coenobium-like collection of bicellular groups. — *h—i Synecho-
cystis minuscula*, in normal cells and bicellular groups, *h* a catenulate collection
of cells. All figs. × 1700.

No kind of movement was observed. On the strange chain-
formation see below.

17. *Pseudanabaena biceps* Böcher. As to this species refer-
ence may be made to the description in Böcher (1946). A few
important observations may be added. In a culture glass filled
with foul mud the surface near the glass was not, as so frequently,
covered by a coating of yellow-green *Oscillatoriae*, but by a dark-
green coating which chiefly consisted of *Pseudanabaena biceps* and

a few species of *Oscillatoria*. There was here a formation of a skinlike "lager", which probably is not otherwise found in *Pseudanabaena*, but certainly in *Oscillatoria*. At the transverse walls there were always very distinct red disc-like bodies. In this material they were so large that they could easily be made out to be gas-vacuoles. The cells in *P. biceps* are always rather hyaline and mostly pale in the centre (fig. 4*h*), but in this material a great many individuals had a darker central filament, which often with a somewhat bent or eccentric direction ran through the central axis of the cell. It seemed that the filament continued through the pore-like connexion between the cells. The formation of the filament is undoubtedly a vital process, for the individuals were just as active in their movements as the others. To all appearance it is a special question of cheritomy, as is known from a few other blue-green algae, e. g. *Oscillatoria Borneti* (see on this in GEITLER's handbooks). In a few cases it could be observed (fig. 4*k*) that from the axial filament some lateral filaments branched off, and these generally led to cyanophycin granules, which nearly always were very close to the filament. In the cytologically different individual depicted in fig. 4*l* the uppermost cell has an axial filament and in connexion with it both cyanophycin and gas vacuoles. In the material this type of cytologically deviating individuals was very rare. They were interesting by highly supporting the hypothesis about a closer connexion between gas vacuoles and cyanophycin granules advanced by CANNABAEUS (1929). The gas vacuoles in the deviating individuals were abnormally placed and near or close to them the refractive, mostly rounded granules were found. In the individuals with an axial filament it was not easy to decide whether there was also parietal plasma. Several observations would seem to indicate that this was so. In connexion with the axial filament it should be mentioned that in preparations treated according to the ordinary technique of staining bacteria with desiccation and staining with carbol-fuchsin, pictures of *P. biceps* like fig. 4*i* were obtained. The cells have shrunk as a result of the treatment, but the connective area has been drawn out as if into a fine thread. The whole filament seemed to be bedded in a slightly stained mucus. The possibility cannot be excluded that the organism is run through by a plasmatic filament which is
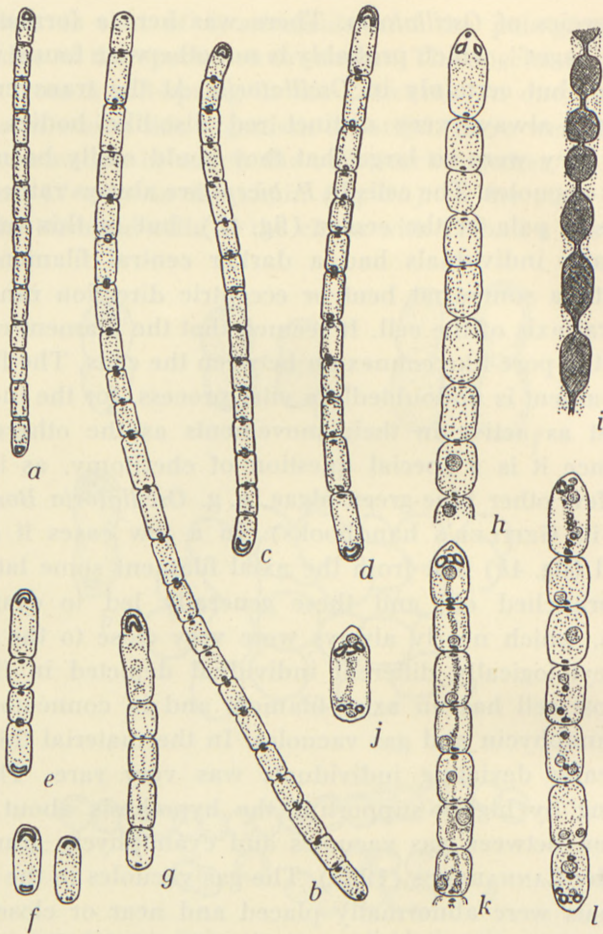
Fig. 4. *a—g Pseudanabaena galeata, a* a small variety of the species, *b* an individual with small gas vacuoles in the terminal cells, *f* unicellular "hormogonia". — *h—l Pseudanabaena biceps, i* stained with carbol fuchsin, *j* unicellular "hormogonium", *k* an individual presumably with cheritomy, *l* an individual with abnormal placing of the gas vacuoles. All figs. × 1700.

only visible under certain conditions. The connective filament between the cells, which is seen in fig. 4 *i*, has a striking similarity to protoplasmatic filaments connecting the cells of *Streptococci* when these are observed in an electron microscope at 20,000 times' magnification, see fig. 261 in FROBISHER (1946). The central plasmatic filament might be supposed to be of importance for the movement of the filaments, which may here be characterized as

a sliding to and fro, often by small starts and sometimes rather quickly, but without a rotation round the longitudinal axis as in most species of *Oscillatoria*.

18. *Pseudanabaena galeata* sp. n. *Cellulae trichomatis* 1.4— 2.2 μ *latae*, 2—5 (7) μ *longae ad genicula inter se plus minusve rotundatae; ambae terminales plerumque ceteris dissimiles, vacuolo aerico magno fornicato galeatae. Septis utrobique vacuolum aericum minus appositum. Chromoplasma a centroplasmate nonnumquam manifesto discretum. Fila* 1—30 *cellularum observata, fluenter lapsa progredientia. Hab. in fundo limoso, foetido lacus Flyndersø Selandiae borealis.*

This alga (fig. 4 b—g) was found partly as single individuals in the same samples as the preceding species, partly in samples without *P. biceps* and then in larger quantities. It is clearly distinct from *P. biceps* by the terminal gas vacuoles, which formed a hood or dome. In some individuals in which the terminal gas vacuoles were in process of development it could be observed that they begin as circular vacuoles. These, however, have a smaller diameter and are closer to the end of the cell than in case of *P. biceps*. During growth the vacuoles change and become galeate, sometimes nearly hemispherical. It is also distinct from *P. biceps* by the terminal cells never being acuminate, but rounded. The gas vacuoles at the transverse walls are also somewhat larger in *P. biceps* than in *P. galeata*. The species further is clearly distinct from *P. catenata* by the very specially equipped terminal cells and the gas vacuoles at the transverse walls.

There is no doubt that the specimens depicted in fig. 4 d and g represent some of the broadest-celled within the species, and most probably fig. 4 c is a typical narrow-celled individual. It is a question which must be left unanswered for the time being whether the still narrower filaments in the material with a breadth of 1.1—1.2 μ (see fig. 4 a) belong to the same species. If so, *P. galeata* as compared with *P. biceps* has a very great width of variation. I am most inclined to think that the thin filaments a little more than 1 μ in breadth belong to a particular species or a variety of *P. galeata*. This new species or variety also distinguishes itself by having very small, often nearly invisible gas vacuoles at the transverse walls and by being less constricted at these.

Both of the *Pseudanabaena* species mentioned multiply by the filaments breaking into a number of pieces. In so far as these consist of several cells, they may simply be termed hormogonia. The parts, as already mentioned in the case of *P. biceps*, however, are often unicellular and such parts may hardly be defined as hormogonia. They are able to move, mostly slowly or by small starts. They might perhaps be termed planococci. As, however, they do not differ from the hormogonia except in the number of cells, it would after all be more advisable to term them unicellular hormogonia (fig. 4 *f* and *j*). They are at any rate very interesting from the point of view of cell physiology. It often seems to be terminal cells that are detached. One end of the cells thus is equipped in the way characteristic of terminal cells while the other end often is not equipped like this. Soon after the detachment of the cell the conditions of polarity seem to change. From being built with two polarly opposite ends, the cell gradually becomes uniform at both ends, but this does not mean that it ceases being polarly built. The difference now manifests itself as a difference between the distal parts and the median part of the cell. When this part after a cell-division becomes the two non-terminal parts of a bicellular hormogonium, these parts appear clearly different from the terminal parts of the two cells.

The formation of hormogonia was particularly frequent in the mucus between other algae. Hormogonia with any number of cells could be found, but it was actually, as in other *Oscillatoriaceae*, impossible to distinguish the hormogonia from other filaments.

19. *Pseudanabaena catenata* Lauterb. Observed here and there in several samples, seems never to have had any gas vacuoles.

20. *Spirulina maior* Kütz. Observed a few times in some of the samples.

21. *Spirulina* cf. *subtilissima* Kütz. In mucus among other algae and sulphur bacteria a few individuals of a *Spirulina* species were found (fig. 5 *f*). They were rather pale green, without visible boundaries between the cells, and the coils were a little more removed from each other than in the typical *S. subtillissima*. Further the coils were not quite regular, for which reason one might also think of relationship with *S. Meneghiniana* Zanard.

Oscillatoria. Some of the most important species of the foul mud belong to this genus. First the blue-green, olive-green, or brownish forms will be mentioned, then the completely or nearly colourless forms, and finally the yellow-green or pale green forms.

22. *Oscillatoria limosa* Ag. Olive-green-brown, cells often 10—14, in some cases 19—22 μ in breadth and 2—2.2 μ in length, granulated at the transverse walls, in some cases, because of the intercalary growth, only at every second transverse wall. Frequent
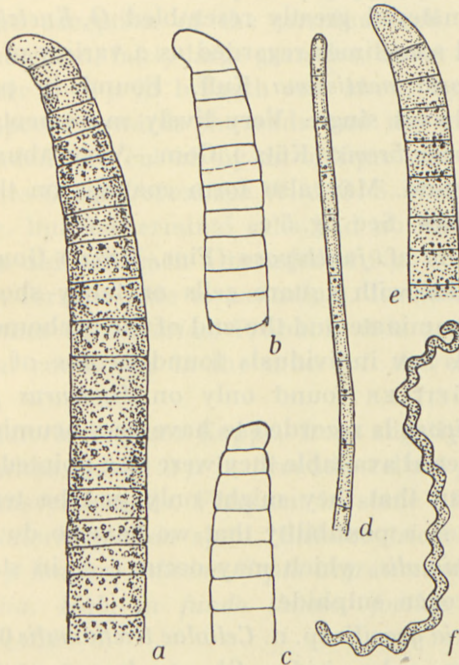
Fig. 5. *a—c Oscillatoria chalybea* ($\times$ 800), *d Oscillatoria gracilis* with granules near the almost invisible transverse walls, *e Oscillatoria brevis, f Spirulina sub-tilissima* (?) (*d—f* $\times$ 1700).

in some of the samples. Survives in culture glasses and may here form coatings.

23. *Oscillatoria chalybea* Mertens. This species was not with certainty found in Flyndersø, but in the foul mud in a small lagoon on Skansehage in the neighbourhood. Here it occurred with large quantities of *O. brevis* and *O. profunda* and species of *Beggiatoa.* The cells showed the measures characteristic of

O. chalybea and the filaments were slightly constricted at the transverse walls. At the ends they were tapering somewhat more than is usually stated of the species, further the colour was different by being olive-green. Hence it may be a variety of *O. chalybea*, cf. further fig. 5 a—e.

24. *Oscillatoria tenuis* Ag. In many samples from Flynderso very abundant, particularly in the surface of the mud. Both var. *natans* Gom. and var. *tergestina* Rabenh. were observed.

25. *Oscillatoria amphibia* Ag. A few filaments in one of the samples. The material greatly resembled *O. Kuetzingiana* Nag., which is indeed sometimes regarded as a variety of *O. amphibia*.

26. *Oscillatoria acutissima* Kuff. Found in practically all samples, but always single. Very lively movements.

27. *Oscillatoria brevis* (Kütz.) Gom. Very abundant on the surface of the mud. May also form coatings on the surface in the culture glasses. See fig. 5 e.

28. *Oscillatoria* cf. *janthipora* (Fior.-Mazz.) Gom. Filaments 6—8 μ in breadth with square cells or fairly short cells. The terminal cells acuminate and the end of the trichome bent almost like a sickle. A few individuals found in one of the samples. According to GEITLER found only on *Hydrurus foetidus* near Rome. *O. janthipora* is recorded to have very acuminate terminal cells. In the material available they were also pointed, but perhaps no more so than that they might only just be termed "spitz-kegelig". There is a possibility that we have to do with a "var. *crassa*" of *O. animalis*, which may occur e. g. in stagnant water containing hydrogen sulphide.

29. *Oscillatoria gracilis* sp. n. *Cellulae trichomatis* 0.7—1 μ *latae*, 2—5 μ *longae, coeruleo-virides. Chromoplasma a centroplasmate nonnumquam distinctum. Septis aegre conspicuis, utrobique interdum granulu minus appositum. Hab. in fundo limoso, foetido lacus Flynderso Selandiae borealis.*

This very narrow species formed coatings in the upper part of the foul mud in some of the culture glasses and single specimens were found in fresh samples from the surface. It is no doubt closely related to *O. angustissima* W. & G. S. West, but has somewhat broader and longer cells, see figs. 5 d and 8 (No. 3). Sometimes it is impossible to discover the transverse walls. In the cases in which the chromoplasm could be distinguished from the centroplasm there were also generally granules at the trans-

verse walls, one granule on each side of the walls. These granules assisted in the discovery of the transverse walls and thus the establishing of the length of the cells.

The following species are very pale and can hardly to any appreciable degree take nourishment by photosynthesis. In the material there was further in a single culture glass a strange *Oscillatoria* species, which unfortunately was observed in few specimens. It had an extremely faintly pale yellow plasma, but this, with the exception of the terminal cell contained some spherical blue-green, fairly large granules, about four in each cell. The cells were 7—8 μ in breadth and about 4 μ in length. The trichomas tapered towards the ends and the terminal cell was broadly rounded and cut off by an oblique wall. Thus it looked like the species *O. subproboscidea* W. & G. S. West described from the Antarctic, but the terminal cells had no thickened wall and the trichomes did not reach a breadth of 9 μ. Of course I cannot decide if this form is able to assimilate. It showed lively movements like other *Oscillatoriae*. Probably it is a modification due to the special conditions in the mud (cf. the experiments with *O. putrida*).

30. *Oscillatoria angusta* Koppe, from slightly bluish to completely colourless, 0.8—1.2 μ in breadth, cells 6 μ in length with indistinct transverse walls. Frequent in some of the samples.

31. *Oscillatoria pallida* sp. n. *Cellulae trichomatis 0.5—0.6 μ latae, 2.5—3 μ longae, pallidae. Septa aegre conspicua. Trichomata valde flexibilia. Hab. in fundo limoso, foetido lacus Flyndersø Selandiae borealis.*

This completely colourless, very narrow species was observed in numerous samples. Its movements are extremely lively. There is nothing particularly characteristic about its exterior. The terminal cells are broadly rounded; there are no constrictions at the transverse walls, which are often almost invisible.

32. *Oscillatoria profunda* Kirchn. Observed as a pale bluish, almost colourless form, with cells 2 μ in breadth which were 2—3 times as long as broad. The trichomes were not wavy. Frequent in several samples.

33. *Oscillatoria guttulata* van Goor. Cells 2.5—3.3 μ in breadth, 7—9 μ in length, pale blue-green with granulated con-

tents, in some cases with dark granules. These did not show the red interference colour, but very much resembled sulphur granules. The species was observed in two of the samples only, being very frequent in one, cf. fig. 8.

The following species are all more or less yellow-green. There is a possibility that the form already mentioned as reminding of *O. subproboscidea* also belongs to this group, in which case it will be closest related to the marine species *O. laetevirens* and *subuliformis*. The species most thoroughly investigated is *O. putrida*, which because of its great abundance and the breadth of the cells invited experiment.

34. *Oscillatoria putrida* Schmidle. A long-celled species which according to Schmidle (1901) has cells 2 μ in breadth and 8—14 μ in length and 1—3 small glistening granules (gas vacuoles) near each transverse wall. As regards the breadth and the small gas vacuoles my material agrees with the original description, the cells, however, not being so long as those in Schmidle's form. They measured 5—10, mostly 7—8 μ. This difference, however, is hardly greater than allowing to consider my material as a short-celled variety of the species. My material no doubt approaches *O. minima* Gicklhorn, the cells of which, however, does not exceed 6 μ in length and which have not the distinct granules along the walls. My material resembles *O. minima* by the filaments often being fairly regularly spirally coiled and by often having a blue lustre ("blauglanz", cf. Gicklhorn 1921).

O. putrida was kept under observation for four years and proved very constant in the characters mentioned, even though conditions slowly changed in the culture glasses. Only once a form that was narrower than the others and as a rule had only one gas vacuole at the transverse walls was found in an old culture glass (fig. 6 *b*). This may be a modification.

In material fixed in Nawashin's fluid, hydrolyzed for 20 minutes in normal hydrochloric acid, and stained for 60 minutes according to Feulgen's method with fuchsin-sulphuric acid a central chromatin apparatus was found in which it was difficult to distinguish details in the form of granules or threads. It was, however, obvious that the chromatin apparatus chiefly consisted of separate bodies or threads and that there was a particular

density at the ends of the long cells. It often seemed as if the chromatin was already divided into two sections, and this agrees very well with other observations showing that the long cells very often must be assumed to be dividing and forming a wall in the middle of the cell, only that this wall is not visible until later.
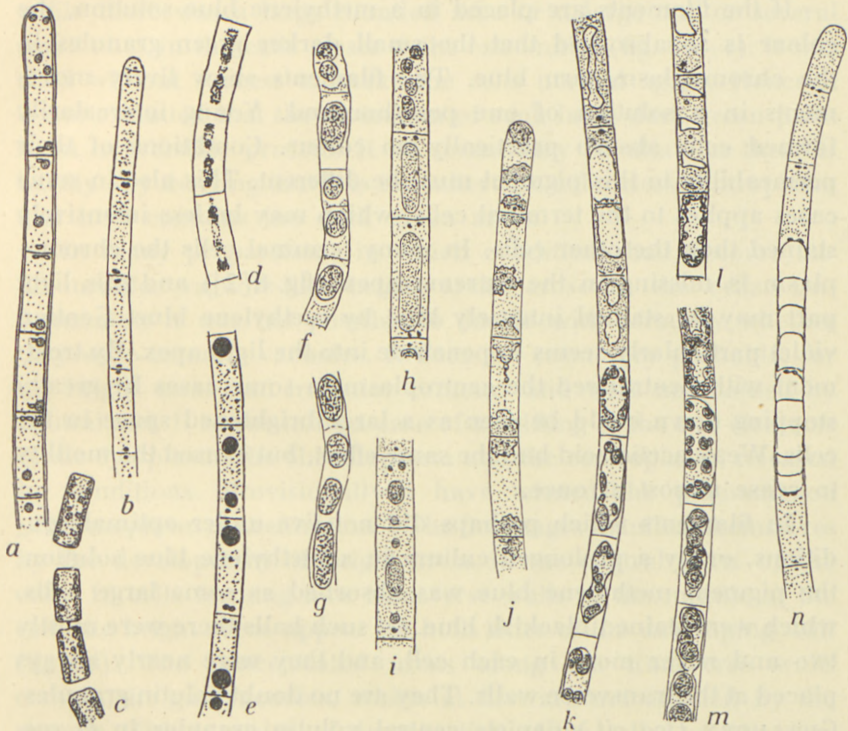

Fig. 6. *Oscillatoria putrida*, *a* cultivated in the dark; yellowish protoplasm with green granules and gas vacuoles near the transverse walls, *b* narrow form from old culture, *c* decay of filament showing plasmodesm, *d* the chromatin apparatus after staining with Feulgen, *e* volutin granules stained with methylene blue, *f—g* spore-like dark green bodies developed after preceding chromoplasm concentration, *h—i* large central dark green areas (volutin?) after treatment of the cells with H₂S, *j* chromoplasm concentration, *k—m* chromoplasm concentration and plasmolysis, *n* nannocyte formation in an otherwise normal motile filament. × 1700.

The chromoplasm is yellow-green with a granulated structure, the granules being small and dark green. According to GICKLHORN yellow-green species in a fluorescence microscope shows the red fluorescence colour of chlorophyll. My material of *O. putrida* in a microspectroscope showed an absorption which nearly corresponded to that of a leaf at light falling through.

The gas vacuoles along the transverse walls are glistening red with interference effect. Centrifugalization does not affect them, but they disappear if 2.5 or 5 per cent. KOH and weak NH_4OH are added, and seem to decrease in size in 4.5 per cent. acetic acid, whereas alcohol does not influence them.

If the filaments are placed in a methylene blue solution, the colour is so absorbed that the small darker green granules in the chromoplasm turn blue. The filaments show lively movements in a solution of one per thousand. Young intercalarily formed cells absorb practically no colour. Conditions of their permeability to this pigment must be different. This also in some cases applies to the terminal cells, which may be less intensively stained than the other cells. In many terminal cells the chromoplasm is missing in the extreme apex (fig. 8 [2]) and this light part may be stained intensely blue by methylene blue. Gentian violet particularly seems to penetrate into the light apex. By treatment with neutral red the centroplasm in some cases by greatly stopping down could be seen as a large brightened space in the cells. Weak acetic acid had the same effect, but caused the motility to cease almost at once.

In filaments which perhaps did not live under optimal conditions, or by a prolonged culture in a methylene blue solution, the pigment methylene blue was absorbed as some large balls, which were stained blackish blue. Of such balls there were mostly two and never more in each cell, and they were nearly always placed at the transverse walls. They are no doubt volutin granules. GICKLHORN (*loc. cit.*) depicts central volutin granules in *O. coerulescens*, which has short cells. Perhaps the situation of the volutin granules in *O. putrida* is connected with the more or less bipartite chromatin apparatus. Terminal cells often have no or small volutin granules.

In some preparations which were kept in constant darkness from the 4th of December to the 14th of March and in which the filaments still were very motile, the chromoplasm was faintly yellow, and the cells contained a number of blue-green spherical granules (fig. 6 a). The similarity to the above-mentioned *O. subproboscidea*-like form was great. It seemed as if the green pigment had preferably concentrated in these granules or drops. The cells were alive and motile. In some other preparations treated in

various ways, thus with addition of H_2S to the water, and in
which conditions obviously were unfavourable, as the movements
of the filaments were slow or had ceased, fairly large dark green
rounded areas developed in the middle of the cells. In the middle
of the filaments there were several separate parts in each cell,
while there was a large rounded area or a large one or several
small ones in the cells closer to the extremities (fig. 6 h—i). It was
tried without success to make the cells normal again. Hence it
is not excluded that the formation of such large dark green parts
is an irreversible process. It all seems very peculiar, as there is
hardly any denying that it is the otherwise colourless centroplasm
that here contains the dark green areas.

In many preparations in which conditions had become un-
favourable, vacuole-like bright areas arose in the cells. Un-
fortunately it was not possible to decide with certainty whether
they were actually vacuoles. It does not seem very probable, for
the bright areas had irregular contours and were not stained by
neutral red. It seems to be a case of a shifting of the two elements
of the cytoplasm, the chromoplasm and the centroplasm, released
by conditions. Provisionally I have termed the phenomenon
,,chromoplasm concentration''. The first stages manifest themselves
by the development of bright areas in the central parts of the
cells. In cells forming new transverse walls in the middle of the
cell, the bright areas appear on both sides of the developing wall
(fig. 6j). The concentrated areas along the transverse walls
contain the gas vacuoles, which at first are not affected by the
process. This is a sign of degeneration of the cells, but they are
no doubt still alive. In a filament with chromoplasm concentration
which was placed under more favourable conditions the develop-
ment continued, the concentrated areas being changed into spore-
like dark green bodies (fig. 6g). Unfortunately an attempt at
making these bodies, which remind of the so-called endospores
in *Beggiatoa*, develop further proved unsuccessful; hence their
nature is obscure. It is more important that cells with chromo-
plasm concentration can be plasmolyzed. As with plasmolysis
experiments with many other blue-green algae, a highly dis-
similar behaviour of the cells was observed by treatment with
low concentrations of NaCl or KNO_3. In some cells, particularly
young ones, the plasma did not or almost not withdraw from

the walls. In these cells only bright areas appeared, in others there was a withdrawal and at the same time the chromoplasm concentration was intensified so that the bright portions reached the surface of the plasma and the dark portions were rounded off into some dark green bodies in the same way as described above. With increasing distance from the non-plasmolyzed cells these dark green bodies increased in size (see fig. 6 *k—m* and further pp. 38—41).

After many of the treatments to which *O. putrida* was exposed there was at last a breakdown of the filament, the cells coming apart. At the same time the gas vacuoles along the transverse walls disappeared. In some cases a plasmodesm between the cells was discovered (fig. 6 *c*).

In a three year old culture glass, in which *O. putrida* throve well, there was a filament in which a formation of nannocytes was observed (see Geitler 1925). Two cells had divided speedily into respectively 4 and 5 small cells (fig. 6 *n*). The gas vacuoles of the original cells could still be seen in the space between and at the ends of the two groups. It is very strange that the nanno-cytes in question had pale blue-green cells without granulated plasma, while the normal cells surrounding them were yellow-green with granulated plasma. The formation of nannocytes has not hitherto been described as regards forms belonging to the *Hormogonales*.

It was tried to cultivate *O. putrida* in water with different con-centrations of H_2S. In all experiments the filaments soon degener-ated, in a much diluted solution, however, a few filaments were motile up to a week after the start of the experiment. The species undoubtedly will stand weak concentrations of H_2S in nature, but does not seem so resistant to this substance as the yellow-green species *O. coerulescens* examined by Gicklhorn.

Low light intensities have a positive phototropic effect on *O. putrida*, higher intensities a negative effect. This appeared from the distribution of the green coating in the culture glasses when these were placed with onesided illumination of different in-tensities.

Measurements of the oxygen pressure in the foul mud in culture glasses in which *O. putrida* was abundant, showed that there was here 0.2 cc oxygen per litre or less.

35. *Oscillatoria subtilissima* Kütz. Observed in a form with cells 1 μ in breadth and about 5 μ in length and with indistinct transverse walls. No gas vacuoles; the filament often very slightly undulating with distinct centroplasm. Pale green chromoplasm. Not so lively movements as in the other yellow-green species. Abundant in some of the culture glasses; not observed in fresh samples; see fig. 7 *a—b*.
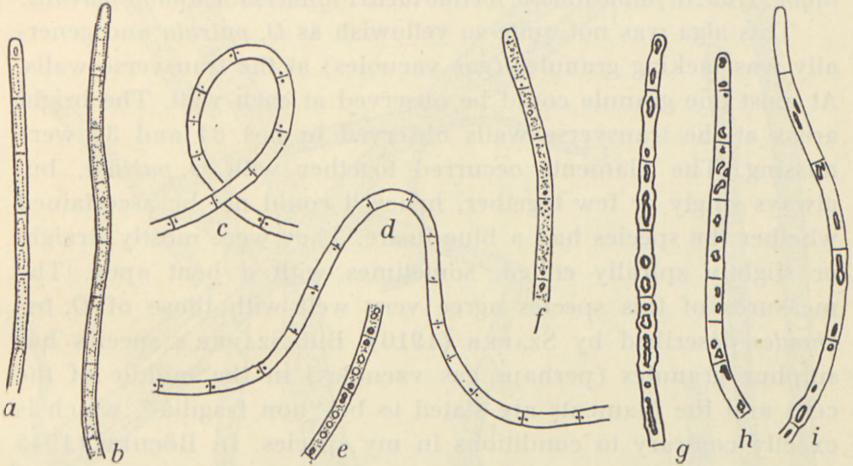
Fig. 7. *a—b Oscillatoria subtilissima, c—f O. mirabilis, g—i O. fulgens.* Gas vacuoles with a thick black contour. × 1700.

36. *Oscillatoria mirabilis* sp. n. *Cellulae trichomatis 1—1.2 μ latae, 2.5—5 μ longae, flavo virides. Septis utrobique vacuolum aericum parvum vel minutum appositum. Trichomata ad 300—350 μ longa, recta, motu proprio praedita, sinibus distantibus retro currentibus instructa. Hab. in fundo limoso, foetido lacus Flyndersø Selandiae borealis.*

This organism was found abundantly in preparation from one of the culture glasses and looked extraordinary by having 1—3 displaceable loops or sinuosities on the otherwise quite straight or slightly curved trichomes. The loop developed at the foremost end, and during the forward movement of the trichome was shifted backwards until it disappeared at the other end. Cytologically the similarity to *O. putrida* was great, the plasma being granulated, now and then with fairly large dark green bodies. At the transverse walls there was always a small gas

vacuole in the form of a larger or smaller reddishly shining granule. These granules mostly, as in *O. putrida*, were situated apart from the chromoplasm in a bright area at the transverse walls. See further fig. 7c—f.

37. *Oscillatoria fragilis* sp. n. *Cellulae trichomatis* 1.2—1.5 μ *crassae,* 4—9 μ *longae, flavo virides de more sine vacuolis aëricis. Trichomata in aqua pura fragilla, in aqua putrida mobilia vegetaque. Hab. in fundo limoso, foetido lacus Flyndersø Selandiae borealis.*

This alga was not quite so yellowish as *O. putrida* and generally was lacking granules (gas vacuoles) at the transverse walls. At most one granule could be observed at each wall. The bright areas at the transverse walls observed in nos. 34 and 36 were missing. The filaments occurred together with *O. putrida*, but always singly or few together, hence it could not be ascertained whether the species had a blue lustre. They were mostly straight or slightly spirally coiled, sometimes with a bent apex. The measures of this species agree very well with those of *O. trichoides* described by SZAFER (1910). But SZAFER's species has sulphur granules (perhaps gas vacuoles) in the middle of the cells and the filaments are stated to be "non fragilia", which is exactly contrary to conditions in my species. In BÖCHER (1945 fig. 6) a small piece of filament of *O. fragilis* has been referred to *O. trichoides*.

The name *O. fragilis* refers to the plasmoptysis which takes place when the filaments are transferred to clear water. Similar phenomena may exceptionally be observed in some of the other *Oscillatoria* species, but in this one the occurrence of plasmoptysis is a rule. The plasmoptysis takes place at the transverse walls, where a colourless mass of plasma is pressed out, the filament at the same time being bent and often later broken. In one case the process took place as follows: At 11^{30} the filaments normal, 11^{40} 4 bends (places of plasmoptysis), no ruptures, 12^{00} 16 bends, no ruptures, motility nearly ceased, 13^{00} 22 bends, 3 ruptures, 14^{40} 20 bends, 7 ruptures. A picture of the plasmoptysis and the ruptures is found in fig. 8 (1), cp. further pp. 38—41.

Under unfavourable conditions there is here as in *O. putrida* a chromoplasm concentration (fig. 8) and at a plasmolysis the cells behave as those of *O. putrida* by being very dissimilar as regards the withdrawal of the plasma from the wall.

38. *Oscillatoria fulgens* sp. n.   *Cellulae trichomatis* 1—1.3 μ
*latae, (3) 4—7 μ longae, laete-virides, 1—4 vacuolis aericis magnis
lobatis rubicundis fulgentibus ornatae, ad vacuola aerica magna
plerumque dilatata. Septa interdum aegre conspicua. Hab. in fundo
limoso, foetido lacus Flynderső Selandiae borealis.*
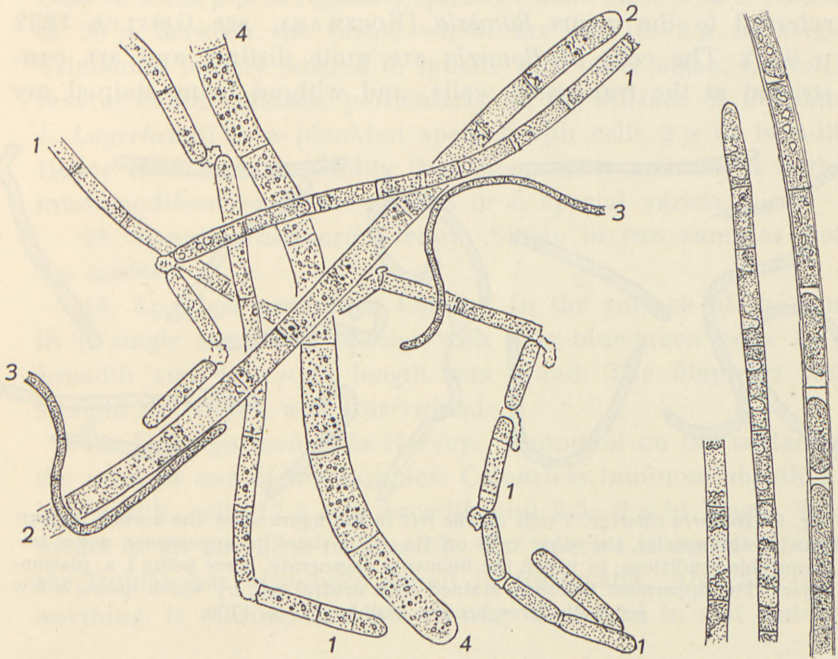
Fig. 8. On the left a small section of a preparation in which filaments of various
Oscillatoria species have been placed in pure water. No. 1 is *O. fragilis*, which
shows zigzag formation, plasmoptysis, and below on the right detachment of a
bicellular piece of filament. No. 2 is *O. putrida*, no. 3 *O. gracilis*, and no. 4 *O. guttu-
lata*. — On the right, chromoplasm concentration and plasmolysis (10 per cent.
NaCl) in *O. fragilis*. × 1700.

This species was very abundant in the material and was also
observed in fresh samples. It is obviously related to *O. Lauter-
bornii* Schmidle, in whose cells there are 1—2 large central lobate
gas vacuoles and whose transverse walls are almost invisible.
O. Lauterbornii differs from the new species by being more than
twice as broad, by having fewer gas vacuoles and by lacking
the swellings at the largest vacuoles. The swellings are simply
due to the fact that the gas vacuoles spread and make the exterior
part of the cell bulge. Young cells, hence often terminal cells,

have no or small gas vacuoles, cp. fig. 7. In this species the colour is pale green, not yellowish green.

39. *Romeria chlorina* sp. n. *Trichomata* 1 μ *crassa, (5)—9—20 μ longa, viridiflava, flexibilia. Septa non conspicua. Hab. in fundo limoso, foetido lacus Flynderso Selandiae borealis.*

A very strange organism, which is not without great hesitation referred to the genus *Romeria* (KOCZWARA, see GEITLER 1932 p. 915). The cells of *Romeria* are quite distinct and are constricted at the transverse walls, and without being stained my
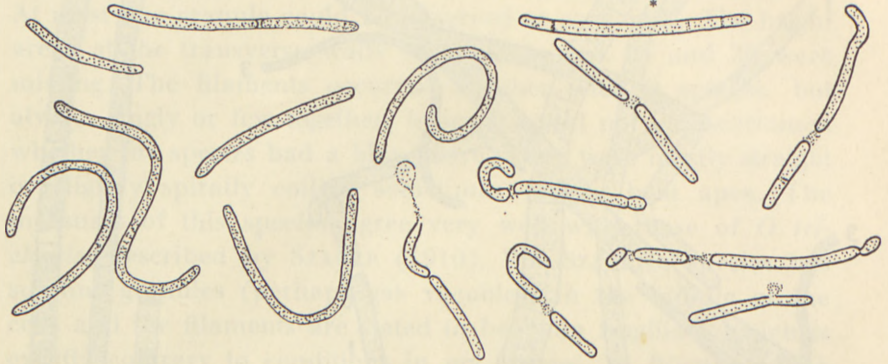
Fig. 9. *Romeria chlorina*. 7 cells on the left in the figure show the normal appearance of the species, the other cells on the right show its appearance under unfavourable conditions, in which the filaments degenerate, there being i. a. plasmoptyses. The uppermost filaments stained with neutral red, by which means a few cell-walls have become visible (*). × 1700.

organism has no visible transverse walls. In this character it approaches *Spirulina*. There are also points of resemblance with *Crinalinum* and *Chlorobacteriales* (see below).

Under unfavourable conditions the trichomes break, as there is plasmoptysis (fig. 9), in which a pale green mass of plasma is pressed out. The smallest pieces probably correspond to cells and are 1.5 μ in length. By staining with neutral red it is possible to observe a few transverse walls (fig. 9), which, if anything, suggests a cell length of 2.5 μ. The latter size probably is the one in best agreement with facts; for the small pieces produced by the plasmoptysis may easily have shrunk somewhat. In preparations in which the organism occurred in water from the foul mud, the filaments moved in a very lively manner changing their form all the time, sometimes they were u-shaped, sometimes rod- or s-shaped. Gas vacuoles were never observed.

40. *Phormidium valderianum* (Delp) Gom. In a single sample from the surface of the mud.

41. *Lyngbya Lagerheimii* (Möb.) Gom. In a narrow form with cells 1.2—1.5 (1.8) μ in breadth and 1—2 μ in length and with blue-green granules along the walls. A fairly thin sheath. Only in some places regularly spirally coiled. Here with a distance of 20 μ between the turns, which are (2—)6—8 μ in height. Trichomes loosely tangled in mucus with other algae. Found in several culture glasses, particularly on the surface of the mud. *L. Lagerheimii* is a plankton species with cells 2 μ in breadth. Hence there is a possibility that the present material is a thin mud modification of the species or a special variety.

42. *Lyngbya aestuarii* Liebm. Singly in two samples from the surface.

43. *Lyngbya perelegans* Lemm. In the surface of the mud in a single sample a species with pale blue-green cells 1 μ in breadth and 4—5 μ in length was found. The filaments were straight or curved and intertwined.

44. *Lyngbya maiuscula* Harvey. Abundant on the surface of the mud in one of the samples. Colourless laminose sheath 5 μ in breadth, cells 17.6 μ in breadth and 2.5—3 μ in length. Filaments in all 26—28 μ in breadth. The species is marine, but in the tropics has also been found in freshwater. Also no. 42, if anything, is marine, and no. 43 may be found in salt water.

Chlorobacteriales.

45. *Pelogloea* sp. (?). It is not without great hesitation that my material of green bacteria is given this systematic name. It is done on the basis of the undoubtedly correct view that the establishment of new species, in so far as bacteria are considered, is hardly of any importance until extensive cultivation experiments revealing the width of variation and physiological properties have been made. The green bacteria in the Flynderso material belongs to the rod-type, but may assume rounded forms or even develop into streptococci. The *Chlorobium limicola* described by NADSON (1912) generally is a coccus the cells of which "manchmal, obwohl seltener, haben das Aussehen ausgesprochener Stäbchen". The question is whether it is imaginable that NADSON's and my material are extremes in a continuous

variation within a single species which may be both chiefly
coccus- and chiefly rod-shaped, or whether there are two different
organisms. If the latter, the chiefly rod-shaped type may come
under the genus *Pelogloea* (Lauterborn), and it might suitably be
termed *P. heteromorpha*, for its width of variation seems very great.

The green bacteria occurred in two manners in the material.

(1) In the cultures originating from the deep soft mud along the
shores of the lake and in which blue-green algae were dominant,
there often, particularly after some time and always in connexion
with increasing abundance of the purple sulphur bacteria,
appeared some small colonies of a rod-shaped green bacterium
(fig. 10 a). The cells were 0.5—0.7 μ in breadth and 1—10 (mostly
2—5) μ in length, immotile, yellowish green and dispersed in
thin mucus, which was pale greenish. The organism had a great
variation in length, but was always distinctly rod-shaped and
hence might perhaps be a *Pelogloea*. It differs from the other
Pelogloea species by the cells being narrower and longer.

(2) In a culture originating from the middle of the lake where
the layer of mud was thin, no filamentous Cyanophyceae ap-
peared at all. Purple sulphur bacteria (*Lamprocystis*), a large
colourless spirillum and, after six months' culture, a green bac-
terium were abundant. The last-mentioned organism formed very
large connected masses of mucus which was so watery that the
spirilla could work their way through them, although with dis-
tinctly reduced speed. The rod-shaped form was dominant, but
the cells were a little thicker than those in the other cultures
(0.7—0.8 μ in breadth), and further there appeared a number of
deviating cell forms which highly reminded of those found in
Chlorobium limicola (see NADSON, *loc. cit.*, Table III). There were
two types of deviating cell forms, involution forms and strepto-
coccus- or diplococcus-forms. The involution forms were dis-
persed among normal rod-shaped cells and might be more
swollen than these, sometimes completely rounded-off with a
bright median part (cf. NADSON's fig. 11), in rare cases somewhat
ramified; cf. fig. 10 e. The diplococcus- and streptococcus-forms
were found here and there among normal rod-shaped cells; see
fig. 10 c, d. These cannot be termed involution forms. In the
material studied by NADSON (*loc. cit.*) and VAN NIEL (1931) the
streptococcus form is dominant, while the rod-shaped and spirillar

forms are considered involution forms. The material studied by
Skuja (1948) contains only the streptococcus form but deviates
with regard to the breadth of the cells (0,3—0,5 μ). It may belong
to *Chloronostoc* (Pascher). There is very little evidence that there
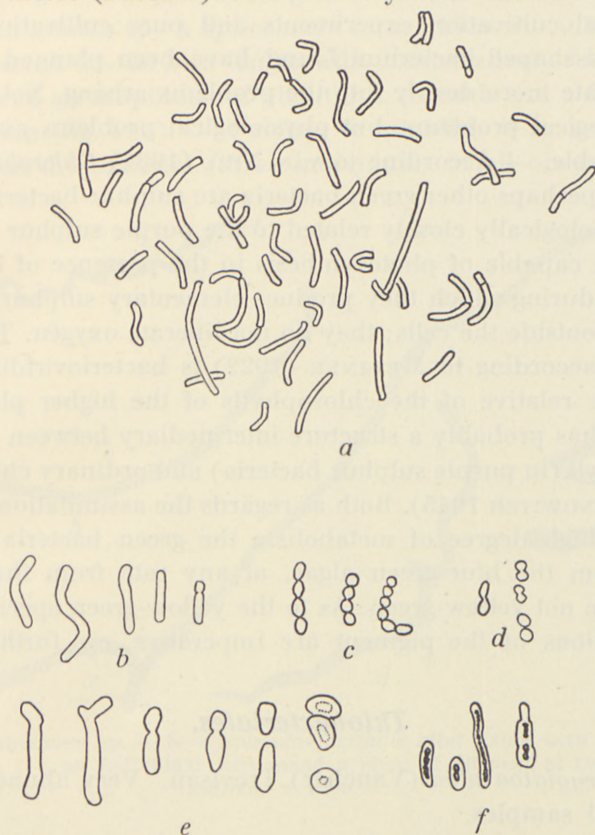
Fig. 10. Material of green bacteria from Flyndersø, *a* colony from mud near the
shore. *b*—*f* examples of cells in large green masses of bacterium mucus from mud
in the middle of the lake, *b* normal or typical cells, *c* streptococcus forms, diplo-
coccus forms, *e* involution forms, *f* cells with gas vacuoles. × 1700.

should be a mixture of two different bacteria in my material; for
there were all possible transitions between the normal rodshaped
cells on the one hand and the involution forms and the diplo-
coccus- and streptococcus-forms on the other. Both types of devi-
ating cells never occurred in groups but always single among normal
cells. Of special interest was the observation of cells with reddishly
shining central areas, presumably gas vacuoles of quite the same

type as those in the *Oscillatoriae* (particularly *O. fulgens*), see fig. 10 *f*.
Cells of this type were particularly frequent in certain parts of the
material and seemed to indicate that here there were special physio-
logical circumstances conditioning the development of gas vacuoles.

Special cultivation experiments and pure cultivation of the
green rod-shaped bacterium found have been planned in order
to penetrate more deeply into the problems arising. Not only the
morphological problems, but physiological problems as well are
innumerable. — According to van Niel (1931) *Chlorobium limi-
cola* and perhaps other green bacteria are sulphur bacteria, which
are physiologically closely related to the purple sulphur bacteria.
They are capable of photosynthesis in the presence of hydrogen
sulphide during which they produce elementary sulphur which is
excreted outside the cells; they do not liberate oxygen. The green
pigment according to Metzner (1922) is bacterioviridin, which
is a close relative of the chlorophylls of the higher plants and
algae; it has probably a structure intermediary between bacterio-
chlorophyll (in purple sulphur bacteria) and ordinary chlorophyll
(cp. Rabinowitch 1945). Both as regards the assimilation pigment
and the high degree of metabolism the green bacteria seem to
differ from the blue-green algae, at any rate from the species
which are not yellow-green. As to the yellow-green species closer
investigations of the pigment are imperative, cp. further p. 42.

Thiobacteriales.

46. *Beggiatoa alba* (Vaucher) Trevisan. Very abundant, but
not in all samples.

47. *Beggiatoa leptomitiformis* (Menegh.) Trevisan. Very com-
mon in the material; constantly occurring in fresh samples.

48. *Achromatium mobile* Lauterb. Very abundant.

49. *Chromatium fallax* (Warming) Kolkwitz. In large quanti-
ties in some of the culture glasses. According to Bavendam (1924)
probably a species of *Thiovolum*. Besides this a rather long,
slightly spirally coiled form was observed, which generally was
without sulphur granules. In size and form it reminded very
much of *Thiospira bipunctata* (Molisch) Wislouch.

50. *Lamprocystis roseo-persicina* (Kütz.) Schröter. Very abun-
dant in particular in old culture glasses.

51. *Thiothece gelatinosa* Winogr. Scattered in old cultures.

Spirochaetales.

52. *Spirochaeta plicatilis* Ehrenberg. Frequent in several samples.

52 a. *Spirochaeta* sp. A *Spirochaeta* form which was 0.5—0.6 μ thick and about 30—50 μ in length with comparatively few coils, which showed an amplitude of about 3 μ. At each end a flagella-like extension (fig. 11 a). — I refuse to establish it as a species at present as the material (three individuals in all observed) is
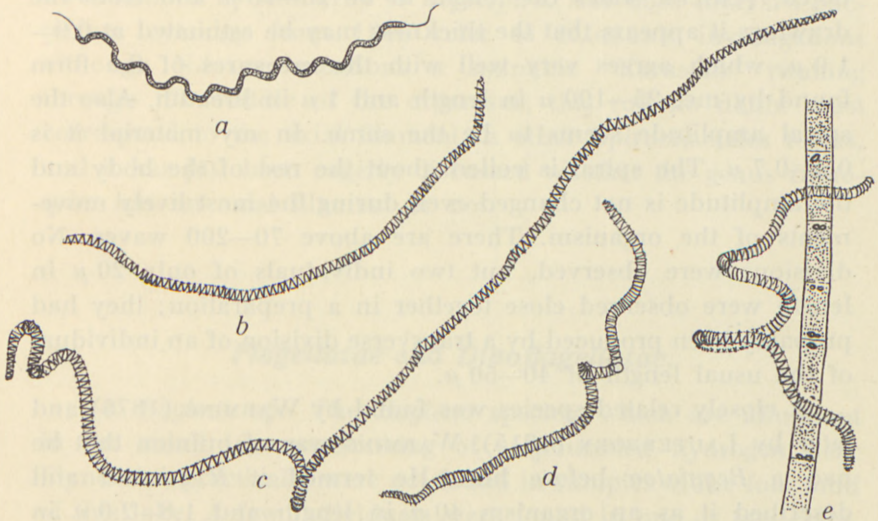
Fig. 11. *a Spirochaeta* sp. — *b—e Spirophis flexibilis* after fixing with La Cour 2 BD; in fig. 11 e an individual coils round a piece of filament of *Oscillatoria putrida.* × 1700.

two small for an exact statement of the measures of length of the species and its other properties. The species may be related to *S. stenostrepta* Zuelser, which is found in water containing H_2S and has pointed ends, but deviates in dimensions (0.25 μ in thickness and 20—60 μ in length, spiral amplitude very narrow with steep windings).

53. *Spirophis flexibilis* Nägler. This remarkable organism occurred in not a few specimens in one of the culture glasses together with *Oscillatoriaceae* and *Pseudanabaena* species. It is extremely motile, its movements show bending rotation, rapid spinning and intermittently active lashing as stated about *Lepto-spira* (Nogouchi 1918). Also its cytological conditions are in good

agreement with *Leptospira*, particularly the thin close permanent coil. The main differences between the two genera are that *Spirophis* is much larger than *Leptospira* and is not bent into a hook at one or both ends, nor is its terminal portions more flexible than the median part. Actually it is a question whether the two genera ought not to be united. If so, the name of *Spirophis* should presumably be adopted for both, as being the oldest name, even though NÄGLER's description of the genus (1909) is somewhat defective.

As to the species *S. flexibilis* the following facts should be noted. NÄGLER states the length to be 20—70 μ and from the drawings it appears that the thickness may be estimated at 0.9—1.0 μ, which agrees very well with the measures of the form found by me, 25—100 μ in length and 1 μ in breadth. Also the spiral amplitude seems to be the same. In my material it is 0.4—0.7 μ. The spiral is coiled about the rest of the body and the amplitude is not changed even during the most lively movements of the organism. There are above 70—200 waves. No divisions were observed, but two individuals of only 20 μ in length were observed close together in a preparation; they had probably been produced by a transverse division of an individual of the usual length of 40—50 μ.

A closely related species was found by WARMING (1876) and later by LAUTERBORN (1915). WARMING was of opinion that he had a *Beggiatoa* before him. He termed it *B. minima* and described it as an organism 40 μ in length and 1.8—2.0 μ in breadth. LAUTERBORN then referred it to *Spirophis* as *S. minima*. Unfortunately this very large species thus came to be named *minima*. LAUTERBORN states its measures to be a length of about 100 μ and a thickness of 1.5—2.0. He does not seem to have calculated the measures of *S. flexibilis* described by NÄGLER and thinks that it is identical with *S. minima*. However, as long as there are two observers who have found individuals of up to 2 μ in thickness and two who have found a thickness of 1 μ only, it seems to me that the two species must be kept apart. Future investigations must decide whether the two species should be united, in which case the new species will have a considerable width of variation as regards the breadth of the cells. This variation increases further if also the very narrow form (breadth 0.5 μ) found by SKUJA (1948) in Sweden is included.

It is rather curious that only two of the large monographs mention Warming's and Nägler's organism. Zuelser (1931) and Bergey (1948) are the only authors who include it in their work. Zuelser mentions it on p. 1671 under water spirochaetes as an uncertain species, which may be due to Nägler's brief mention and Bergey mentions it under the name of *Spirochaeta flexibilis* as an uncertain species due to inadequate description, and on p. 1053 he does not give any description of its characters. Nor is it mentioned in Nogouchi (1928) and nobody seems to have noticed its similarity to *Leptospira*. Nor does Knaysi's bacterium cytology from 1946 refer to Nägler's investigations although Nägler mentions a stainable "Kernstab" running through the middle of the organism; this rod no doubt must correspond to the axial filament in other Spirochaetales forms, and it has just been eagerly discussed whether the genus *Leptospira* has an axial filament or not.

Flagellatae and *Dinoflagellatae*.

54. *Euglena* sp. The *Euglena* species, which are abundant in the small lagoons stinking of sulphuretted hydrogen near Flyndersø, practically were not found in samples of the foul mud of this lake. A few individuals were found in one or two cases, but they were not determined. *Euglena* is probably an accidental visitor to the mud in spite of the fact that the genus includes greatly saprophilous species.

55. *Ochromonas viridis* Böcher. Apart from what has been stated in my paper (1945) it may only be said about this species that it is not common in fresh samples. It has been observed in two samples in all only, and never in great quantities in newly made preparations. On the other hand, conditions in such preparations in which the water with the organisms was surrounded by an edge of vaselin or paraffin oil, obviously were particularly favourable to it so that it could here reach abundance in few days.

56. *Peridinium cinctum* Ehrb. In the surface of mud in samples taken in October this plankton organism was fairly abundant.

Chlorophyceae.

57. *Pediastrum integrum* Näg. var. *scutum* Raciborski.

58. *Pediastrum duplex* Meyen var. *coronatum* Raciborski.

59. *Pediastrum Boryanum* (Turpin) Menegh.

These three *Pediastrum* species were found in surface samples taken in October, but not in great numbers. Most cells were dead or dying.

60. *Scenedesmus bijugatus* (Turp.) Kütz. This species, which is considered slightly mesosaprobous, was so constantly present in the samples that it may be considered enter naturally in the mud vegetation; but it was never present in great numbers and did not multiply very rapidly in the preparations.

61. *Coelastrum proboscideum* Bohlin. In a single surface sample very frequent and greatly variable.

Conjugatae.

62. *Closterium Leibleinii* Kütz. In a single sample this species had multiplied at a great rate on the surface of the mud.

63. *Staurastrum alternans* Breb. Dying individuals observed in the surface of mud in a sample taken in October. In the same sample several other *Desmidiaceae* belonging to the genera *Cosmarium* and *Euastrum* were seen. These were not determined and also were dying. Without doubt mud of this type is not a natural habitat to *Desmidiaceae.*

Diatomeae.

Determination and counting done by ERIK JØRGENSEN, M.Sc.

Table 1.

Species	Number of Individuals	Percentage	Place in KOLBE'S Halobion System
64. *Achnantes flexella* (Kütz.) Brun	26	9.0	Halophobous
65. *Amphora coffaeiformis* Ag.	+	—	Mesohalobous
66. — *ovalis* Kütz.	5	1.7	Indifferent
67. *Anomoeoneis sphaerophora* (Kütz.) Pfitzer	+	—	Halophilous

Table 1 (continued).

Species	Number of Individuals	Percentage	Place in KOLBE's Halobion System
68. *Caloneis alpestris* (Grun.) Cleve......	1	0.3	Indifferent
69. — *silicula* (Ehrb.) Cl. var. *truncatula* (Grun.) Cl.	+	—	,,
70. *Cymbella aequalis* Sm.	12	4.1	,,
71. — *lesatii* (Rabh.) Grun........	1	0.3	Halophobous (?)
72. — *helvetica* Kütz.	31	10.9	Indifferent
73. — *incerta* Grun..............	10	3.4	Indifferent (?)
74. — *parva* (W. Sm.) Cl.	3	1.0	Indifferent
75. *Diploneis ovalis* (Hilse) Cleve........	1	0.3	,,
76. *Epithemia argus* Kütz..............	151	52.2	,,
77. — *turgida* (Ehrb.) Kütz......	+	—	,,
78. — *zebra* (Ehrb.) Kütz........	1	0.3	,,
79. *Eunotia arcus* Ehrb................	3	1.0	,,
80. *Gomphonema intricatum* Kütz.	1	0.3	,,
81. *Mastogloia Braunii* Grun...........	2	0.7	Mesohalobous
82. — *elliptica* Ag.	1	0.3	,,
83. — *Smithii* Thw.	8	2.8	Indifferent[1]
84. — — var. *amphicephala* Grun.	4	1.4	,,
85. — — var. *lacustris* Grun.	3	1.0	,,
86. *Navicula oblonga* Kütz.	4	1.4	,,
87. — *radiosa* Kütz.	7	2.4	,,
88. *Nitzschia denticula* Grun............	7	2.4	,,
89. — *vermicularis* (Kütz.) Grun. .	+	—	Halophobous (?)
90. *Pinnularia gentilis* (Donkin) Cleve ...	+	—	Indifferent
91. *Rhopalodia gibba* (Kütz.) O. Müll.....	8	2.8	,,
	290	100.0	

[1] Perhaps mesohalobous (cf. BOYE PETERSEN 1943 p. 76).

4. Summarizing Remarks on the Flora and Vegetation.

It appears from the preceding treatment of the flora that some species must be considered typical mud organisms, while others may be considered more or less accidental visitors. The typical exclusive species, i. e. species which in plant sociology are generally called character species, ought to be those which lend their names to the community. There can be no doubt that the yellow-

3*

green Oscillatoriae and the *Pseudanabaena* species are the best
character species. Hence the community may suitably be named
Oscillatorietum putridum, a saprobous community particularly
bound up with shallow ponds with *Characeae*. Strictly speaking
the *Chara* species have their lower parts growing in the mud,
and so it might with some right be said that this *Oscillatorietum
putridum* after all was a synusia in the bottom vegetation, a kind
of "mould flora" in the "Chara wood". But the ecological con-
ditions in the mud are so specific that however the community
is considered, it will be most natural to treat it as something
quite apart.

HAYRÉN (1921, 1933, and 1944) mentions a highly meso-
saprobous community which he names *Oscillatorietum benthoni-
cum*. It is found in foul mud in slightly salt seawater. As character
species he mentions *Oscillatoria amphibia, chalybea* and *tenuis*.
Of these *O. chalybea* did not with certainty appear in my material
from Flyndersø, but in a small lagoon smelling strongly of H_2S,
in which there was much rotting seaweed and plenty of *Euglena
proxima* (see p. 15). Here all the yellow-green *Oscillatoriae* were
missing, and HAYRÉN does not mention them as occurring in his
community in Finland. Thus there are in the mud vegetation at
any rate two distinct *Oscillatorieta*, of which *O. putridum* most
likely is oligohalobous and slightly mesosaprobous whereas *O.
benthonicum* is meso-euhalobous and highly mesosaprobous.

As character species of *Oscillatorietum putridum* I consider
nos. 17, 18, 34—39, 45, and 53.

As character species common to the two *Oscillatorieta* and
perhaps even more related associations: nos. 24, 32, 46, 47, 49,
and 52.

Natural elements in the vegetation: nos. 1, 10, 13, 15, 16, 22,
26, 27, 29—31, 33, 41, 44, 48—50, 58, 60, 61, 75, and 91.

More or less accidentally occurring species: nos. 2—4, 7—9,
12, 40, 42, 56.

On the basis of the investigations of the diatoms mentioned
on pp. 34—35 we may for the foul mud in Flyndersø set up a
Diatom-Halobion Spectrum. This spectrum has in Table 2 been
compared with a similar spectrum adduced from BOYE PETERSEN
1943, Table 26. BOYE PETERSEN's spectrum originates from
scrapings off stones on the bottom of Flyndersø. Strangely enough

there is rather a considerable difference between the two spectra,
a difference inviting closer study. *Achnantes flexella* (*Eucocconeis
flexella*) was not found on the stones at all by Boye Petersen,
but is frequent in the foul mud between the stones. It is halo-
phobous. As there also in the very sample from the stones are
several meso- and euhalobous species, this might seem to indicate
that the flora of the foul mud was less halobous than the flora
of the stones. In all 12 species only are common to the two
samples, and the abundant species are also different: in the mud
Epithemia argus and on the stones *Achnantes minutissima*.

Table 2.

Diatom Halobion Spectra, Flyndersø.

		Sample of bottom mud analyzed by Erik G. Jørgensen		Scrapings off stones according to Boye Petersen 1943, Table 26	
		Number of forms	Percent-age of indivi-duals	Number of forms	Percent-age of indivi-duals
Oligohalobous	halophobous......	1	9.0	0	0.0
	indifferent........	20	*86.3*	18	59.7
	halophilous.......	1	0.0	7	*26.1*
Mesohalobous...................		3	1.0	7	*12.3*
Euhalobous		0	0.0	1	0.0
? ? ?...........................		3	3.7	1	1.9
		28	100.0	34	100.0

In several culture glasses in which purple sulphur bacteria
developed to some degree, it was impossible at the microscopy
not to notice that particularly certain yellow-green *Oscillatoriae*
and an immotile pale green species belonging to the *Oscillatoriaceae*
and needing a closer study formed a mosaic with the red bacteria.
In the picture, which formed rich colour contrasts, the sulphur
bacteria often constituted spindleshaped islands surrounded by
the filamentous green species. There were many things indicative
of a kind of symbiosis. Perhaps the sulphur bacteria get oxygen
from the green species. In fresh samples such a contact between

the two kinds of organisms was not observed. However, a partner-
ship of this type is very probable also in nature, but here the
organisms occur more sporadically in the mud and hence visible
evidence of such a partnership will rarely be found.

5. Some Plasmolysis and Plasmoptysis Experiments with Oscillatoriae.

The strange species *Oscillatoria fragilis* which would not stand
being put into pure water (p. 24), but broke here after plasmo-
ptysis, invited a closer study of the plasmoptysis and the con-
ditions needed to produce it. It was probable that *O. fragilis* was
a particularly characteristic inhabitant of the mud, adapted to
live at a fairly high concentration of osmotically active sub-
stances, but would not stand low concentrations in the surrounding
liquid. As for marine species, particularly *O. proboscidea*, a similar
breakdown of the filaments in connexion with plasmoptysis has
been described by STROH (1925). This worker could produce
plasmoptysis experimentally by first placing the filaments in a
hypertonic solution and then transferring them to a hypotonic
solution. The hypertonic solution produced plasmolysis, after
which the cell contents gradually became isotonic with the plasmo-
lyzing fluid. By being transferred to water from the city supply
the cells in some cases absorbed the water so rapidly that
they burst.

My experiments included the species *O. fragilis* and *putrida*,
putrida alone, and *O. brevis* and *profunda*. Isosmotic concentra-
tions of cane sugar, KNO_3, and NaCl were used. The fluids had
concentrations corresponding to pressures of 1, 2, 5, 10, 20, or
40 atmospheres.

In the first experiments filaments of *O. fragilis* and *putrida*
were placed for two hours in the solutions, after which they were
transferred to water from the city supply and observed. The
result corresponds very well to that of STROH's. The zigzag for-
mation, which is due to plasmoptysis near the transverse walls,
and the subsequent decay of the filaments became more pro-
nounced the higher the concentration of the fluid used at the
introductory treatment. The two species clearly behaved differ-

ently, the plasmoptysis in *O. fragilis* being produced by fluids of introductory treatment with lower concentrations than those which produced plasmoptysis in *O. putrida*. Further it was evident that KNO_3 had a different effect from the other two solutions, even though isosmotic concentrations were used. KNO_3 had a much stronger effect than the others, a fact that may be due to a particularly high degree of permeability in KNO_3. Moreover, the conditions of permeability must be very different in the different cells in the filaments. Often plasmolysis and plasmoptysis were observed in one part of a filament of a thread and apparently unaffected cells in another part. It was peculiar to see that the plasmolysis in some cells could hold out long after the filaments had been transferred to water. Thus it seemed that the process might be irreversible, or the cells very slowly returned to their original state.

In an experiment in which only *O. putrida* was used and in which the observations were protracted until 13 days after the beginning of the experiment, it could be demonstrated that 20 atmosphere concentrations always caused a permanent degeneration, whereas high motility could be re-established after introductory treatments with a solution of sugar or NaCl with osmotic values of 10 or 5. KNO_3 caused permanent degeneration, i. e. breakdown of the filaments and dissolution of the cells, and this even after an introductory treatment with a solution corresponding to 5 atmospheres. Still lower concentrations (1 and 2 atmospheres) had no injurious after-effect.

In one more experiment with *O. putrida*, in which only sugar and KNO_3 with an osmotic value of 10 were used, but in which the time in which the filaments were exposed to the plasmolyzing solution was varied ($\frac{3}{4}$, 2, and 4 hours), it could, in the case of the preparations with the sugar solution, be ascertained that the injurious after-effect increased the longer the duration of the introductory treatment. Such a difference could not be observed in preparations treated with KNO_3; all the three spaces of time gave the same picture: plasmoptysis, „chromoplasm concentration", (see p. 21), decay, and dissolution.

Experiments with *O. brevis* and *profunda* with introductory treatment for two hours with the same concentrations as used in the experiments first mentioned, on the whole gave the same

result. *O. profunda*, however, was more liable to plasmoptysis than *O. brevis*. NaCl had a slight influence, sugar a somewhat greater, and KNO$_3$ the greatest influence. After an introductory treatment with solutions with an osmotic value of 5, a great many bends appeared in *O. profunda*, still the bends very often appeared near hormogonia already developed. In *O. brevis* the effect was different in different parts of the filaments. Some pieces of filaments which were particularly light and undoubtedly represented terminal or intercalarily developed young pieces of filament, were particularly apt to plasmoptysis and detachment from the other parts. It was interesting here to observe how the refractive concave cells which are so characteristic of this species very often formed a boundary between the young and the older parts of the filaments; thus they came to function in a similar way as heterocysts. In concentrations corresponding to 10 to 20 atmospheres similar conditions were observed, but also interior disturbances in the cells of *O. brevis*, which reminded of the above-mentioned "chromoplasm concentration". In a few cases filaments were seen which had been exposed to numerous plasmoptyses at one end, but were quite normal at the other. These normal ends were motile and dragged the part bent in zigzags after them.

In some of the experiments it seemed that the plasmolysis held out in spite of the transfer to water and that later ruptures of the filaments occurred in these places. In order to investigate this question in more detail, filaments of *O. putrida*, *fragilis*, and *brevis* were placed in NaCl and KNO$_3$ with osmotic values of 5, 10, and 20, and were observed for three weeks in these solutions. The plasmolysis held out and the motility ceased, at the same time chromoplasm concentration arose, which also held out or became more and more pronounced (fig. 6*k—m*), but the most curious thing was that both in NaCl with an osmotic value of 10 and in all the three concentrations of KNO$_3$, some bends appeared with escape of plasma at the place of the rupture. This was particularly clear in *O. fragilis*. It all looked completely as a case of plasmoptysis, but, indeed, it can only with difficulty be interpreted like this. Perhaps it may be a question of the organism itself by a vital process producing states in the cells which lead to plasmoptysis. It is not improbable that we have here a similar process to that described as autolysis in *Beggiatoa alba* (see
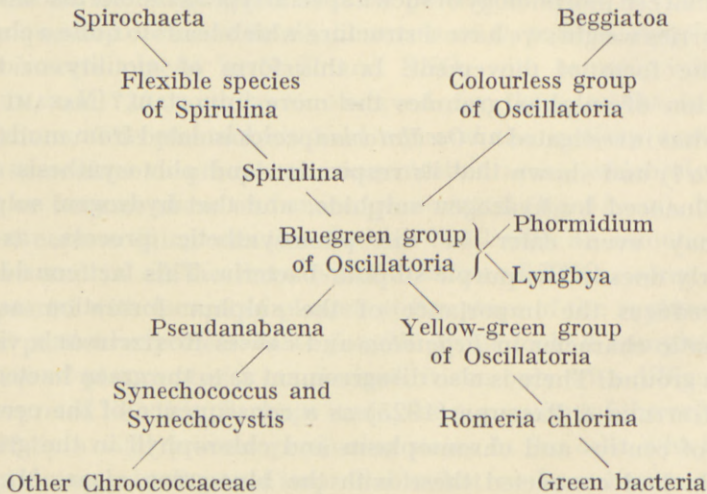
D. ELLIS 1932, pp. 94—98); this autolysis is induced by many different unfavourable conditions and involves escape of mucus between the cells, zigzag formation and decay and dissolution of the cells. It must be left for future investigations to make out the relation between genuine plasmoptyses and such autolyses.

6. Remarks on the Relationship of the Oscillatoriaceae.

In the case of microorganisms the unravelling of relationship must always be uncertain. The comparatively few characters is one of the chief reasons for the uncertainty. In certain bacteria the great morphological variability is a further factor of uncertainty. Hence it is not strange that, instead of these, physiological characters are extensively adduced at the judgment of relationship, indeed, in many cases physiology has been considered decisive. This has led to several disagreements of views. Thus *Beggiatoa* because of physiological accordance with colourless sulphur bacteria is generally counted among the bacteria. From the point of view of cell morphology, however, it is closely related to the *Oscillatoriaceae*, which made ROSENVINGE (1913) place *Beggiatoa* as a colourless type within *Oscillatoriaceae*. The question is which is the more correct view? Undoubtedly everybody will admit that cell morphology of such a special type as the one discussed here carries weight; we have a structure which leads to quite a characteristic form of movement. Is this form of motility or the formation of sulphur granules the more important? NAKAMURA (1938) has investigated an *Oscillatoria* species isolated from mud (*O. neglecta*?) and shown that its respiration and photosynthesis are not influenced by hydrogen sulphide, and that hydrogen sulphide may even enter in the photosynthetic process, as it regularly does in the purple sulphur bacteria. This fact considerably reduces the importance of the sulphur formation as a systematic character in *Beggiatoa* and causes ROSENVINGE's view to gain ground. There is also disagreement as to the green bacteria. After GEITLER & PASCHER (1925) as a consequence of the occurrence of centro- and chromoplasm and chlorophyll in the green bacteria had connected these with the blue-green algae, METZNER's investigations (1922) of the pigment and VAN NIEL's studies

(1931) on the great metabolism and physiological similarity to
the sulphur bacteria led to the green bacteria being considered
bacteria. van Niel even writes (*loc. cit.* p. 73) that the group of
green bacteria "has nothing to do with the group of bluegreen
algae," and (p. 92) "So much is certain, that these green bacteria
cannot be considered as small bluegreen algae". Indeed, these
are strong words, which one might be tempted to change into:
"The evidence would seem to indicate that the green bacteria
are more closely related to the bacteria than to the blue-green
algae". For it must be kept in mind that their pigment (bacterio-
viridin) is considered intermediary between chlorophyll and bac-
teriochlorophyll and that there are a long series of *Cyanophyceae*
of the same pale green colour, hence perhaps bacterioviridin, and
finally that certain blue-green algae physiologically approach to
the green bacteria by their relation to hydrogen sulphide.

For my part I see no reason whatever for such a sharp
distinction between bacteria and blue-green algae. The boundaries
between these groups is actually blurred. From the genus
Oscillatoria as the centre with may draw radiating lines to other
groups of organisms, several of which belong to the bacteria.
These lines are based on similarity between the forms. Probably
many of them also denote relationship. The following survey
shows my view:

Spirochaeta   Beggiatoa
           \   /
       Flexible species   Colourless group
        of Spirulina   of Oscillatoria
                    \   /
                 Spirulina
                        \   /
                    Bluegreen group \ / Phormidium
                     of Oscillatoria } \ Lyngbya
                    /   \
          Pseudanabaena   Yellow-green group
               /   of Oscillatoria
      Synechococcus and   \
       Synechocystis   Romeria chlorina
           /   \
  Other Chroococcaceae   Green bacteria

Besides the lines indicated in the survey there are undoubtedly many others; but I cannot throw light on them on the basis of material observed by myself. The line *Chroococcaceae—Pseudana-baena—Oscillatoria* is of particular interest; for there is a possibility that this is an evolutionary line so that it would be possible to derive the *Oscillatoriaceae* direct from the *Chroococcaceae*. The connexion is supported by the following facts, viz. that *Synecho-cystis* may form chains, that *Synechococcus* may form polarly arranged gas vacuoles like those in *Pseudanabaena*, and that motility has been observed in several species of *Synechocystis* and *Synechococcus*.

The genus *Pseudanabaena* which GEITLER did not consider as a natural group seems now to be fully established. In addition to the discussion in BÖCHER (1946b) of *P. biceps*, SKUJA (1948) has described several new species and concludes that the genus is well characterized and presumably a progressive group. In *P. constricta* he mentions »Anlagen von Heterocysten« which, however, cytologically resemble the ordinary vegetative cells. If these cells have anything to do with genuine heterocysts, there is a possibility of a relation between *Pseudanabaena* and *Anabaena*.

7. Literature.

BAVENDAMM, W. 1924. Die farblosen und roten Schwefelbakterien. Pflanzenforschung Heft 2. Jena.

BERGEY, D. H. 1948. Manual of Determinative Bacteriology. 6th Edition by R. S. BREED, E. K. D. MURRAY and A. P. HITCHENS. Baltimore.

BOYE PETERSEN, J. 1943. Some Halobion Spectra (Diatoms). Det Kgl. Danske Vidensk. Selskab, Biol. Medd. **17**, No. 9, pp. 1—95.

BÖCHER, T. W. 1945. Ochromonas viridis sp. n., a Green Flagellate Belonging to the Chrysomonadinae. Vidensk. Medd. fra Dansk naturhist. Foren. **108**, pp. 233—238.

— 1946a. Dichothrix gelatinosa sp. n., its Structure and Resting Organs. Det Kgl. Danske Vidensk. Selskab, Biol. Skrifter **4**, No. 4, pp. 1—15.

— 1946b. Pseudanabaena biceps, a New Sapropelic Species from Bottom Mud. Botaniska Notiser 1946, pp. 281—284.

CANNABAEUS, L. 1929. Über die Heterocysten und Gasvakuolen der Blaualgen und ihre Beziehungen zueinander. Pflanzenforschung Heft **13**, Jena.

ELLIS, D. 1932. Sulphur Bacteria, a Monograph. London, New York and Toronto.

FROBISHER, M. 1946. Fundamentals of Bacteriology. Philadelphia and London.

GEITLER, L. 1925a. Synoptische Darstellung der Cyanophyceen in morfologischer und systematischer Hinsicht. B.B.C. II. Abt. **41**.

— 1925b. Cyanophyceae. Pascher: Süsswasserflora. Heft 12, pp. 1—450.

— 1932. Cyanophyceae. Rabenhorst's Kryptogamenflora 14, pp. 1—1196.

— 1936. Schizophyzeen. Handb. d. Pflanzenanatomie 4, 1, B.

— & PASCHER, A. 1925. Cyanochloridinae = Chlorobacteriaceae. Pascher: Süsswasserflora, Heft 12, pp. 451—463.

GICKLHORN, J. 1921. Über den Blauglanz zweier neuer Oscillatorien. Österreich. Botan. Zeitschrift **70**, pp. 1—11.

HAYRÉN, E. 1921. Studier över föroreningens inflytande på strändernas vegetation och flora i Helsingfors hamnområde. Bidrag t. Kännedom af Finlands Natur och Folk 80, No. 3, pp. 1—128.

— 1933. Förorening och strandvegetation i Helsingfors hamnområde år 1932. Ibid. 84, No. 5, pp. 1—38.

— 1944. Studier över saprob strandvegetation och flora i några kuststäder i Södra Finland. Ibid. 88, No. 5, pp. 1—120.

KNAYSI, G. 1946. Elements of Bacterial Cytology. Ithaca, New York.

LAUTERBORN, R. 1913. Zur Kenntnis einiger sapropelischer Schizomyceten. Allgem. Bot. Zeitsch. 19. Jahrg., pp. 97—100.

— 1915. Die sapropelische Lebewelt. Verhdl. d. Naturhist.-mediz. Vereins zu Heidelberg, N. F. 13, pp. 395—481.

METZNER, P. 1922. Über den Farbstoff der grünen Bakterien. Ber. d. deutsch. Bot. Gesellschaft 40, pp. 125—129.

NADSON, G. A. 1912. Mikrobiologische Studien. 1. Chlorobium limicola Nads., ein grüner Mikroorganismus mit inaktivem Chlorophyll. Bulletin du Jardin Imp. Bot. de St.-Pétersbourg 12, pp. 83—87.

NAKAMURA, H. 1938. Über die Kohlensäureassimilation bei niederen Algen in Anwesenheit des Schwefelwasserstoffs. Acta Phytochimica 10, pp. 271—281.

NÄGLER, K. 1909. Eine neue Spirochäte aus dem Süsswasser. Centralblatt f. Bakt. u. Parasitenk. 1. Abt. 50, pp. 445—447.

NIEL, C. B. VAN 1931. On the Morphology and Physiology of the Purple and Green Sulphur Bacteria. Archiv f. Mikrobiologie 3, pp. 1—112.

NOGOUCHI, H. 1918. Morphological Characteristics and Nomenclature of Leptospira (Spirochaeta) icterohaemorrhagiae. Journ. Exper. Medicine 27, pp. 575—592.

— 1928. The Spirochaetes. Jordan-Falk: The Newer Knowledge of Bacteriology and Immunology. Chicago.

OLSEN, S. 1944. Danish Charophyta. Det Kgl. Danske Vidensk. Selskab, Biol. Skrifter 3, No. 1, pp. 1—240.

RABINOWITCH, E. I. 1945. Photosynthesis and Related Processes 1. New York.

ROSENVINGE, L. K. 1913. Sporeplanterne. Kjøbenhavn og Kristiania.

SCHMIDLE, W. 1901. Neue Algen aus dem Gebiet des Oberrheins. B.B.C. 10, pp. 179—180.

SKUJA, H. 1948. Taxonomie des Phytoplanktons einiger Seen in Uppland, Schweden. Symbolae Bot. Upsal, IX, 3, pp. 1—399.

STROH, L. 1938. Über prämortale Mazeration bei Oscillatorien. Archiv f. Protistenkunde 91, pp. 187—201.

SZAFER, W. 1911. Zur Kenntnis der Schwefelflora in der Umgebung von Lemberg. Bull. Internat. de l'Académie des Sciences de Cracovie. Classe Sciences Mathém. et Nat. Sér. B. 1910, pp. 161—167.

WARMING, E. 1876. Om nogle ved Danmarks Kyster levende Bakterier. Vidensk. Medd. fra den naturhist. Forening i Kjøbenhavn 1875, Nr. 20—28, pp. 1—116 (307—420). Kjøbenhavn.

ZUELSER, M. 1911. Über Spirochaete plicatilis Ehrbg. und deren Ver-
    wandschaftsbeziehungen. Arch. f. Protistenkunde **24**, pp. 1—59.
— 1921. Biologische und systematische Spirochätenuntersuchungen.
    Centralblatt f. Bakt. u. Parasitenkd. I. Abt. **85** (Beih.),pp. 154—167.
— 1931. Die Spirochäten. Handb. d. pathogenen Protozoen heraus-
    gegeb. v. S. von Prowazek. **3**, pp. 1627—1797.