

STUDIES ON THE PLANKTON
IN THE LAKE OF
FREDERIKSBORG CASTLE

BY

KAJ BERG AND GUNNAR NYGAARD
(FRESHWATER-BIOLOGICAL LABORATORY, THE UNIVERSITY OF COPENHAGEN)

WITH 6 PLATES AND 27 FIGURES IN THE TEXT

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATHEM. AFD., 9. RÆKKE, I. 4



KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL

BIANCO LUNOS BØGTRYKKERI

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Introduction.

Problems concerning temporal variation in plankton organisms in fresh water, and the probable significance of such variation to the organisms themselves, have for many years — indeed ever since the appearance of the fundamental works on this subject by C. WESENBERG-LUND (1900) and W. OSTWALD (1902) — occupied the minds of biologists, and new works are constantly being published dealing with different aspects of this subject, the variation of the Cladocera having more especially furnished material for investigation. Also the present work owes its existence to the discussion raised by these problems, and for this reason it has been considered expedient to quote briefly in the following some of the principal points of view already advanced on this subject.

In conformity with the said works by WESENBERG-LUND and OSTWALD, it is rather commonly accepted that the variable organs of the plankton organisms — notably the variable organs (crest, rostrum, spina, mucro etc.) of the Cladocera — are buoyancy organs, and it is further supposed that the enlargement taking place in these organs in summer, serves to augment the form-resistance of the animals, thus furnishing some compensation for the diminished bearing power of the fresh water during the summer half year.

In his work "Über Funktion, Herkunft und Entstehungsursache der sogen. Schwebefortsätze pelagischer Cladoceren", R. WOLTERECK has advanced a hypothesis in direct opposition to the above conception. According to WOLTERECK, the function of the buoyancy organs of the Cladocera is neither to increase their form-resistance to sinking, nor to serve as balancing organs, maintaining the equilibrium of the organism. The latter consideration may perhaps in rare cases play some slight part, but the most important and common function of all these organs is "dass sie die Schwimmrichtung regulieren, indem sie einerseits geradlinige Fortbewegung ermöglichen, andererseits vorweichend horizontale Schwimmbahnen bewirken". The organs are therefore described as "Richtungsorgane" and play a role partly as steadying planes ("Führungsflächen"), partly as rudders ("Steuer") (WOLTERECK 1913, pp. 488—489). A close study of the swimming hypothesis of WOLTERECK and the reasons given in support of it would take us too far; further information may be gathered from the above-mentioned work and from a treatise by WOLTERECK from 1921 (especially pp. 49—69). But the reader is invited to

pause for a moment at a question of far more interest from the point of view of the following work, namely the question of the possible usefulness of the "Richtungsorgane" to the pelagic Cladocera. What ecological advantage may these organisms be supposed to obtain from the possession of the straightlined movements? The organs are supposed to cause the animals to adopt a horizontal swimming-direction, but why should the pelagic Cladocera have any fixed direction at all for their jump?

WOLTERECK answers these questions in their relation to several other propositions, more especially that of the nourishment of the animals (1913, p. 520 & 1921, p. 53). It is true that knowledge on this point is extremely limited, no precise information, based on reliable observations, being available. But according to WOLTERECK's opinion (1908, p. 871), the nourishment of the pelagic Cladocera consists of small algae etc. collectively described as "Nannoplankton" (after LOHMANN), of which it is supposed — partly on the authority of works by his pupils H. DIEFFENBACH & R. SACHSE (1911) and K. LANTSCH (1914) — that they occur in summer in quite definite waterlayers. In each lake there is, therefore, from spring to autumn, supposed to be distinct "Nahrungsschichten" or "Wohnschichten" for each separate species of *Daphnia* and *Bosmina*, and the "Richtungsorgane" make it possible for them to reside in that particular layer. — Furthermore, WOLTERECK suggests that the daily vertical ascents and descents of the pelagic Cladocera in the waterlayers might perhaps be looked upon "zum Teil als Folgeerscheinung des Auf- und Absteigens ihrer Nahrung" (1913, p. 522); he also makes similar statements later (1921, p. 55).

The main points in WOLTERECK's swimming hypothesis, as well as a series of other questions connected with these problems, have been made the object of very thorough investigation by WESENBERG-LUND in a work dealing with the Biology and Morphology of the Genus *Daphnia* (1926, especially pp. 158—200). In this treatise, the different arguments advanced against the older buoyancy theory are carefully tried, point by point; in order to throw light on the questions, the author's own former observations from "Plankton Investigations of the Danish Lakes" (1904—08), new studies on the genus *Daphnia*, and the entire literature written after 1908 and contributing something of importance in regard to the subject in hand, were brought out and investigated. The principal result of the cogitations is that the hypothesis of WOLTERECK cannot in the main be regarded as correct; on the other hand WESENBERG-LUND maintains that "if we take our stand on the buoyancy theory, it cannot be denied that WOLTERECK has to a very high degree, especially with regard to the *Bosmina* body, contributed to solve the question of how the organisms adjust themselves to the augmenting rate of sinking during the summer; and limnology will then always be in great debt to him for what he in this way has yielded" (1926, p. 194). Finally WESENBERG-LUND expresses his conception in the following terms: "In my eyes the buoyancy theory as it was set forth in its fundamental lines in 1900—1910 is just as necessary now as then, if we

want to understand the biology and morphology of the plankton organisms of the freshwater" (1926, p. 200).

The above brief presentation of certain main points in the discussion that has been carried on regarding the buoyancy organs of the plankton organisms, will be sufficiently comprehensive to indicate the basis and background of the following treatise. There has been no intention of recapitulating the whole of the buoyancy theory, the authors being actuated merely by a wish to offer a contribution to the discussion by furnishing certain information in regard to one of the disputed problems, namely the question whether the vertical distribution of the plankton-Cladocera (their possible "Wohnschicht") is dependent on the vertical distribution of the phytoplankton (the possible "Nahrungsschicht"). A few authors seem to look upon WOLTERECK's conception of these ecological conditions as being of "grosse Bedeutung" (A. THIENEMANN, 1914, p. 679).

As a natural complement to the said main topic of this work, an investigation of some other plankton problems has been included; the work will, therefore, deal with the following questions:

1. It is attempted to throw light on the main topic by furnishing material calculated to answer this question: is it possible in a very shallow lake in the summer to point out a "Wohnschicht", i. e. a waterlayer preferred by the Cladocera, especially by a form like *Daphnia cucullata* with a pronounced seasonal variation? If this is not the case, how then is the vertical distribution in a shallow lake?

The reason why it is especially stressed that information is desired in regard to a very shallow lake, is that a such information seems to us to be most valuable as a means of solving the above mentioned problems. For it will be able to supplement a number of results already arrived at in consequence of investigations carried out, partly in quite shallow ponds, partly in rather deep lakes. Of these investigations, the following may be mentioned:

In the "Hestesko pond" situated near Hillerød, which has a depth of only $\frac{1}{2}$ —1 metre, contains a plentiful supply of organic material, and in summer has a large maximum of *Microcystis*, a dwarf variety of *Daphnia cucullata* has been found. The locality does not appear to be particularly well suited for this species; the animals generally only attain a diminutive size, the crests decrease in length at the very time when they are augmented in the lakes, and a slow reproduction causes a minimum to occur, just when the maximum develops in the lakes. Under these circumstances the usual cyclomorphosis of the genus must be said to have been severely modified, a change which can hardly be ascribed merely to altered conditions of temperature; it is far more probable that the cause of the said change is in some way connected with the assimilation (WESENBERG-LUND 1926). In the vicinity of Leipzig, WOLTERECK and WAGLER also found dwarf races; some of which were entirely without cyclomorphosis. WAGLER has attempted to explain the nature of the pond-races, and his first conception was that they were "Hemmungsrassen"; subsequently he sought the reason for their peculiar qualities in the

fact that the animals become ripe at an earlier stage, 1 or 2 ecdysis before the other races. This again was supposed to be attributable to the larger amount of nourishment to be found in the ponds and to their temperature, which is higher than that of the lakes (WAGLER 1923, p. 292). Several objections may, however, be raised to this explanation. It is, for instance, difficult to understand why the pond-races should stop growing soon after arriving at maturity, although the mass of nourishment available and the temperature of their surroundings would seem to be particularly favourable (compare WESENBERG-LUND 1926, p. 142). All the same, it must be admitted that the said investigations have considerably enlarged our knowledge of the pond-races and their external conditions.

Other new plankton researches — principally carried out in deeper lakes — are also of importance from the point of view of the problems now under discussion. UTERMÖHL, for instance, in his great work on the phytoplankton of the lakes in Holstein, has some chapters dealing with the vertical distribution of the algæ. The main points of his result may be rendered as follows: In the cold season, during the period of circulation that occurs in the spring and autumn, all the algæ in the phytoplankton are almost uniformly distributed in all waterlayers; in winter they are also nearly uniformly distributed; yet a different distribution may occur, for instance under ice and in wind-sheltered places, where many flagellates and a few bacteria show a definite layer-distribution. In regard to the state of things prevailing during the hot season — a matter of especial interest to us — UTERMÖHL remarks that the above-mentioned statements about the almost uniform distribution in all waterlayers “gilt in schwächerem Masse für viele Formen in winddurchwühlten, meistens flacheren Seen”; in other lakes with epilimnion and hypolimnion, the distribution of the separate forms may be more or less stratified. As far as the epilimnion species are concerned, this is, for instance, the case with forms having flagella, under quite definite conditions viz. “bei länger anhaltendem ruhigem Wetter”; these forms “halten sich, so weit sie gefärbt sind, am Tage — genauer: um die Mittagsstunden — in bestimmten der Art, vielleicht sogar den Rassen nach, verschiedenen Wasserschichten auf” (UTERMÖHL 1925, p. 501—502). — UTERMÖHL's plan of research did not include any attempt to find out whether a vertical stratification occurred in the case of the Cladocera, corresponding to the stratification observed in some of the phytoplankton species. It is doubtful whether it would have been possible to obtain definite information on this point — more especially when one considers that although a stratification has certainly been proved to exist at certain times, under certain conditions, among a number of phytoplankton species, it is most probable that the maxima of these species occur at somewhat different levels, thus to some extent neutralising one another, so that the vertical displacements in the total quantity of nourishment in the different waterlayers will only be slight.

UTERMÖHL does not overrate the significance of the stratification observed by him among certain species of phytoplankton; on the contrary, to a certain extent

he adopts the opinion advanced by RUTTNER (1914, p. 293) that "wir werden daher beim Phytoplankton auch in der Zeit der Sommerstagnation grosse Unterschiede der Volksdichten in dem von Windströmen durchzogenen Epilimnion nicht zu erwarten haben . . .". In this connection UTERMÖHL writes (1925, p. 165) that "die RUTTNERSCHE Auffassung (trifft) auch für die ostholsteinischen Seen eher zu, falls man den Begriff "grosse Unterschiede" nicht zu eng fast".

In the great work by BIRGE and JUDAY on Lake Mendota (1922) there is no mention of stratification of nannoplankton within the epilimnion; a single investigation in the month of August shows that of the total quantity of plankton contained in the lake, 36.7 p. c. is to be found at a depth of 0—5 metres, 30.6 p. c. at 5—10 metres (1922, p. 197). There is, therefore, not much difference between the contents of plankton at these levels, which both belong to the epilimnion of the lake. On the other hand, the epilimnion and metalimnion (0—13 metres below the surface) contained about $2\frac{1}{2}$ times as much nannoplankton per cubic metre as the hypolimnion (depth: 14—20 metres); in regard to the netplankton the difference was still greater¹).

2. In the second place the quantity of nourishment of the animals will be studied in order to throw light on the question: Is it justifiable to ascribe a more frequent appearance of Cladocera in certain waterlayers rather than in others, to the presence of plentiful nourishment in the former?

3. It will also be expedient at certain times to take several sample collections in the course of 24 hours, so as to procure at any rate some material likely to furnish points of support in the answering of the question: Is there in a shallow lake, in the evening twilight, a distinct wandering of Cladocera towards the surface?

4. If this is the case, may these ascents — as WOLTERECK is inclined to suppose (1913, p. 521) — be said to coincide with a corresponding change of level of the food of the animals?

5. The quantitative investigations should extend over a space of time long enough to make it possible to establish the main points of the periodicity both of the Cladocera and of the phytoplankton. This will furnish an opportunity to compare the periodicity of the Cladocera in a quite shallow lake with that in our larger and deeper lakes, concerning which we already possess full knowledge (WESENBERG-LUND, 1904—1908).

6. In conjunction with the quantitative phytoplankton researches (vide points 2 & 5) it will be natural to undertake qualitative researches, so as to obtain a

¹) In connection with the above researches we may mention a recently published work by TER-POGHOSSIAN (1928). In Klostersee near Seon he has observed that *Daphnia cucullata* chiefly inhabits the warm epilimnion, while *D. longispina* also occurs in the hypolimnion — and sometimes even collects there in large numbers. No information is given as to whether the cause of this distribution is to be found in differences in the distribution of the phytoplankton; the phytoplankton of the lake is not dealt with in the work. — It is possible that the varied distribution of the species is merely due to the fact that they are not equally termophile.

knowledge of the species of phytoplankton of importance — either while they are alive or through the detritus left by them at their death — as elements of food for the Cladocera. As mentioned on page 228, it is especially the smallest species, the nannoplankton, that is considered an important source of nourishment, and for this reason it would, naturally, not do to ignore these forms; indeed, the list of species ought to be as complete as possible, in order to convey an impression of the great wealth of food-producing organisms available.

It is well known that the term “nannoplankton” was first used by LOHMANN (1909, p. 201) as a name for “jene kleinsten Auftrieborganismen die uns im Wesentlichen erst durch die Fangapparate der Appendicularen und die Zentrifugierung kleinster Wassermengen zugänglich werden”. The different species of nannoplankton are not caught even in the finest plankton-nets, being so small as to pass through the meshes; small varieties have a length of only 1μ , individuals 25μ long must be described as large (LOHMANN 1911, p. 3). BIRGE and JUDAY have, however, drawn attention to the fact that many of the freshwater organisms that pass through the finest plankton-nets are in reality considerably larger than 25μ ; for practical reasons they therefore use the expression nannoplankton in speaking of all the plankton organisms that pass through the finest silk gauze used for plankton-nets (Swiss silk gauze Nr. 20), and they arrive at very interesting results — obtained through weighing — in regard to the quantity of nannoplankton in Lake Mendota. Taken as an average for the whole year, the nannoplankton in this lake contains five times as much organic material as the netplankton; it is true that at times the quantities may be almost equal, but at other times the nannoplankton contains about 25 times as much organic material as the netplankton (1922, p. 96).

There are also other thorough investigations conveying an impression of the importance of the nannoplankton, for instance the studies carried out by UTERMÖHL on the phytoplankton in the lakes in Holstein, in the course of which he has made use of centrifugal methods and has counted the species in a KOLKWITZ chamber.

Nevertheless it is advisable to look upon some of the statements published in regard to the nannoplankton with a certain amount of caution. It is true that RUTTNER and some others use the expression in the same sense as LOHMANN, but WESENBERG-LUND has pointed out instances in which other “authors have quite forgotten the original meaning of the term and use it as a substitute for the old term phytoplankton” (1926, p. 189).

For the purpose of satisfying, in the best possible manner, the requirements of the qualitative phytoplankton research, especially with regard to the nannoplankton, it would obviously be most convenient to have this part of the examination carried out by a botanist; GUNNAR NYGAARD has undertaken this work and gives the results of his investigation in part II of this treatise, while the above-mentioned points 1—5 are dealt with in part I.

The work has been carried out at the Freshwater-Biological Laboratory of the University of Copenhagen, and both the authors are anxious to seize this opportunity of expressing their sincere thanks for the great interest with which the Chief of the Laboratory, Professor, Dr. phil. C. WESENBERG-LUND, has followed the progress of their work.

The determination of the quantity of phytoplankton has been worked out by KAJ BERG in the Laboratory of Zoophysiology, University of Copenhagen. We beg the Director of the Laboratory, Professor, Dr. phil. AUGUST KROGH, to accept our sincere thanks for his kind helpfulness, and for the valuable advice offered by him when the work was first planned and prepared.

Part I.
Zoological Investigations

by KAJ BERG.

Methodics.

The lake of Frederiksborg castle was chosen as the scene of investigation, and for collecting samples, a water hauler constructed by F. N. BRØNSTED (F. N. BRØNSTED and C. WESENBERG-LUND 1911—12, p. 437) was used. At each sample taking, the waterhauler gathers 0.5 litre of water, the temperature of which is immediately taken. All temperatures given are in the centigrade scale.

On each day of research, the following 2 sets of samples were collected:

1st set: 4 samples ("crustacea samples"), one from each of the following levels: Surface, 1 metre, 2 metres and 3 metres below the surface. These samples were, by means of the Kolkwitz filtering apparatus, filtered through a coarse strainer, so as to allow a considerable portion of the phytoplankton to escape. The crustacea, which were all retained, were then counted up in the Kolkwitz counting-chamber.

2nd set: 4 samples ("phytoplankton samples"), similarly one each from the surface, from a depth of 1 metre, of 2 metres and of 3 metres. According to the result of the counting of the crustacea, these 4 phytoplankton samples were treated in one of the following 2 ways:

a. If the counting of the 4 crustacea samples resulted in none of the crustacea showing any great difference in number at the different depths, 125 cm³ of each of the 4 phytoplankton samples were taken (after careful shaking!), that is to say, 4 × 125 cm³ or 500 cm³. The remainder from each sample, 375 cm³, was mixed with 16 cm³ of "concentrated" formalin (by which is meant the usual trade liquid, containing about 40 p. c. of formaldehyd). The result was a watersample containing about 4 p. c. of formalin. The plankton sediment formed therein was used as material for Mr. GUNNAR NYGAARD's botanical examination (See part II). — The 500 cm³, of which, then, each fourth part originates from a separate water-layer, were filtered through the Kolkwitz apparatus, the filter used in this case being a membrane of nitrocellulose with a maximum pore-width of 2 μ. All crustacea were carefully removed from the sediment thus obtained and which contains all the plankton organisms of the sample and all the detritus measuring in diameter

2 μ and above. The remainder, consisting of the phytoplankton and detritus in which the principal nourishment of the Cladocera is to be found, was poured into glass tubes with a fluid containing about 4 p. c. of formalin, and was subsequently weighed in the manner described below. In this way, an estimate was arrived at of the contents per litre of nutritive material contained in the castle lake, on the day the sample was collected¹) (Table 3, p. 260—261, vide also below under *b*).

b. If the counting of the 4 crustacea samples showed that one or more of the species were distributed so as to leave a considerable difference between the numbers of individuals caught at the various depths, it became desirable to obtain information in regard to possible corresponding differences in the quantities of nutriment derived from the waterlayers in question. It would then be possible to decide whether any correlation existed between the vertical distribution of the foodmaterial and the Cladocera. All 4 phytoplankton samples were, in that case, filtered in a Kolkwitz apparatus through a nitrocellulose membrane with a maximum pore-width of 2 μ . The crustacea were carefully removed from all of the four lots of sediment, and they were dealt with in the same way as the sediment from the 500 cm³ mentioned above under *a* — that is to say, they were put into glass tubes, weighed etc. In this manner information was obtained about the food material contained in each waterlayer at the time when the quantity of crustacea had also been determined by means of counting (table 2, p. 260—261). From the contents of the 4 water-layers, a comprehensive estimate of the quantity of foodstuff per $\frac{1}{2}$ litre on the day of examination could then be found (table 3, p. 260—261, in which will also be found the terminations mentioned under *a*). — In the case mentioned under *b*, 4 extra samples, in which the plankton was deposited with formalin, as described above, served as material for Mr. NYGAARD's botanical examination.

Weighing gives a better valuation of the quantity of material available as nourishment, than would be yielded by counting the species of phytoplankton, because it includes in the estimation, not only the quantity of allochthonous and autochthonous detritus, but also all the organisms (bacteria and others) that are bigger than the maximum pore-width of the filter (2 μ). In view of the present, not too minute, knowledge of the effective nourishment of the filtering zooplankton organisms, this must be considered an advantage. Already in 1908 WESENBERG-LUND (Plankton Investigations of the Danish Lakes, p. 279) emphasises the fact that the freshwater zooplankton "has to a very great extent to live upon detritus in the northern, temperate lakes". At a later date, E. NAUMANN and other writers have laid stress on the important part that dust-fine detritus and bacteria must be supposed to play as sources of nourishment (1918—25). In shallower waters, rich in foodstuffs, with a summer temperature of more than 16 Centigrades — that is, the type to which the

¹) It was not possible to remove the Rotifera. With the exception of a few spring samples they are probably so few in number that their influence on the weight may be looked upon as negligible in this connection.

lake of Frederiksborg castle belongs — NAUMANN is, however, of opinion that the zooplankton is “von dem Phytoplankton direkt abhängig, wenn auch oft in einer ganz indirekten Weise, indem das Phytoplankton wahrscheinlich minder an und für sich als vielmehr eben als Detritusproduzent — und zwar theils aber auch erst bei ihren Absterben — von einer grundlegenden Bedeutung wird.” (NAUMANN 1918, p. 39).

A method which, like the one mentioned, determines not only the quantity of nutriment found in the shape of organisms, but also that represented by detritus is, therefore, preferable. The nitrocellulose membrane used as a filter has, as already mentioned, a maximum pore-size of 2μ : for technical reasons, a still smaller one could not be chosen. The advantage gained by using this size of pores lies in the fact that besides larger organisms and particles the so-called nannoseston is retained, the minimum size of which is estimated at about 5μ and which includes small protists, certain bacteria and finer detritus; in addition, a good deal of ultra-seston, of a size smaller than 5μ , is also included. — Another argument that may be advanced in favour of weighing rather than counting is the avoidance of errors due to the fact that the same sort of phytoplankton may often vary in size at different times. By weighing rather than space-measuring the phytoplankton plus detritus one also avoids the error caused by the circumstance that loosely built, voluminous but relatively unsubstantial organisms during certain months dominate the phytoplankton. An instance of the appearance of such organisms is given on p. 243.

Before the weighing process commenced, the clear, formalin-containing fluid standing above the sediment in the glasstubes was removed by means of a pipette. After rinsing with distilled water and renewed deposition, the liquid was again removed, and the samples were then cleaned of any trace of formalin. They were then left to dry in a thermostat at about 80° C. After being thoroughly dried and allowed to cool, the tube with the material contained therein was weighed, and the tube was then thoroughly cleaned and again weighed. The difference between the first and second weighing gives the contents of phytoplankton and detritus of the sample in question, which in the following pages, for the sake of brevity, is merely called the quantity of phytoplankton.

A number of the most remarkable facts have been illustrated by means of diagrams, which more easily than a table draw attention to the more important features of the distribution. In the graphical representations showing the vertical distribution of a species in a column of water (vide plate I), the usual spherical curves have been employed in a manner similar to that used by RUTTNER (1914, p. 277) and many others, as first suggested by LOHMANN (1908, p. 192). The number of individuals in half a litre of water has been used as a basis for the representation, and from this the radii in the corresponding spherical volumina have been calculated, using the formula $V = \frac{4}{3} \pi r^3$ or $r = \sqrt[3]{\frac{V}{4} \pi}$ being supposed to equal 3

(V = the number of individuals in $\frac{1}{2}$ litre of water, r = the radius of the sphere). The calculated radii are placed along the abscissa, the value 1 being made equal to $\frac{1}{2}$ cm.; the depth of the lake is indicated along the ordinate (1 metre represented by 1 cm.). — Spherical curves, which render the maxima in a more gradual and descriptive manner than the linear curves, have, besides, been mentioned so often that in regard to their qualities and construction it is only necessary — in addition to the above authors — to refer to COLDITZ (1914, p. 629), BIRGE & JUDAY (1922, p. 58) and UTERMÖHL (1925, p. 90).

In the diagrams showing the contents of crustacea at the surface and at the bottom, by day and night (plate II), and in the text-figures showing the periodicity of the animals, linear curves have been used to emphasize the difference in the distribution. For purposes of greater emphasis, UTERMÖHL, too, often prefers the linear representation, and even LOHMANN himself sometimes uses this mode of illustration.

The Lake of Frederiksborg Castle and its Scale of Temperatures.

The lake of Frederiksborg castle is longest in the direction north—south and here measures about 700 metres; the width is just over half that size. The castle of Frederiksborg cuts a few small portions off from the western part of the lake, and these are connected with the lake proper by canals. The area of the lake is about 0.22 km.², calculated in accordance with the Ordnance Survey¹). Its greatest depth is 3—3 $\frac{1}{2}$ metres, and great parts of the lake only have a depth of 2 and 3 metres. The collecting of samples took place in the middle of the lake, S.E. of the castle, where the depth, even in summer, when the water is low, made it possible to collect a sample at a depth of 3 metres without scraping the bottom.

At its southern end, the lake receives a covered influx from the Teglgaard Sø and is, in its turn, depleted by a similarly covered outlet to Pølaa, which flows into Arre Sø. The water, which is somewhat soiled by waste water, has late in the summer a very conspicuous water bloom, caused by a great maximum of Cyanophyceae. On still days, these algæ form, on the surface of the lake, a kind of form that sometimes assumes a bluish colour, and near the shore the surface may be covered by large oily stains; when this is the case, the water spreads a most offensive smell.

The proportion of oxygen has in summer on a few occasions been found to be fairly large, namely 9.3 cm.³ per litre, both at the surface and at the bottom. Similarly, a rather great proportion of lime was found after filtering through *Ca*-free filter: 68 mgr. *CaO* per litre, (GUNNAR NYGAARD, April 1928).

¹) H. MICOLETZKY has erroneously stated the size of the lake to be about 200 hectares (= 2 km.²) (1925, p. 67).

Some tests made at noon during the spring and summer in order to determine the reaction of the water show an alkaline reaction; the following figures show a growing pH value from spring to summer:

March	12th	1927	$pH = 8.3$	Temp. 5.5	
April	2nd	—	— = 8.3	— 6.8	
May	18th	—	— = 9.1	— 12.0	
June	1st	—	— = 9.2	— 16.0	
	—	15th	—	— = 9.1	— 17.0
	—	28th	—	— = 8.5	— 15.0
July	7th	—	— = 9.2	— 22.0	
	—	21st	—	— = 9.1	— 20.0
August	15th	—	— = 9.2	— 20.0	

The comparatively low pH value on June 15th was measured at a time of violent showers and a strong wind.

The margins of the lake are partly artificial, especially on the northern side, where there is a stone setting. There is but a slight development of reed-marsh, chiefly along the north-eastern shore, where there is a narrow belt of *Phragmites*. Plants with floating leaves are still rarer; only in a few places may one find a little *Polygonum amphibium*. Submerged plants are also rather scarce; yet in places *Potamogeton crispus* abounds and in others *Myriophyllum* occurs.

In the following, the most important temperature conditions in the lake of Frederiksborg castle will be stated, and later, when mention is made of the zooplankton species, the significance of the temperature for these organisms will be dealt with.

The castle lake belongs to FOREL's group of temperate lakes, with water temperatures that in summer exceed 4 centigrades and in winter are below this figure. When such temperate lakes have been covered with ice in winter, and this melts in the spring, the surface water is rather quickly warmed up to 4° C, the temperature at which its specific gravity is greatest. Consequently, convection currents are formed, causing the colder water from the bottom to rise to the surface and be heated in its turn to 4° (the homotherme of spring). Subsequently, the surface water attains a higher temperature than 4° and becomes lighter. At this point the deep temperate lake enters into the period of summer stagnation, its longest period, characterised by a direct division in horizontal layers, with falling temperature from the surface to the bottom. The fall of temperature is particularly pronounced in the so-called thermocline, which marks the limit of the daily fluctuations of temperature. During this period we find, therefore, warmer and lighter water above colder and heavier.

The conditions outlined above refer to fairly deep, temperate lakes; yet similar observations have been made in a shallow temperate lake, COLDITZ having found

in Mansfelder See, which has a depth of 7 m., a summer stagnation lasting from the end of May till the end of July. All through this period, on every day of observation, a thermocline was, with great regularity, found between 1 and 3 metres below the surface, with a difference of temperature from 3.5° to 0.7° , while the difference between the other depths was smaller. Notwithstanding the great biological significance attributed to this summer stagnation, the author says: "Durch heftige Wellenbewegungen und grössere Niederschläge kann plötzlich eine thermische Ausgleichung der Wasserschichten eintreten". (COLDITZ 1914, p. 531).

Now how does the castle lake with its depth of only about 3 metres react in respect of this period of summer stagnation?

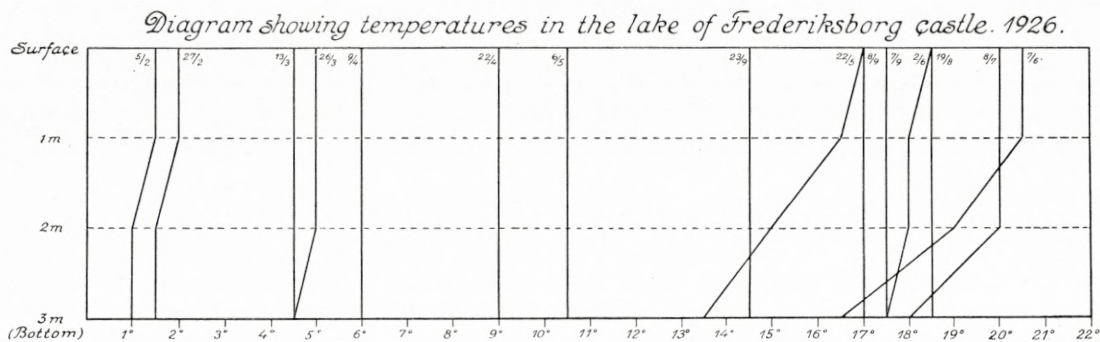


Fig. 1.

A consideration of table 1 (vide p. 260—261) will clearly show that while the water is duly heated in the spring and during the high summer temperatures lasting till the month of September, there is, in the castle lake with its depth of only about 3 m., no such thing as a period of stagnation with a settled state of warmer water above colder — the so-called "Temperaturschichtung". For, it has often happened that the same temperature was found to prevail through all the water-layers examined, for instance on $15/6$ 25, $25/6$ 25, $22/4$ 26, $6/5$ 26 and $19/8$ 26. At other times a greater or smaller diminution of temperature from surface to bottom has been recorded. There is, however, no definite spring-layer, conditions being quite erratic, as shown by the statement given in the table of the differences of temperature between the surface and a depth of 1 metre, between 1 and 2 metres and between 2 and 3 metres beneath the surface (p. 261—262). The differences of temperature may occur solely in the upper water-layer ($25/5$ 25), in the middle layer ($28/7$ 26) or in the bottom layer ($18/7$ 25 and $26/8$ 26). They may also be distributed throughout the layers examined ($19/8$ 25, $22/5$ 26) or be found in 2 layers and be missing in the 3rd ($11/6$ 25, $7/6$ 26 and $21/6$ 26) — owing to the varying influence of wind and hot sun, the castle lake is, therefore, during the spring and summer, in a constant state of change, in which uniform temperatures in all water layers alternate

with temperatures that decrease from surface to bottom without regularity. Text-fig. 1 shows such temperature profiles from 1926.

As might be expected, the maximum differences of temperature between surface and bottom do not amount to much — the greatest difference found is 4° ($^{20/7}$ 25 and $^{7/6}$ 26). More frequently, there was a difference of 2—3 degrees; they occur on still, hot days, exclusively in the summer. At other seasons there was at most a difference of 1° . That there are never very great differences between surface and bottom, will easily be gathered from text-fig. 2, which illustrates the series of temperatures registered at the surface and at the bottom in 1925 and 1926.

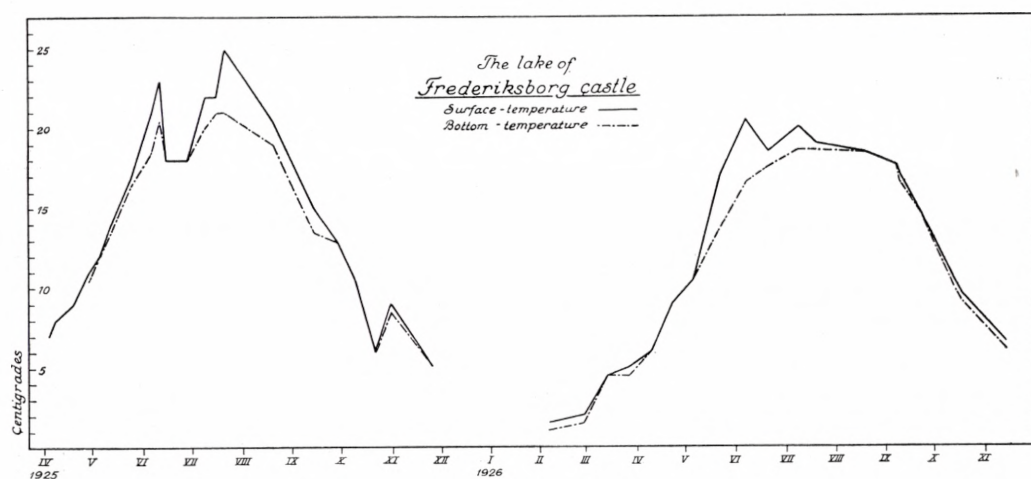


Fig. 2.

When the water is cooling down, during the autumn, measurements taken in September and later nearly always show the same temperature at all levels; only on rare occasions is there a slight difference. Both the autumn gales and the convection currents, which carry the cooled, heavier water of the surface downwards, may contribute to produce this equalisation of temperature.

During the greater part of February 1926, the castle lake was icebound and only thawed for a few days. The 2 records then taken showed the upper water-layers to be of a slightly higher temperature than the lower ones (See table 1, p. 260—261). As we are dealing with temperatures under 4° C, the slightly warmer surface water is also relatively heavy, though it has not yet sunk to the bottom, and for this reason, the equilibrium had not been established yet when the temperature was measured.

With reference to the above-mentioned summer conditions of temperature, there may be occasion to make the following remarks: WOLTERECK is of opinion that not only is the ecological significance of the seasonal variation of the Cladocera to be found in the fact that the animals, thanks to the flattened swimming courses, are enabled to spend the summer in layers that are well stocked with food,

but he also thinks that the majority of a lake's daphnia population thus avoids the colder water beneath the thermocline (1913, p. 522). WOLTERECK, however, finds conditions somewhat complicated, and his cogitations in this connection have been discussed by WESEBERG-LUND (1926, p. 179). — E. WAGLER seems to see the matter in a clearer light. He does not, like WOLTERECK, attach much importance to the chance enjoyed by the Cladocera of remaining in water-layers well stocked with food: "Ich glaube nicht, dass WOLTERECK mit seinen Hypothesen Recht hat. Die Abflachung der Schwimmbahn erleichtert weder das Auffinden der Nährschicht noch schützt sie vor der Berührung mit dem Wasserspiegel (WAGLER 1927, p. 298). To him "scheint aber ein anderes Grund massgebend to sein", namely the reason

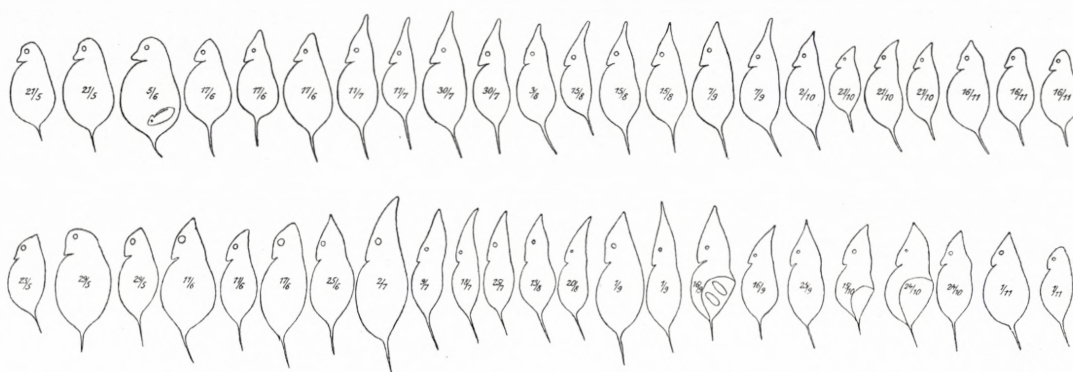


Fig. 3. *Daphnia cucullata* G. O. Sars. The upper series from the lake of Frederiksborg castle, the lower series from Fure Sø. (After C. Wesenberg-Lund).

that the animals, on account of the flattened swimming courses, avoid the danger of sinking from the warm epilimnion into the cold hypolimnion. (WAGLER 1923, p. 300). WESEBERG-LUND arrives at a quite similar result on the basis of his fundamental starting-point in the buoyancy theory (1926, p. 143).

The observations made in the lake of Frederiksborg castle cannot, of course, either confirm or weaken the opinions regarding the importance to the Cladocera of great vertical changes of temperature. As explained above, there are only small and constantly changing differences of temperature in this lake, there is no cold hypolimnion — consequently there is no danger of the Cladocera being submerged therein. Yet the species of *Daphnia cucullata* living in this lake has such a marked seasonal variation that WESEBERG-LUND, who has minutely illustrated and described it (1926, pp. 128—134), considers it most probable that it would be impossible to distinguish the species from that existing in Fure Sø, our deepest lake. (See fig. 3).

The vertical Distribution and Periodicity of the Quantity of Phytoplankton.

Before dealing with the vertical distribution and periodicity of the separate species of crustacea, it may be expedient to give a short review of these conditions as regards the quantity of phytoplankton. As mentioned on p. 235, the vertical distribution of the phytoplankton of the lake has been measured on those days of investigation when the position of the crustacea in the levels of the water has rendered such information desirable. In table 2, p. 260—261, will be found the results

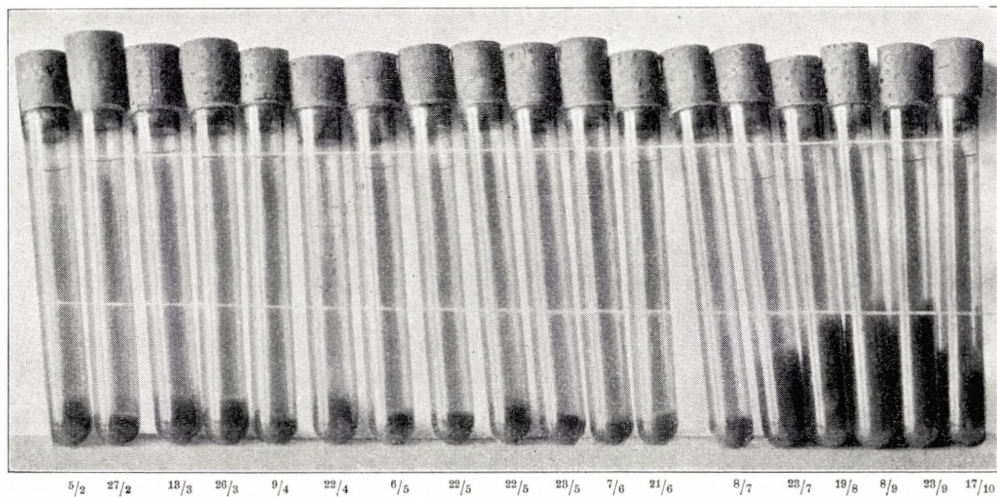


Fig. 4. Phytoplankton samples from the lake of Frederiksborg castle, 1926.

of these measurements. As will be seen, the phytoplankton of the castle lake does not, taken as a whole, form any reliable "Nahrungsschicht" during the six summer months. Sometimes the maximum will occur at one level, sometimes at another; sometimes the difference is but slight, at other times very considerable.

On certain days, several series of hauls have been taken at various hours throughout the day and night. They do not seem to indicate the occurrence of any regular "Dämmerungswanderung" or "Nachtwanderung" of the phytoplankton as a whole, with which the wandering of the crustacea might be connected. RUTTNER, too, is of opinion that vertical wandering has not, up to the present, been unmistakably observed in any species of phytoplankton (1914, p. 309), and COLDITZ has arrived at a similar result as regards Mansfelder See (1914, p. 606). For a few groups other information is, however, available. LANTZSCH (1914, p. 689), for instance, states that the Flagellata show evidence of active, phototactical wanderings. UTERMÖHL (1925, p. 191—218) says the same thing about a series of species provided with flagella. — After a few hours, the quantity varies at a certain depth, or in all 4

samples, and the difference is often considerable. This, however, is not surprising, since the variation in the quantity of the waterbloom may at times indicate the rapid alterations caused by wind and current when, for instance, water containing large masses of Cyanophyceae is washed into the lake from canals and bays near the castle.

Table 3, p. 260—261 shows the main points in the yearly variation of the quantity of phytoplankton. From the end of November 1925 till the beginning of February 1926, the quantity has decreased, and it reaches its minimum at the end of February. In the course of March and April, the quantity increases, and at the end of May a spring maximum occurs, followed by a summer minimum in June. This minimum is, however, not nearly so small as the winter minimum. In the course of July and, more especially, of August, the quantity increases once more and culminates at the beginning of September in a maximum far greater than that of the spring. Decreasing during the month of October, the quantity of phytoplankton, in November, reaches a level similar to that of the previous year. (In the graphic representations in text-fig. 5—10 the quantity of phytoplankton is measured per litre in the same way as the quantity of crustacea).

The illustration, text-fig. 4, shows glass tubes from 1926, each containing the quantity of phytoplankton from half a litre of water. As will be seen, the great autumn maximum, which is mainly due to the Cyanophyceae especially *Microcystis*, is even more remarkable for its volume than for its weight.

The vertical Distribution and Periodicity of the Entomostraca.

Daphnia cucullata G. O. Sars (table 4, p. 262—263).

Vertical distribution. From June or July till about the middle of October, the species is so abundant that the number of individuals found in the samples is sufficient to demonstrate the vertical distribution. At other seasons, the quantity is insufficient for this purpose, numbers being then so small as to render it impossible to decide whether the difference between the hauls taken at various depths is merely accidental, or whether it may be trusted to be genuine.

By means of the numbers given in the table or, more easily perhaps, by studying the spherical curves given on plate I (figures 1—18), the following chief features in the distribution of *D. cucullata* will be observed. The rather erratic distribution found in the daytime is first dealt with, and subsequently some remarks are made regarding conditions prevailing in the evening and during the night.

1. The layers of water immediately under the surface, in the daytime, are often poorer in individuals than other layers (fig. 1—7). This sparsely populated

layer seems to be fairly shallow; already one metre under the surface, the organisms are generally found in greater abundance.

2. On some days, a distinct maximum will occur at certain levels (fig. 1, 4, 6, 7, 8, 9, 10, 11 & 12). Nevertheless, no definite "Wohnschicht" has been established, seeing that the maximum may occur at the surface (fig. 10) and at depths of 1 metre (fig. 9), 2 metres (fig. 8), and 3 metres (fig. 11 & 12) below the surface.

3. The absence of a "Wohnschicht" is further proved by the fact that on other days there may be but slight variations between the population at different levels (fig. 13 & 15). Also fig. 2 and 5 show an even distribution; only the surface seems to be shunned.

In other words, the only rule determining the vertical distribution of *D. cucullata* in the lake of Frederiksborg castle in the daytime during the summer months appears to be, that the layers just beneath the surface often contain a considerably larger number of animals than the lower strata. Apart from that, the distribution may be almost uniform in all layers or with a maximum at any depth — conditions being probably largely influenced by wind currents and light.

If a comparison is drawn between the vertical distribution of the quantity of phytoplankton contained in the lake (table 2, p. 260—261) and that of the *D. cucullata* (table 4, p. 262—263), it will be seen that in some cases the maximum of *D. cucullata* is found in the same layer of water in which the greatest quantity of phytoplankton occurs; but this is merely accidental and does not establish any rule. On the contrary, the largest number of individuals of the *D. cucullata* is just as frequently found to occur at any other depth. Nor can the lake of Frederiksborg castle claim to possess any special "Nahrungsschicht", in which the species exists more abundantly than elsewhere.

The curve fig. 4, plate II gives an idea of the varying numbers of individuals found at the surface in the course of several consecutive days and nights. The same figure also shows the variations observed in the bottom population during the same days and nights — (the corresponding numbers will be found in table 4). The curve drawn for the surface shows a distinct resemblance between the different days, in as much as it indicates higher values for observations made just before sunset than for hauls taken in broad daylight. It is obvious that, when twilight sets in, a wandering of individuals takes place towards the upper layers of water. That this rise towards the surface occurs in a greater or smaller degree on the different test evenings, is clearly shown by the curve. — The curve relating to the bottom population shows minima during the night.

Even when the rising process causes a considerable maximum to occur at the surface, it does not, however, deplete the lower levels, a fact which is clearly illustrated in figs. 16, 17 & 18, plate I.

Periodicity (text-fig. 5). At the time of the first counting, $\frac{25}{6}$ 25, each litre was found to contain on an average barely 5 individuals, but the number increased

steadily till $20/7$, when it was 4 times the previous average. A still more marked increase took place in the course of the following month, reaching a maximum of 176 individuals per litre on August 19th. After that numbers declined rapidly and

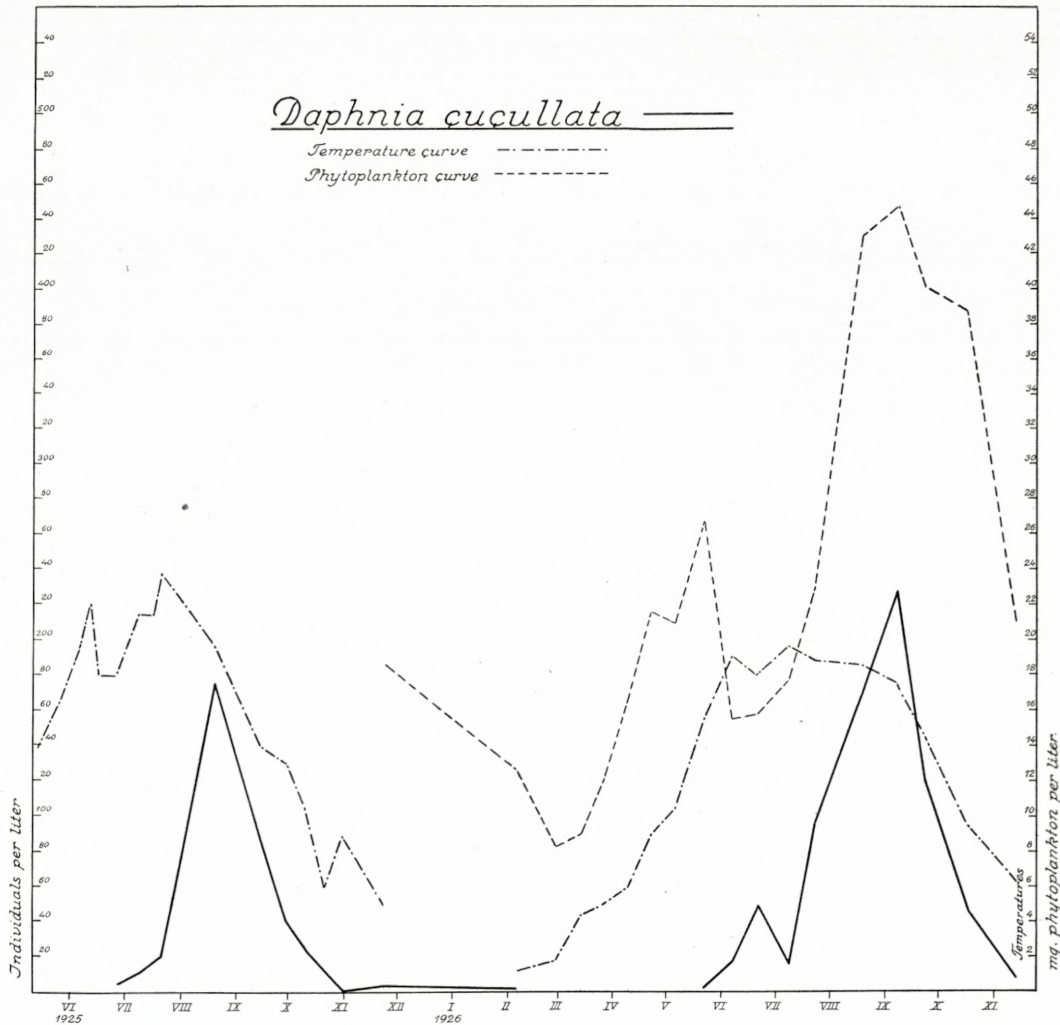


Fig. 5.

more or less regularly during the months of September and October, falling to a minimum of 3—5 individuals per litre in November. Having wintered in small quantities under the ice the species slowly increases during the spring in the main due to hatched ephippia; these ephippia have been produced in large quantities during the intensive sexual period of the autumn and in still weather might be found by the thousand, floating in the surface of the water. They are gradually, by wind and stream, carried to the shore and may there form actual coatings on

stones and fragments of plants. From this wintering place, the water layers of the lake are stocked in the spring, more especially in the month of April, with freshly hatched young animals.

By the end of May, the average number of *D. c.* is still only 2—3 individuals per litre, but through June, July and August the number steadily grows, until it culminates, at the beginning of September, in a maximum of more than 200 individuals per litre; simultaneously, the sexual period starts. Soon after, a rapid decline commences, like the previous year, and about the middle of November the average is only about 7 individuals per litre.

In dealing with the periodicity of *D. c.* in the lake of Frederiksborg Castle, WESENBERG-LUND states (1926, p. 134) that "the periodicity is the same as in larger lakes", in regard to which we know "that the maximum of the species occurs at the end of the summer half-year, from the end of July until October; in some lakes the maximum ceases already in Oct. — — —" (WESENBERG-LUND 1908, p. 181).

The figures arrived at in regard to the lake in question, fully bear out the above statement. They also show the very definite aspect of the maximum. During the period from the end of July till the beginning of October, in which *D. c.* is abundant, a very sudden increase and decrease in quantity may be observed; in the course of 2—4 weeks, numbers may be doubled or halved. The rule has, furthermore, been confirmed that the highest point of the maximum coincides with the highest temperatures of the lake (WESENBERG-LUND 1904, p. 170). The latter, as regards the castle lake, are about 18—24 centigrades, and it is just during such hot periods that the maxima culminate. The curve (text-fig. 5) also shows, however, that both in 1925 and 1926 the point of culmination only occurs at the very end of the hot period, with a day temperature above 18 centigrades, the temperature of the lake having then been high for some 2—3 months. — Finally, we would draw attention to the simultaneous increase in the quantity of phytoplankton and the number of individuals of *D. c.* in July and August 1926, as well as the simultaneous culmination in September. —

In a consideration of the selective value of the early stages of variation, WOLTERECK also meditates (1921, p. 71) on the number of *Daphnia* "in einem kleinen nur einige Meter tiefen See" — like our castle lake — and arrives at the conclusion that an immense number of *Daphnia* must perish. In support thereof, he states, that in spite of a very vigorous reproduction "ist in Wirklichkeit im July und August die Zahl der Daphnien entweder gar nicht oder nicht wesentlich grösser, jedenfalls nicht zehnmal so gross als im Juni". — The research carried out in the castle lake, nevertheless, shows the number during the August maximum in 1925 to be at any rate 35 times as great as in June of the same year; in 1926 it is, at the end of August, about 20 times larger than at the beginning of June. It is, therefore, obvious, that a selection as intense as that suggested by Woltereck cannot take place — not even if it is taken for granted that his supposition of the very intensive reproduction is in agreement with the actual facts in nature.

D. brachyurum does not winter as a plankton-organism. At its reappearance in the plankton in the spring of 1926 it was so rare that not until the end of June was it possible to catch it with the water hauler. During the month of July the number increased suddenly and, as in 1925, a maximum was observed at the end of the month. The population then averaged 14 individuals per litre. After that, the number declined so rapidly that not even 1 individual per litre could be found by the end of August. The species may, therefore, be said to have a very brief and marked maximum occurring about the middle of the period characterised by the highest temperatures occurring in the lake — that is to say, some 4—6 weeks before the maximum of the *Daphnia cucullata*. At the time when *D. b.* culminated in 1926, the quantity of phytoplankton was in process of increase, and the *D. b.* maximum disappeared while the phytoplankton continued to increase, and the temperature remained at about 18°.

In regard to the habits of *D. brachyurum* in our larger lakes, WESENBERG-LUND states (1904, p. 161) that "Maximum is reached at the highest temperature of the water and is greatest from the middle of July till the middle of August". — As shown above, the result arrived at during the investigation carried out in the castle lake is in fairly accurate agreement with this statement.

Chydorus sphaericus O. F. Müller (table 6, p. 262—263).

Vertical distribution. *C. s.* shows a marked difference in number at the different depths. Most frequently, the day-distribution shows an increase of individuals from the surface towards the bottom (fig. 19—26, plate I). Here, near the bottom, one may sometimes find twice as many individuals as at a depth of 2 metres. Less frequently, a maximum occurs at a depth of 2 metres (fig. 27—31, plate I), and very rarely it will appear in the daytime at a depth of 1 metre (fig. 32, plate I) or at the surface (fig. 33, plate I), or it will be replaced by an approximately even distribution (fig. 34, plate I).

The commonest vertical distribution, with the greatest number near the bottom and the smallest number at the surface is replaced at night by a more even distribution at all levels. This will easily be seen if a comparison be made between fig. 22 and fig. 35, showing, respectively, the conditions prevailing at noon and at midnight; see also fig. 25 and fig. 36 (plate I). — The curves fig. 2 & 6 plate II, showing the number of individuals to be found at the surface at different hours during several consecutive days and nights, will convey an idea of the far greater frequency with which *C. s.* appears at the surface at sunset and during the night than in the daytime.

A comparison between the vertical distribution of *C. s.* and of the quantity of phytoplankton (tables 6 & 2) will show that an accumulation of *C. s.* in certain layers of water does not depend on the occurrence of abundant quantities of phytoplankton at that particular depth. Simultaneous maxima at the same level only occur very occasionally.

C. s. has been observed as a plankton-organism in several of our larger lakes. In other lakes it is missing in that capacity. Where it appears "as a plankton-organism, it is a surface form, apparently missing at the lower levels". (WESSEN-

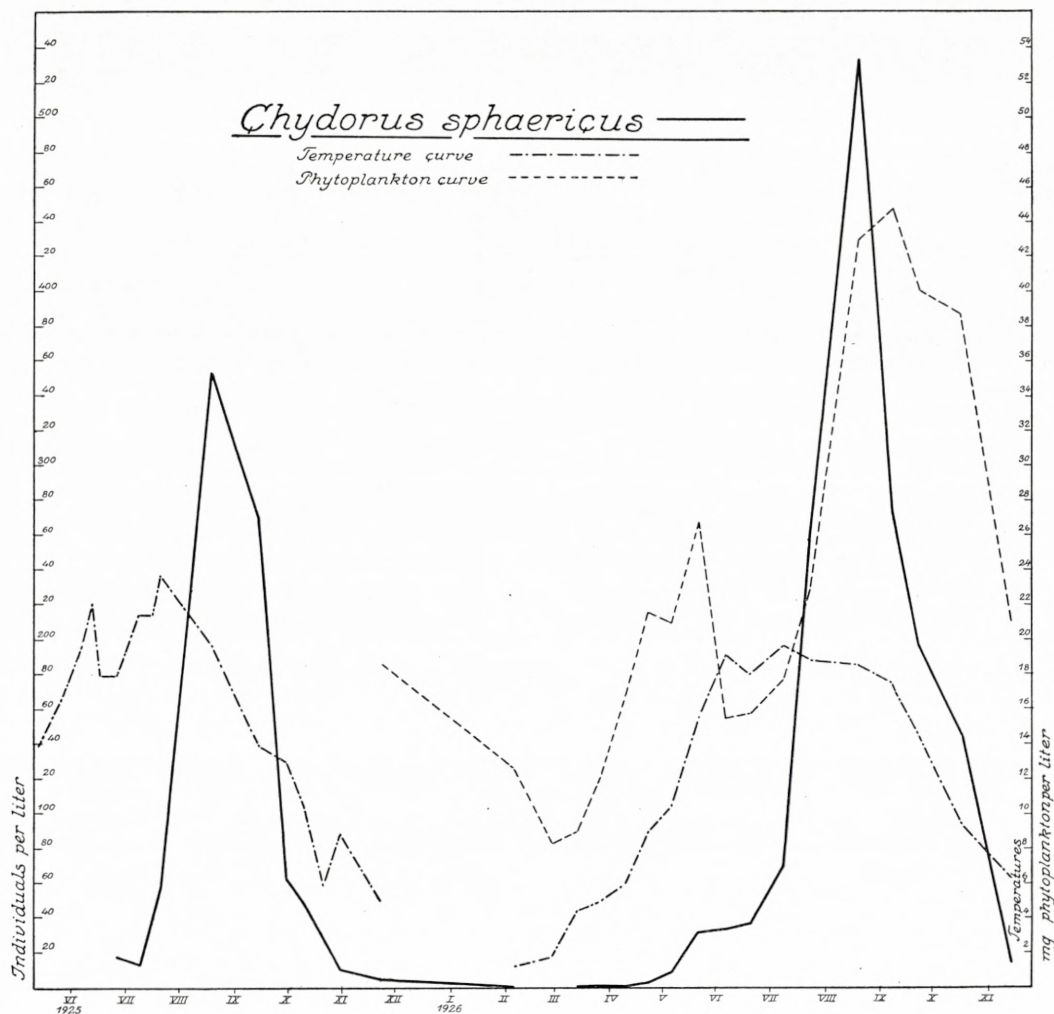


Fig. 7.

BERG-LUND 1904, p. 178). We find, therefore, a marked contrast between the condition prevailing in our great and deep lakes and the vertical distribution in the shallow castle lake, with the above-mentioned occurrence of organisms at all levels, most frequently increasing in number from the surface towards the bottom.

Periodicity (text-fig. 7). At the end of June and the beginning of July 1925, *C. s.* averages about 10—20 per litre. But at the end of July, at a temperature which for about 2 months has been above 18°, the number quickly increases, at-

taining in the month of August the great maximum of about 350 per litre. In the course of September and October, while the temperature gradually falls to some 6—8°, the number of *C. s.* also declines to about 10 per litre, and by ²³/₁₁ it has fallen still lower, being then about 5 individuals per litre.

C. s. winters in small numbers. As early as March 1926, at temperatures of 4—5°, a few individuals were taken with the waterhauler. After that, the number rises — rapidly from April till May, more slowly in June, and in July again very quickly — culminating in August with more than 500 individuals per litre, a still greater number than that recorded the year before. Through September, October and November the number again declines, till it reaches a minimum similar to that of the previous autumn. The curve of periodicity consequently shows a similar course of development for both years of research.

As mentioned above, there seems to be a considerable difference between the vertical distribution of the species in the lake of Frederiksborg castle and that of our deeper lakes in which it occurs, but in regard to its seasonal distribution, no such difference has been observed. The species has, for instance, been found to be present in very large numbers in Skanderborg Sø, Mos Sø and Jul Sø about the end of July and the beginning of August. It is only in Viborg Sø that the maximum occurs somewhat later, in October (WESENBERG-LUND 1904, p. 178).

When the maximum reaches its highest point in the lake of Frederiksborg castle, the day-temperature of the water has, as indicated, for a couple of months been about 18 centigrades or more, the maximum therefore culminates at the end of the hot season. In 1926, the rapid and heavy increase of the number in July and August is seen to be simultaneous with a quick and vigorous increase in the quantity of phytoplankton, this increase being mainly due to the growth of the Cyanophyceae. This coincidence has also been observed and pointed out by earlier investigators. Already BIRGE, who recorded a somewhat varying periodicity for *C. s.* during several consecutive years in Lake Mendota, is of opinion "that these periods of abundance are correlated with the abundance of *Anabaena* and allied algae in the water" (1897, p. 342), and APSTEIN states that the species occurs pelagically in lakes where *Chroococcaceae* (*Clathrocystis*) are plentiful, but not in his so-called *Dinobryum*-lakes (1896, p. 95—96). Dealing with the conditions prevailing in large Danish lakes, WESENBERG-LUND writes (1904, p. 178): "Taken altogether, one may say that this phenomenon (the appearance of large quantities of *C. s.* in the pelagic region) is rarest in deep, cold and clear lakes (Fure Sø, Esrom Sø, Tjustrup Sø, Hald Sø), but that it may be very marked in lakes with high *Cyano-phyceae maxima* (Viborg Sø, Jul Sø)".

WEIGOLD has arrived at a result, in regard to periodicity, that differs considerably from those quoted above. Taking all the Saxe localities examined under one head, he mentions no less than 4 annual maxima for the species: in April (the greatest), June, August, and November (1910, p. 34). It may be doubtful whether more precise methods than those employed by WEIGOLD would really confirm a

periodicity of this description. In any case, there is no indication of several consecutive maxima in the course of one single year in the lake of Frederiksborg castle.

Bosmina longirostris (O. F. Müller) (table 7, p. 264—265).

Vertical distribution. It is only for a couple of months — May and June in 1926 — that *B. l.* occurs in sufficient quantities to make it possible to define its vertical distribution; but during those 2 months it forms a tremendous maximum. During the day, *B. l.* seems as a rule to be most abundant near the bottom (fig. 37—40, plate I). Towards evening and during the night, a great many of the animals ascend towards the surface, without, however, leaving the other levels quite deserted (compare fig. 38 to fig. 41 & 42, plate I). Fig. 3, plate II plainly shows that upon examinations on $^{22/5}$ and $^{23/5}$ 26, the surface was most thickly populated in the evening, and that the bottom shows a distinct minimum at night.

There is no sign of any connection between the vertical distribution of *B. l.* and the quantity of phytoplankton, respectively, in the sense that the species should occur most plentifully at the levels containing the greatest quantity of phytoplankton (tables 2 and 7).

Periodicity (text-fig. 8). In 1925 *B. l.* was only found most sparingly in the plankton of the lake from June till October. The number was so small that some of the test collections taken with the waterhauler contained no specimen at all of the species. By November it had risen to about 8 per litre, and in samples from February 1926 a similar number was observed. A small minimum may perhaps be said to occur in March, but in any case the number increases in April, and in May the development is so extremely swift that by $^{22/5}$ the number was 50—60 times as great as that noted on $^{22/4}$, that is to say, some 950 individuals per litre — or about 1 per cm^3 . From this great spring maximum the quantity abruptly decreases during June, being at about the same low level in July, August and the beginning of September as in the corresponding months of the previous year. And once more an increase takes place during the autumn, occurring, however, somewhat earlier and reaching greater values in 1926 than in 1925.

The said periodicity corresponds exactly to the conditions observed in our larger lakes, where *B. l.* usually attains a maximum that may be exceedingly high, in May and the beginning of June. After that, it suddenly disappears from the pelagic region being, as a rule, entirely absent until the autumn, when it reappears in small numbers (WESENBERG-LUND 1904, p. 177); this author also states that in the central regions of small lakes, the species shows different habits, being present in large numbers all the year round.

The rapid growth in April and May, culminating in the latter month, and declining in June, is contemporary with a similar increase and decrease in the

quantity of phytoplankton; the simultaneous spring maxima of the quantity of phytoplankton and of *B. l.* occur at a temperature of 15° C., before the lake has reached its high summer temperature.

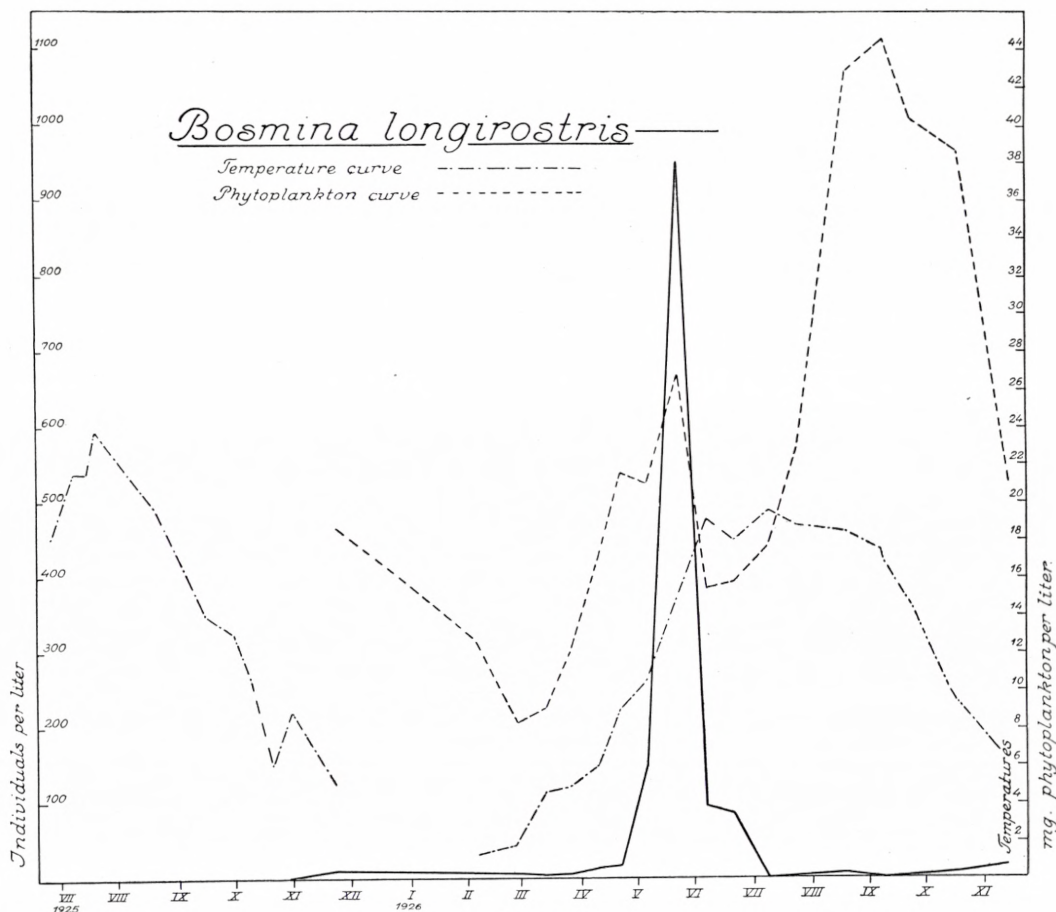


Fig. 8.

Cyclops strenuus Fischer (table 8, p. 264—265).

Vertical distribution. In August 1925, in February 1926, and from May till August 1926, *C. s.* occurred in the samples in such large numbers as to furnish reliable information in regard to the vertical distribution, the result arrived at being that there is no preference for any particular level, not even during the summer months. A maximum may occur at any depth, and sometimes there is a fairly even distribution through all the waterlayers. As a general rule it may be said, that the surface is shunned in the daytime (fig. 43—47, plate I); this comparatively deserted layer is, however, only of an inconsiderable depth.

Towards evening and during the night there is a general ascent towards the

surface. Fig. 1, plate II shows how the population of the surface increases at the said hours, declining once more the following morning. This figure also shows the bottom population to be scantiest at sunset and during the night. The same state

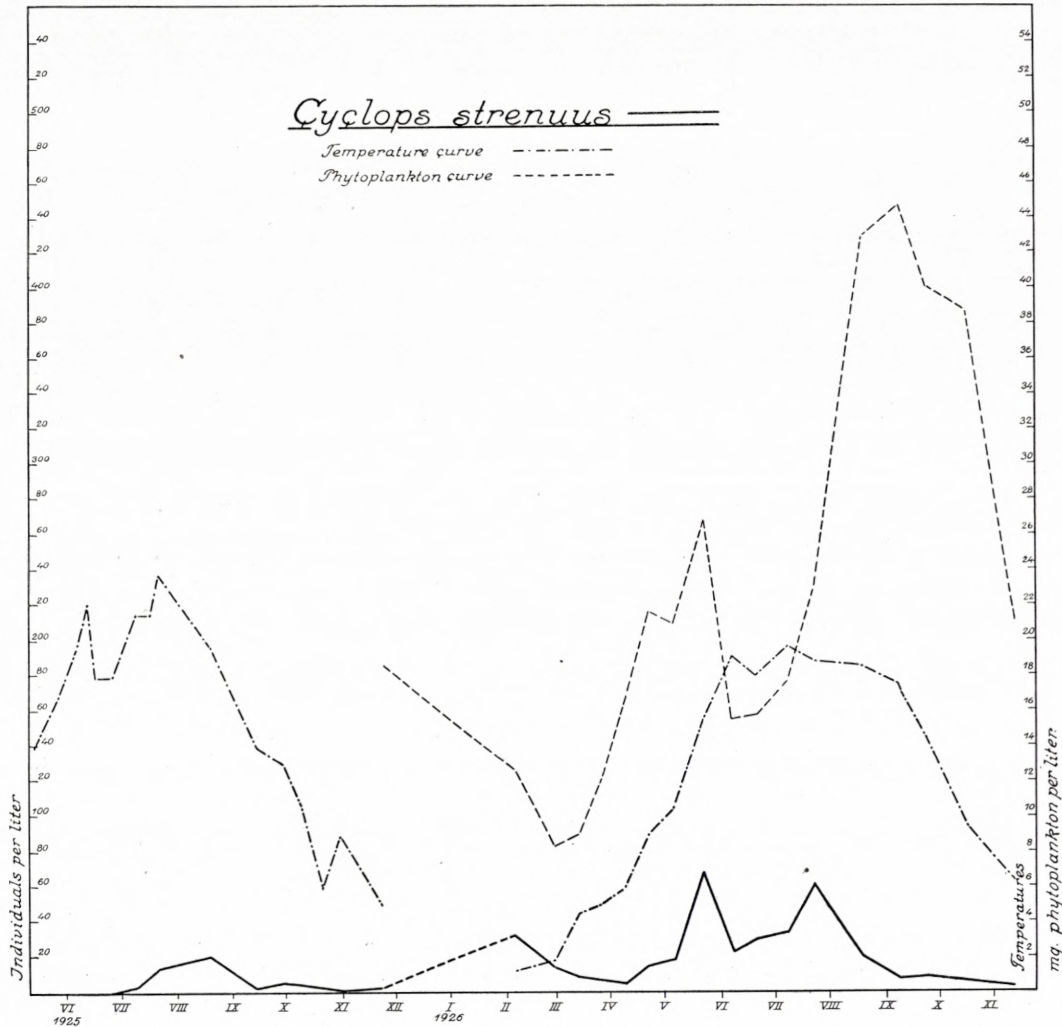


Fig. 9.

of things is clearly illustrated in fig. 43 in conjunction with figs. 48 and 49 (plate I), which also show that, notwithstanding the marked surface maximum at night, the deeper levels are by no means depopulated.

If a comparison be drawn between the vertical distribution of *C. strenuus* and that of the quantity of phytoplankton (tables 8 & 2), it will be seen that *C. strenuus* is no more frequent in the samples collected in the layers that are richest in phytoplankton, than in other layers.

Periodicity (text-fig. 9). In 1925 a maximum was observed at the end of July and in August. In the course of the autumn the number decreased, but by February 1926 it had risen once more, which makes it justifiable to speak of a winter maximum, declining again during March. In the course of April and May the number increased, until an important spring maximum was reached at the end of the latter month, numbering some 60—70 individuals per litre. In June and the beginning of July the quantity was again considerable smaller, but at the end of July a summer maximum occurred of about the same proportions as the spring maximum, whereafter the number decreased during the autumn, as in 1925.

According to WESENBERG-LUND (1904, p. 193) *C. s.* has been found in the pelagic region of our larger lakes, but only plays a prominent part in two of them, namely Esrom Sø and Viborg Sø. In these, a spring maximum has been observed, as in the lake of Frederiksborg castle, but during the hot summer season the species is not, as a rule, abundant, as is the case in the castle lake. Nothing corresponding to the autumn maximum of the great lakes has been observed in the castle lake, but, as already stated, the species is fairly frequent in February.

***Diaptomus graciloides* Lilljeborg (table 9, p. 264—265).**

Vertical distribution. In the months of June to August, *D. g.* occurs in sufficient numbers to make it possible, to gather some information in regard to its vertical distribution. It is obvious that no particular level can be said to be preferred; a maximum may occur at any depth, and sometimes there is an even distribution throughout all levels. This species has not been proved to show any conspicuous inclination to appear in smaller numbers at the surface than elsewhere. Fig. 5, plate II plainly shows the rise in surface numbers that takes place about sunset.

A comparison between the vertical distribution of the quantity of phytoplankton and of *D. g.* (tables 2 & 9) would seem to indicate that *D. g.* is not more abundant at those levels which, at the time of test collections, have been proved to contain larger quantities of phytoplankton, than at other levels.

Periodicity (text-fig. 10). In 1925 *D. g.* was frequent in June, July, and August; in the last named month the largest number was found — 65 per litre. After this summer maximum the number fell during September, being by October reduced to less than 10 per litre. The number now remained almost stationary in November and was still about the same in February 1926, when the ice had so far subsided as to make it possible to recommence sample collection. Subsequently there seemed to be some slight diminution; the number was, at any rate, strikingly small from March till the end of May. By $\frac{22}{5}$ the number of individuals was still only 4—5 per litre, but then it quickly rose. In June, July, and August the species was abundant, as in the previous year; but the maximum reached its highest point already at the end of June and was about of the same proportions as that of 1925. Also

the autumn showed features similar to those already recorded: a rapid fall in September and then no changes in October and November; the number was then, like the year before, less than 10 per litre.

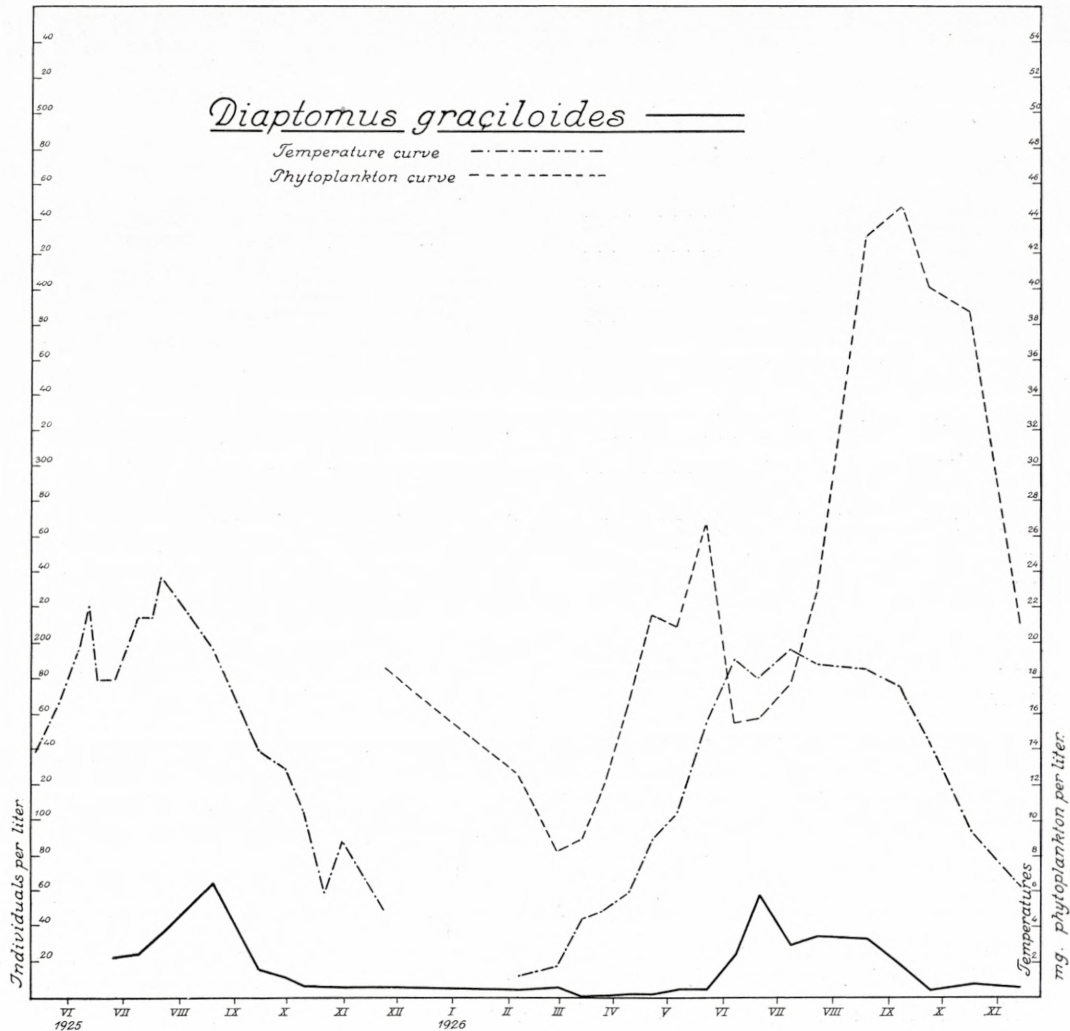


Fig. 10.

The plentiful appearance of *D. g.* from the beginning of June and during the subsequent summer months is in exact agreement with conditions observed in our larger lakes, Esrom Sø, Sorø Sø, Tjustrup Sø and Hald Sø, where — after a very sharply defined sexual period in March—May — large numbers of young animals appear in the plankton during the summer (WESENBERG-LUND 1904, p. 147).

Concluding Remarks.

It will be clearly seen from the above description of the periodicity of the Cladocera, as well as from many other similar works, how marked are the maxima that occur in the career of these animals. In the course of a few weeks their number is many times multiplied, only to decrease again in an equally short period. A comparison will show that the values reached by the various species differ considerably. They are here listed in the order indicated by the largest number per litre that has been recorded:

<i>Bosmina longirostris</i>	952	individuals	per	litre	(²²⁻²³ / ₅ 26)
<i>Chydorus sphaericus</i>	355	—	-	-	(¹⁹ / ₈ 25)
<i>Daphnia cucullata</i>	229	—	-	-	(⁷⁻⁹ / ₉ 26)
<i>Diaphanosoma brachyurum</i>	25	—	-	-	(²⁰ / ₇ 25)

For purposes of comparison the Copepodes are quoted as well:

<i>Cyclops strenuus</i>	67	individuals	per	litre	(²²⁻²³ / ₅ 26)
<i>Diaptomus graciloides</i>	65	—	-	-	(¹⁹ / ₈ 25)

In dealing with *Daphnia cucullata* (p. 246) an instance is given of the erroneous conclusions that may be drawn, when the investigator fails to take into due consideration such quantitative conditions in nature — more especially the tremendous variations. In the following lines, another such example is briefly related.

F. K. REINSCH has recently carried out a quantitative examination purporting to show the different distribution of the Entomostrac-fauna in relation to the Macroflora in ponds (1925, p. 253). With a net that had been constructed especially for this purpose and by means of which it was possible to catch crustacea existing on and about definite plants within a certain space, samples were collected at different times in pure belts of *Phragmites*, *Scirpus*, *Chara*, *Potamogeton natans*, *Helodea* etc. Then every species of crustacea found in each of the samples was counted. The thus obtained absolute expressions for the appearance of the separate species of Cladocera on and around a certain sort of plant were then recalculated and converted into relative figures, i. e. percentages of the total number of crustacea.

If now the above-mentioned periodicity of the Cladocera be taken into consideration, with its very high, clearly defined maxima, it will be obvious that such percentages, calculated at different times or from samples collected in different places, are altogether unsuited to illustrate the abundance with which a certain species appears; comparisons in this case would be quite unjustifiable. If, for instance, a certain species occurs in the same or approximately the same number per litre in 2 samples compared, a totally different percentage will nevertheless result if one of the samples be taken during the maximum of another species, and the other sample outside such a maximum. In other terms, the percentages for

one species are entirely dependent on the strong oscillations in the periodicity of the other species. The researches of Reinsch have therefore — as might be expected — already been criticised (V. LANGHANS 1925, p. 481).

As mentioned when the separate species of Cladocera were dealt with, a remarkable coincidence was observed in 1926, between the maxima of the quantity of phytoplankton and those of the Cladocera (text-fig. 5—8). It is least plain in the case of the *Diaphanosoma brachyurum*, although its heavy increase in June—July is simultaneous with a growing mass of phytoplankton. The spring maximum of the *Bosmina longirostris*, on the other hand, coincides to a marked degree with the spring maximum of the phytoplankton; the late summer maxima of the *Daphnia cucullata* and the *Chydorus sphaericus* also occur at the same time as the late summer maximum of the phytoplankton. None of the Cladocera have maxima at the time when the summer and winter minima of the phytoplankton take place.

The facts here pointed out naturally offer no definite proof of the possible connection of cause. All the same, the simultaneous occurrence of great quantities of phytoplankton and great Cladocera maxima is hardly quite accidental. It seems more reasonable to look upon the increase in the quantity of phytoplankton as a contributory cause of the occurrence of the maxima of the Cladocera. As far as I know, such a dependence between the phytoplankton and the zooplankton is not in conflict with events occurring elsewhere. On the contrary, it has often been pointed out in the course of other quantitative investigations.

It is certainly true that EINAR NAUMANN has laid strong emphasis on the significance of the allochthonous mass of detritus as nourishment for the Cladocera in lakes containing a great deal of *humus*, and has expressed himself thus: “Um eine Abhängigkeit zwischen Phyto- und Zooplankton kann hier gar nicht gesprochen werden; das eine ist stets arm entwickelt, das andere kann gleichzeitig luxurieren” (1918, p. 34). Besides in lakes rich in *humus*, situated in regions where the ground is rock without much chalk, the Cladocera — according to NAUMANN — also have to be content with detritus-food in very deep lakes, independently of the geographical situation. But in lakes characterised by NAUMANN as “seichtere Gewässer nährstoffreicher Gebiete, mit einer nicht zu tiefen sommerlichen Mitteltemperatur (über 16° C.)” — in other terms a category comprising several lakes in Denmark and North Germany, also the lake of Frederiksborg castle — “besteht das nährende Filtrat überwiegend aus mehr oder minder ausgesprochen unversehrten Algen in Kombination mit den leicht kollabierenden Flagellaten bzw. mit Peritripton einer vorwiegend planktogener Herkunft”. For this reason, NAUMANN thinks of these lakes that “Die Produktion an Zooplankton ist somit hier von dem Phytoplankton direkt abhängig, wenn auch oft in einer ganz indirekten Weise indem das Phytoplankton wahrscheinlich minder an und für sich als vielmehr eben als Detritusproduzent — und zwar teils durch Produktion von im Wasser später ausflockenden Assimilaten, teils aber auch erst beim ihren Absterben — von einer grundlegenden Bedeutung wird”. (1918, pp. 38—39).

The above-mentioned coincidence between the maxima of the phytoplankton and the Cladocera in the castle lake seems to support the supposition of a dependence, so that the increase in the quantity of phytoplankton should influence the occurrence of the maxima of the Cladocera. It is true that the spring maximum of *Bosmina longirostris* might also conceivably be caused by the hatching of the ephippia; but in the case of the species having their marked maximum in the late summer — *Daphnia cucullata* and *Chydorus sphaericus* — it seems reasonable to imagine a dependence on the contemporary, equally marked, maximum of the phytoplankton. In which way this happens, to how great an extent it is due to nourishment supplied in the shape of the algae themselves, through allogenous detritus or through assimilatives exuded by the algae in the water and there appearing as fluff, these are matters which have not yet been adequately explained. Nor has it been ascertained whether it is the total quantity of foodstuffs that regulates the production of zooplankton; it may well be merely a certain part thereof that — varying with the total quantity — turns the scale. In this connection we remind the reader that with the weighing method employed to determine the quantity of phytoplankton, particles of detritus, bacteria and the like, of a size above 2μ , are also included (Compare p. 235).

In spite of the supposed dependence of the zooplankton-production on the phytoplankton-production — a supposition which, as already mentioned, is accepted by E. NAUMANN in the case of lakes well stocked with phytoplankton — this author also considers it proved that all nutritive particles in the shape of algae s. str., with the exception of the *Chlamydomonadae*, pass quite unaltered through the digestive canal of the filtering Cladocera, so that in the main only very delicate flagellates and bacteria collapse in the intestine (1921, p. 22). Consequently NAUMANN also thinks that dust-fine detritus of allogenous origin, together with bacteria, are, "unter allen Umständen", the most important source of nourishment for the animal-limnoplankton of the filtering type.

In this connection it should, however, be pointed out that — as far as we know — NAUMANN's doctrine, regarding the predominant part played by detritus in humus-lakes poor in phytoplankton, is still without the complement of a similar investigation in respect of lakes rich in phytoplankton, carried out with a correspondingly indisputable result. If detritus and bacteria were only of importance in the last named lakes, there ought to exist there, in the digestive canal of the filtering Cladocera, a large number of unaltered algae in the process of passing through it. In my experience this is by no means the case; it seems, on the contrary, that Biedermann's words about the intestinal contents of the copepodes (1911, p. 65): "dass es sich doch gerade um eine amorphe grüne Masse handelt, in der sich geformte Zellen nicht nachweisen lassen" hold good to a great extent, also in respect of the Cladocera in the plankton region of our lakes. It has, therefore, hardly been proved that the tiny algae, which the Cladocera, owing to the functioning of their feeding apparatus, are bound to filter from the water, do not themselves possess a considerable nutrimental significance in lakes with plenty of phytoplankton.

The most important results of the zooplankton-investigation in the lake of Frederiksborg castle may briefly be summarised as follows:

1. There is in the castle lake no definite water-layer — “Wohnschicht” — preferred by *Daphnia cucullata*. Yet the layer immediately below the surface often contains fewer individuals in the daytime than the other water-layers.

WOLTERECK's hypothesis about the ecological significance of the so-called buoyancy organs in the Cladocera — that, namely, of enabling the animals to remain in quite definite water-layers — has not therefore been confirmed as far as this lake is concerned.

2. The vertical distribution of *Chydorus sphaericus* is, in the daytime, most frequently one of numerical increase from the surface towards the bottom. Something of the same kind happens in the case of the *Bosmina longirostris*, but exceptions often occur in either case.

3. On those occasions when the vertical distribution of the Cladocera has shown maxima at certain depths, the appearance of such maxima have not, as a rule, been attributable to a great mass of phytoplankton at these levels.

4. A rise into the upper layers of the lake has been observed to take place at sunset, the rise including *Daphnia cucullata*, *Chydorus sphaericus*, *Bosmina longirostris*, *Cyclops strenuus* and *Diatomus graciloides*.

5. No corresponding regular readjustment of the quantity of phytoplankton seems to occur.

6. The principal features of the periodicity of the Entomostraca in the lake of Frederiksborg castle have been established.

7. When the maxima of the Cladocera occur, their number increases exceedingly quickly. *Daphnia cucullata*, for instance, during the August maximum 1925, numbered 35 times as many individuals as in June of the same year, and numbers of similar proportions may be quoted in the case of the other species as well.

Hillerød, 15-1-28.

Postscript.

After the above had been got ready for publication, a couple of treatises have been published, dealing with similar problems and written by WOLTERECK (1928), TER-POGHOSSIAN (1928) and ROBERT (1928). WOLTERECK's paper once more gives an exposition of his conception of the seasonal variations of the Cladocera, and a reply to the criticism brought to bear upon it by WESENBERG-LUND; no new material is produced, but reference is made to several recently published works which, in WOLTERECK's opinion, support his own hypothesis; more especially does he seek confirmation of his views in TER-POGHOSSIAN's paper from Klostersee near Seon (1928). The maximum depth of this lake is 15 metres, its summer temperature at the surface about 20 centigrades and at the bottom about 10°. The thermocline is to be found at a depth of about 6 metres. The lake contains both *Daphnia cucullata*, which in summer has a high crista, and *D. longispina*. TER-POGHOSSIAN has now pointed out that *D. cucullata* principally inhabits the hot epilimnion, while *D. longispina* lives both in epi- and hypolimnion and sometimes occurs very plentifully in the latter. According to Ter-Poghossian, the species with the high crista, therefore, has a “Wohnschicht” in Klostersee. — ROBERT's treatise contains, among other things, a critical review of both WESENBERG-LUND's and WOLTERECK's plankton-theories; he thinks that both contain elements of truth, but that they are both too much inclined to generalise.

Table 1. Temperatures in

Date	1925																
	2/4	7/4	18/4	28/4	5/5	12/5	25/5	6/6	11/6	15/6	25/6	8/7	15/7	20/7	19/8	14/9	20/9
Surface	7.0	8.0	9.0	11.0	12.0	14.0	17.0	21.0	23.0	18.0	18.0	22.0	22.0	25.0	20.5	15.0	13.0
Depth 1 m.	6.0	7.5	9.0	11.0	11.5	14.0	16.5	20.0	23.0	18.0	18.0	22.0	22.0	25.0	20.0	14.0	13.0
— 2 m.	6.0	7.0	8.5	11.0	11.5	14.0	16.5	18.5	22.0	18.0	18.0	22.0	21.0	24.0	19.5	13.5	13.0
— 3 m.	6.0			10.5	12.0	13.5	16.5	18.5	20.5	18.0	18.0	20.0	21.0	21.0	19.0	13.5	13.0
Average temperature...	6.3	7.5	8.8	10.9	11.8	13.9	16.6	19.5	22.1	18.0	18.0	21.5	21.5	23.8	19.7	14.0	13.0
Difference between:																	
0 and 1 m.	1.0	0.5	0	0	0.5	0	0.5	1.0	0	0	0	0	0	0	0.5	1.0	0
1 m.—2 m.	0	0.5	0.5	0	0	0	0	1.5	1.0	0	0	0	1.0	1.0	0.5	0.5	0
2 m.—3 m.	0			0.5	0.5	0.5	0	0	1.5	0	0	2.0	0	3.0	0.5	0	0
Surface and bottom...	1.0			0.5	0	0.5	0.5	2.5	2.5	0	0	2.0	1.0	4.0	1.5	1.5	0

Table 2. Weight in milligrams of phytoplankton from

Date	22/4	6/5	22/5			23/5	21/6
			Noon	9 P. M.	Midnight		
Surface	10.79	8.57	16.67	9.91	12.68	13.07	5.87
Depth 1 m.	10.04	11.14	13.41	19.26	8.24	9.45	8.07
— 2 m.	12.45	10.69	13.39	14.09	15.84	10.79	9.71
— 3 m.	9.14	11.56	15.90	15.11	16.78	9.86	7.95

Table 3. Average weight in milligrams of phytoplankton from

Date	23/11 25	5/2 26	27/2 26	13/3 26	26/3 26	9/4 26	22/4 26	9/5 26
Weight	9.35	6.34	4.16	4.52	6.08	8.35	10.61	10.49

the lake of Frederiksborg castle.

1926																							
9/10	21/10	31/10	23/11	5/2	27/2	13/3	26/3	9/4	22/4	6/5	22/5	7/6	21/6	8/7	23/7	19/8	7/9	8/9	9/9	23/9	12/10	17/10	13/11
10.5	6.0	9.0	5.0	1.5	2.0	4.5	5.0	6.0	9.0	10.5	17.0	20.5	18.5	20.0	19.0	18.5	17.5	17.0	17.0	14.5	10.5	9.5	6.5
10.5	6.0	9.0	5.0	1.5	2.0	4.5	5.0	6.0	9.0	10.5	16.5	20.5	18.0	20.0	19.0	18.5	17.5	17.0	17.0	14.5	10.0	9.5	6.5
10.5	6.0	9.0	5.0	1.0	1.5	4.5	5.0	6.0	9.0	10.5	15.0	19.0	18.0	20.0	18.5	18.5	17.5	17.0	17.0	14.5	10.0	9.5	6.0
10.5	6.0	8.5	5.0	1.0	1.5	4.5	4.5	6.0	9.0	10.5	13.5	16.5	17.5	18.5	18.5	18.5	17.5	17.0	16.5	14.5	10.0	9.0	6.0
10.5	6.0	8.9	5.0	1.3	1.8	4.5	4.9	6.0	9.0	10.5	15.5	19.1	18.0	19.6	18.8	18.5	17.5	17.0	16.9	14.5	10.1	9.4	6.3
0	0	0	0	0	0	0	0	0	0	0	0.5	0	0.5	0	0	0	0	0	0	0	0.5	0	0
0	0	0	0	0.5	0.5	0	0	0	0	0	1.5	1.5	0	0	0.5	0	0	0	0	0	0	0	0.5
0	0	0.5	0	0	0	0	0.5	0	0	0	1.5	2.5	0.5	1.5	0	0	0	0	0.5	0	0	0.5	0
0	0	0.5	0	0.5	0.5	0	0.5	0	0	0	3.5	4.0	1.0	1.5	0.5	0	0	0	0.5	0	0.5	0.5	0.5

 $\frac{1}{2}$ litre of water. (The lake of Frederiksborg castle, 1926).

8/7	8/9			9/9			23/9		17/10
	Noon	7 ¹⁵ P. M.	Midnight	6 ⁴⁵ A. M.	2 P. M.	6 ³⁰ P. M.	Noon	6 ³⁰ P. M.	
12.23	18.65	32.26	27.71	18.98	27.44	26.21	14.24	21.61	23.23
9.18	22.59	21.22	16.91	27.88	20.69	21.89	17.19	27.08	18.59
7.21	29.29	22.62	17.39	20.12	12.94	28.69	18.14	25.56	16.07
6.77	22.02	27.17	16.70	19.46	15.81	20.92	16.63	20.90	19.55

 $\frac{1}{2}$ litre of water. (The lake of Frederiksborg castle 1925 & 1926).

22/5 & 23/5 26	7/6 26	21/6 26	8/7 26	23/7 26	19/8 26	8/9 & 9/9 26	23/9 26	17/10 26	13/11 26
13.40	7.78	7.90	8.85	11.45	21.45	22.31	20.17	19.38	10.57

Table 4. *Daphnia*

Numbers of individuals in $\frac{1}{2}$ litre of water from	1925															
	25/6	8/7	20/7	19/8	14/9	29/9	9/10	31/10	23/11	5/2	27/2	18/3	26/3	9/4	22/4	6/5
Surface	4	8	4	25	22	19	12	0	0	0	0	0	0	0	0	0
Depth 1 m.	1	7	1	87	48	21	13	3	4	0	0	0	0	0	0	0
— 2 m.	1	6	36	140	47	15	16	1	0	1	0	0	0	0	0	0
— 3 m.	4	2	0	100	54	28	9	2	5	0	0	0	0	0	0	0
Average number of individuals per litre	5.0	11.5	20.5	176.0	85.5	41.5	25.0	3.0	4.5	0.5	0	0	0	0	0	0

Table 5. *Diaphanosoma*

Numbers of individuals in $\frac{1}{2}$ litre of water from	1925															
	25/6	8/7	20/7	19/8	14/9	29/9	9/10	31/10	23/11	5/2	27/2	18/3	26/3	9/4	22/4	6/5
Surface	3	2	16	0	0	0	0	0	0	0	0	0	0	0	0	0
Depth 1 m.	1	1	17	2	0	0	0	0	0	0	0	0	0	0	0	0
— 2 m.	0	3	15	5	1	0	0	0	0	0	0	0	0	0	0	0
— 3 m.	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
Average number of individuals per litre	2.0	3.0	25.0	3.5	0.5	0	0	0	0	0	0	0	0	0	0	0

Table 6. *Chydorus*

Numbers of individuals in $\frac{1}{2}$ litre of water from	1925															
	25/6	8/7	20/7	19/8	14/9	29/9	9/10	31/10	23/11	5/2	27/2	18/3	26/3	9/4	22/4	6/5
Surface	4	12	7	35	38	30	0	1	1	0	0	0	0	1	0	4
Depth 1 m.	4	6	14	160	171	26	18	6	5	0	0	1	0	0	0	1
— 2 m.	10	8	81	153	207	46	27	6	2	0	0	0	0	0	2	1
— 3 m.	19	2	15	361	126	25	54	8	2	0	0	0	2	1	3	12
Average number of individuals per litre	18.5	14.0	58.5	354.5	271.0	63.5	49.5	10.5	5.0	0	0	0.5	1.0	1.0	2.5	9.0

ucullata.

1926																							
22/5			23/5		7/6	21/6	8/7	23/7	19/8	7/9			8/9			9/9			23/9		17/10	18/11	
Noon	9 P. M.	Mid-night	3 ³⁰ A. M.	6 A. M.						Noon	7 ¹⁵ P. M.	Mid-night	5 ⁴⁵ A. M.	Noon	7 ¹⁵ P. M.	Mid-night	6 ⁴⁵ A. M.	2 P. M.	6 ³⁰ P. M.	Noon			6 ³⁰ P. M.
1	1	0	2	1	9	32	7	37	76	41	546	174	61	50	68	66	54	58	129	55	83	3	1
1	1	5	1	0	16	28	5	16	73	130	403	162	149	127	70	50	78	67	90	35	62	9	7
1	0	2	3	2	9	24	3	55	84	111	144	105	117	118	74	72	119	106	62	71	60	19	5
0	0	1	1	1	0	13	17	81	106	124	135	64	111	129	120	45	68	68	103	39	55	58	2
2.5					17.0	48.5	16.0	94.5	169.5	228.5									120		44.5	7.5	

brachyurum.

1926																							
22/5			23/5		7/6	21/6	8/7	23/7	19/8	7/9			8/9			9/9			23/9		17/10	18/11	
Noon	9 P. M.	Mid-night	3 ³⁰ A. M.	6 A. M.						Noon	7 ¹⁵ P. M.	Mid-night	5 ⁴⁵ A. M.	Noon	7 ¹⁵ P. M.	Mid-night	6 ⁴⁵ A. M.	2 P. M.	6 ³⁰ P. M.	Noon			6 ³⁰ P. M.
0	0	0	0	0	0	1	4	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	3	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	2	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0.5	4.5	14.0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0

phaericus.

1926																							
22/5			23/5		7/6	21/6	8/7	23/7	19/8	7/9			8/9			9/9			23/9		17/10	18/11	
Noon	9 P. M.	Mid-night	3 ³⁰ A. M.	6 A. M.						Noon	7 ¹⁵ P. M.	Mid-night	5 ⁴⁵ A. M.	Noon	7 ¹⁵ P. M.	Mid-night	6 ⁴⁵ A. M.	2 P. M.	6 ³⁰ P. M.	Noon			6 ³⁰ P. M.
1	6	14	4	5	2	10	28	171	258	68	170	147	125	34	117	142	216	61	192	58	76	3	5
2	12	11	8	4	12	12	38	114	211	294	200	250	178	100	88	91	253	115	32	76	137	25	7
3	19	21	37	10	38	9	34	118	289	178	161	236	154	93	94	112	282	142	40	134	72	136	9
17	22	16	33	73	15	42	40	114	308	254	134	192	121	148	120	106	205	66	183	160	71	126	7
32.0					33.5	36.5	70.0	258.5	533.0	273.5									196.0		145.0	14.0	

Table 7. *Bosmina*

Numbers of individuals in $\frac{1}{2}$ litre of water from	1925															
	25/6	8/7	20/7	19/8	14/9	20/9	9/10	31/10	23/11	5/2	27/2	13/3	26/3	9/4	22/4	6/5
Surface	0	1	0	0	0	0	0	1	1	5	0	3	3	4	7	54
Depth 1 m.	0	0	0	0	0	0	0	0	3	0	2	1	3	15	15	82
— 2 m.	0	0	0	0	0	0	0	0	4	0	6	2	1	7	10	68
— 3 m.	0	0	0	1	0	1	0	1	8	10	6	1	4	5	2	100
Average number of individuals per litre	0	0.5	0	0.5	0	0.5	0	1.0	8.0	7.5	7.0	3.5	5.5	15.5	17.0	152.0

Table 8. *Cyclops*

Numbers of individuals in $\frac{1}{2}$ litre of water from	1925															
	25/6	8/7	20/7	19/8	14/9	20/9	9/10	31/10	23/11	5/2	27/2	13/3	26/3	9/4	22/4	6/5
Surface	1	2	13	22	0	3	1	1	1	9	2	2	5	4	5	4
Depth 1 m.	0	3	10	6	4	5	2	0	3	4	2	3	3	4	11	14
— 2 m.	1	1	3	9	2	3	2	2	1	3	12	5	1	2	12	2
— 3 m.	0	2	3	4	1	1	4	1	2	49	12	7	2	0	2	16
Average number of individuals per litre	1.0	4.0	14.5	20.5	3.5	6.0	4.5	2.0	3.5	32.5	14.0	8.5	6.5	5.0	15.0	18

Table 9. *Diaptomus*

Numbers of individuals in $\frac{1}{2}$ litre of water from	1925															
	25/6	8/7	20/7	19/8	14/9	20/9	9/10	31/10	23/11	5/2	27/2	13/3	26/3	9/4	22/4	6/5
Surface	21	17	18	35	0	1	2	1	0	4	0	0	0	0	0	0
Depth 1 m.	6	19	18	19	15	12	5	4	1	0	4	0	0	2	2	1
— 2 m.	12	8	35	16	8	9	5	4	3	1	2	0	1	1	3	0
— 3 m.	8	6	1	40	10	3	2	3	9	4	6	0	1	1	0	8
Average number of individuals per litre	23.5	25.0	36.0	65.0	16.5	12.5	7.0	6.0	6.5	4.5	6.0	0	1.0	2.0	2.5	4.5

ongirostris.

1926

22/5			28/5		7/8	21/6	8/7	28/7	19/8	7/9			8/9			9/9			28/9		17/10	18/11	
Noon	9 P. M.	Mid-night	3 ³⁰ A. M.	6 A. M.						Noon	7 ¹⁵ P. M.	Mid-night	5 ⁴⁵ A. M.	Noon	7 ¹⁵ P. M.	Mid-night	6 ⁴⁵ A. M.	2 P. M.	6 ³⁰ P. M.	Noon			6 ³⁰ P. M.
338	627	434	326	269	18	1	0	2	14	0	0	0	0	0	1	1	0	0	0	1	0	2	11
353	655	705	369	324	35	2	0	0	0	1	0	0	0	0	0	0	0	0	0	3	2	2	13
408	353	401	457	499	54	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2	1	0	12
522	374	298	522	1287	86	175	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	15	5
952.0					96.5	89.0	0	0.5	7.0	0.5									3.0		9.5	20.5	

trenuus.

1926

22/5			28/5		7/8	21/6	8/7	28/7	19/8	7/9			8/9			9/9			28/9		17/10	18/11	
Noon	9 P. M.	Mid-night	3 ³⁰ A. M.	6 A. M.						Noon	7 ¹⁵ P. M.	Mid-night	5 ⁴⁵ A. M.	Noon	7 ¹⁵ P. M.	Mid-night	6 ⁴⁵ A. M.	2 P. M.	6 ³⁰ P. M.	Noon			6 ³⁰ P. M.
20	58	99	28	11	6	12	17	25	4	1	5	8	2	1	3	2	0	4	10	11	4	2	0
40	49	61	29	31	16	14	26	36	12	5	7	3	0	2	7	1	4	1	3	5	4	0	3
26	20	24	31	37	19	14	19	33	12	4	5	5	8	9	2	1	1	5	0	5	4	7	3
28	12	11	25	31	4	20	5	27	11	4	3	9	3	8	3	2	2	1	1	2	0	2	0
67.0					22.5	30.0	33.5	60.5	19.5	7.5									9.0		5.5	3	

raciloides.

1926

22/5			28/5		7/8	21/6	8/7	28/7	19/8	7/9			8/9			9/9			28/9		17/10	18/11	
Noon	9 P. M.	Mid-night	3 ³⁰ A. M.	6 A. M.						Noon	7 ¹⁵ P. M.	Mid-night	5 ⁴⁵ A. M.	Noon	7 ¹⁵ P. M.	Mid-night	6 ⁴⁵ A. M.	2 P. M.	6 ³⁰ P. M.	Noon			6 ³⁰ P. M.
0	3	5	4	0	16	27	21	12	16	4	19	5	6	6	13	11	11	4	22	5	2	1	0
1	2	5	4	5	24	31	13	17	14	8	12	9	10	1	5	5	9	7	11	0	2	0	5
5	1	0	2	2	8	27	13	17	19	12	11	9	7	25	15	9	7	6	3	2	1	3	4
3	2	0	0	0	0	31	13	17	18	9	3	10	5	3	10	8	8	5	8	3	0	12	4
4.5					24.0	58.0	30.0	35.5	33.5	17.5									4.0		8.0	6.5	

Part II.
Botanical Investigations

by GUNNAR NYGAARD.

Methodics.

At the end of 1926 I received a rather large amount of plankton material from the lake of Frederiksborg castle. This material, which I was to investigate, consisted of not less than 146 samples, collected through two years. As to the methods used in the collection and the deposition of the organisms see part I, p. 234. As some Flagellates and Dinoflagellates and also certain inner structures of the cells of Chlorophyceae easily become irrecognisable and indistinguishable after fixation in formaline, the phytoplankton of the lake was, in addition, studied alive during the spring of 1927.

Originally I meant to determine the relative frequency of each species at an estimate: ccc-cc-c-+-r-rr-rrr, but it soon became apparent that although this method might be employed with advantage for the larger species with very distinct maxima, it would give an unsatisfactory idea of the life-cycle of a great part of the Nannoplankton-forms. This question being comparatively little known required special attention, so the following method was employed. Having made sure which species occurred in the sample to be examined, I took out ten different fields of view (magnification 735 times), gradually moving the slide. Every time a certain species occurred in one of the ten fields of view, it was marked with a cross in the table. If it occurred in all ten fields of view, it was characterised as common (c), if there were many individuals in each field of view, its relative frequency was estimated at cc, and if nearly all the organisms in each field of view belonged to the same species, the frequency was estimated at ccc. The two latter degrees of frequency, roughly estimated, were used of one organism only, *Scenedesmus armatus* var. *Chodati*, because in the case of *Microcystis aeruginosa*, which was likely to reach a very great frequency, the colonies only, not the single cells were counted. None of the remaining plankton-organisms of the lake has the frequency cc. As an instance of the method of investigation the following table shows the composition of the plankton on May 5th, 1925.

In order that the method applied might be as accurate as possible, I took, by means of a siphon, so much water from each sample in which the plankton had been deposited, that the volume of water above the plankton was estimated to be

Table showing composition of the plankton on May 5th, 1925.

Species	0 m (surface)	1 m depth	2 m depth	3 m depth
<i>Actinastrum Hantzschii</i>				+
<i>Ankistrodesmus convolutus</i>	+	+		
— <i>falcatus acicul.</i>	+			
<i>Closterium subulatum</i>	+			
<i>Coelastrum microporum</i>	+	+	+	+
<i>Cryptomonas ovata</i>	++	+	+	+++
<i>Dictyosphaerium pulchellum</i> ..	+	+	+++	
<i>Glenodinium pulvisculus</i>	+			
<i>Lagerheimia longiseta</i>			+	
— <i>wratislaviensis</i> ...	+			
<i>Melosira granulata</i>	+	+	+	+
— <i>italica subarctica</i>	+	+	++	+
<i>Micractinium pusillum</i>	+++++++	+++++++	+++++++	+++++++
<i>Microcystis firma</i>	+	++	+	++
— <i>aeruginosa</i>	+		+	
<i>Oocystis parva</i>	++	++	++	++
<i>Pandorina morum</i>	++	++	+	+++
<i>Pediastrum Boryanum</i>	+++++	+++	++	++++
— <i>incisum</i>	+	+		
<i>Pteromonas angulosa</i>	+	+		
<i>Scenedesmus armatus Chodati</i> ++++++++	+++++++	+++++++	+++++++	+++++++
— <i>dimorphus</i>	+			
<i>Staurastrum tetracerum</i>	+			
— <i>paradoxum</i>	+			
<i>Stephanodiscus dubius</i>	+++++++	+++++++	+++++++	+++++++
— <i>Hantzschii</i>	+	++		+
— — <i>pusilla</i>	++++	+++	++	++
<i>Tetraedon minimum</i>		+		
— <i>muticum</i>	++	+		
<i>Tetrastrum apiculatum</i>	+			
— <i>staurogeniaeforme.</i>	+++++++	+++++++	+++++	+++++++
<i>Trachelomonas hispida</i> var....	+	+		
— <i>volvocina</i>	+	+		

the same as that of the plankton itself. Then the glass was shaken, and immediately after a drop of a certain size was taken from it by means of a pipette. This drop, together with a small drop of gentian-violet solution was put on a glass slip, a cover-glass was lowered over it, and the edges were cemented, first with paraffine, then with Canada balsam, and at last with Gram-Rützou varnish. All the samples were treated in this way. Slides, made in this manner, show the organisms coloured and with distinct outlines. In slides made with glycerine the outlines are often difficult to see; this is more especially the case with the diatoms. It is true that slides, made after the above method, often dry up after one or two

years, according to the care with which the cementing is carried out; but in an investigation of this kind, which lasted for about one year, it highly facilitated the work always to have a satisfactory slide at hand. Two sorts of slides were made of Diatoms: slides where the diatoms were heated to red heat on the cover-glass, and such where the material was treated with sulphuric acid and potassic nitrate. As a mounting medium was used not styrax, but potassium iodide and periodide of mercury dissolved in glycerine, in which it is easy to make the frustules of the diatoms roll, so that they can conveniently be seen both in valvular view and in girdle-view.

By means of the above-mentioned determination of relative frequency it is possible to give a picture of the periodicity of the species. In order to make a comparison between their relative abundance I have calculated their annual averages. By the *absolute annual average* of a species is understood the sum of the individuals per litre, of each sample, divided by the number of the samples. In the table on p. 271, however, not the absolute, but the *relative annual average* is given. It has been calculated in the following way. The crosses which a species has obtained by the count for the whole year, are added up, and the sum is divided by the number of collecting-days. As an instance may be given the calculation of the relative annual average of *Tetrastrum staurogeniaeforme*:

Table showing calculation of the relative annual average of *Tetrastrum staurogeniaeforme* Lemm.

Apr. 2nd, 1925	10 +	Feb. 2nd, 1926	1 +
— 7th, —	11 +	— 27th, —	3 +
— 18th, —	22 +	Mar. 13th, —	10 +
— 28th, —	27 +	— 26th, —	14 +
May 5th, —	31 +	Apr. 9th, —	24 +
— 12th, —	30 +	— 24th, —	27 +
— 25th, —	10 +	May 7th, —	20 +
Jun. 6th, —	18 +	— 23rd, —	5 +
— 11th, —	18 +	Jun. 7th, —	1 +
— 25th, —	24 +	— 22nd, —	9 +
Jul. 8th, —	21 +	Jul. 9th, —	4 +
— 15th, —	23 +	— 23rd, —	4 +
— 20th, —	6 +	Aug. 19th, —	1 +
Aug. 19th, —	1 +	Sep. 7th, —	0
Sep. 14th, —	0	— 23rd, —	0
— 29th, —	0	Oct. 12th, —	0
Oct. 9th, —	0	Nov. 13th, —	0
— 21st, —	0		
— 31st, —	0		
Nov. 23rd, —	3 +		
20 collecting days . . .	255 +	17 collecting days . . .	123 +
Thus the relative annual average is		Thus the relative annual average is	
$\frac{255 +}{20} = 12.75.$		$\frac{123 +}{17} = 7.25.$	

The relative annual average thus becomes 4 times the result obtained at division by the number of samples (compare with the table on p. 267), which, however, would give a less convenient survey, as the figures by this means become small, and in the case of most of the species should be given with several decimals.

At the calculation of the relative annual average of *Scenedesmus armatus* var. *Chodati*, which, as mentioned in p. 266, is the only organism to be characterised by cc and ccc, thus lying outside the calculation, the relative frequency cc is estimated at 80+ and ccc at 120+, which figures are by no means too high. The table, made in this way, of the relative annual averages — as mentioned in more detail on p. 270 — gives a rough estimate of the relative significance of the most important species of the lake of Frederiksborg castle. In viewing the table it should be remembered that only the colonies, not the individual cells, have been taken into account in making the count. This explains why *Microcystis aeruginosa* shows such a small number in comparison with *Scenedesmus armatus* var. *Chodati*. Of course it cannot be seen from the table whether a species has a short period of vegetation with a distinct maximum, as e. g. the *Anabaena*-species, *Synedra acus* var. *delicatissima*, *Micractinium pusillum* et al., or if it occurs in small numbers nearly all the year round, as e. g. *Trachelomonas volvocina* and *hispida* var., *Pediastrum Boryanum* et al. But such information as to the periodicity will be given under the separate species. The figures of the table from 1926 give a more correct idea of the facts than those of 1925, the 17 collecting days of 1926 being distributed over the period from Febr. 5th to Nov. 13th, while the 20 collecting days of 1925 are only distributed over the period from Apr. 2nd to Nov. 23rd.

The curves showing the relative frequency, which are figured in this paper, have as their abscissa the time and as their ordinate the sum of the crosses which the species has obtained at the investigation of the four samples from a certain date, e. g.: *Micractinium pusillum* attained the relative frequency (the ordinate) of 34+ on May 5th (s. p. 267 and text-fig. 23).

Now how is an estimate of the quantitative proportion of the individual species in the lake of Frederiksborg castle to be obtained through the counting method employed here? Of course a certain amount of errors have slipped in here — as also in other counting methods — because of the limited number of microscopic fields of view used here. Further the method, as emphasised above, only gives the composition of the plankton, the frequency which one species attains in comparison with the others. The absolute frequency (the number of individuals per litre) is not arrived at by this method, as the quantitative production of plankton is quite different at the different seasons. E. g. *Scenedesmus armatus* var. *Chodati* attains c (40+) on March 26th, 1926; it reaches the same relative frequency on Sept. 7th, 1926. However, there is a great difference between the two c's. The first of them means c of the plankton production 8 mgr.s per litre (see curve on p. 274), and the second means c of the plankton production 45 mgr.s per litre. Thus the absolute frequency of *Scenedesmus armatus* var. *Chodati*

is much greater on Sept. 7th than on March 26th. So we get an estimate of the quantitative proportion of the individual species by comparing its bio-curve with the quantitative phytoplankton-curve on p. 274.

General Remarks.

It is a well known fact that the eutrophic lakelets and ponds are the seat of a great number of unicellular Chlorophyceae and, what is more conspicuous, of certain Cyanophyceae, especially *Microcystis*- and *Anabaena*-species.

The lake of Frederiksborg castle has a very rich plankton flora. In this investigation no less than 74 species have been found, apart from varieties. Of course a great number of these species are very rare.

A look at the tabular survey below gives an impression of what species predominate in the composition of the plankton. Within the Cyanophyceae *Microcystis aeruginosa* is by far the most conspicuous; further *Microcystis firma* and *Lyngbya limnetica* play a rather prominent part. *Anabaena incrassata* and *Anabaena flos aquae* characterise the plankton for a short time in the middle of the summer, but for the rest of the time they are lacking. Within the Diatomaceae *Stephanodiscus dubius* and *Melosira italica* subsp. *subarctica* are predominant. *Melosira granulata* with its variety *angustissima*, *Asterionella gracillima* together with *Stephanodiscus Hantzschii* var. *pusillus* are rather prominent, the two last-mentioned, however, not every year. Of Flagellatae several species of *Trachelomonas* are found, but only *Trachelomonas volvocina* forma *minuta* occurs in quantity, though not every year. Further *Cryptomonas ovata* must be noticed. Volvocales are somewhat better represented. *Phacotus lenticularis* and *Pandorina morum* are the most conspicuous, together with two species of *Pteromonas* and *Chlamydomonas Braunii*, the latter only in 1925. Within the Chlorophyceae the species of *Scenedesmus armatus* var. *Chodati* exceeds all the other phytoplankton-organisms in abundance. Of the rest *Tetrastrum staurogeniaeforme* occurs most abundantly, further *Ankistrodesmus convolutus* var. *minutus*, *Oocystis parva* and *Pediastrum Boryanum* together with *Micractinium pusillum*, *Coelastrum microporum* and several species of *Ankistrodesmus*. Conjugatae stand considerably below the other groups, qualitatively as well as quantitatively; still *Closterium subulatum* must be mentioned.

Beside the 3 new species *Anabaena incrassata* n. sp., *Gymnodinium inversum* n. sp. and *Closterium polymorphum* n. sp. several of the organisms mentioned in the systematical part have not been found before in this country. Organisms like *Mallomonas akrokomos*, *Trachelomonas* sp., *Trachelomonas volvocina* forma *minuta*, *Heleronema* sp., *Pteromonas aculeata*, *Tetraedron Schmidlei* var. *euryacanthum*, *Tetraedron limneticum* var. *simplex* must all be characterised as more or less rare species.

With reference to their periodicity the plankton-organisms may be divided into 3 groups: the obligatorily periodical, the facultatively periodical, and the perennial organisms.

Table showing the relative annual averages of the chief species.

Species	Relative annual averages	
	1925	1926
Cyanophyceae.		
<i>Microcystis aeruginosa</i>	12	11
— <i>firma</i>	6	7
<i>Gomphosphaeria lacustris</i>	1.5	1.5
<i>Oscillatoria Agardhii</i>	0.25	1
<i>Lyngbya limnetica</i>	7	4.5
<i>Anabaena flos aquae</i>	1.5	0.75
— <i>incrassata</i>	2	1
Diatomaceae.		
<i>Stephanodiscus dubius</i>	17	15
— <i>Hantzschii</i>	1.5	5
— — <i>var. pusillus</i>	7	0
<i>Melosira italica</i> subsp. <i>subarctica</i>	?	13
— <i>granulata</i> and <i>var. angustissima</i>	3.5	3.5
<i>Asterionella gracillima</i>	?	2
<i>Synedra acus</i> <i>var. delicatissima</i>	?	3
Flagellatae.		
<i>Trachelomonas volvocina</i>	2	2.5
— — <i>forma minuta</i>	?	8
— <i>hispida</i> <i>var.</i>	1.5	2
<i>Cryptomonas ovata</i>	3.5	5.5
Volvocales.		
<i>Chlamydomonas Braunii</i>	3	0
<i>Phacotus lenticularis</i>	4	3.5
<i>Pteromonas angulosa</i> and <i>P. aculeata</i>	2	2.5
<i>Pandorina morum</i>	3.5	0.5
Chlorophyceae.		
<i>Ankistrodesmus longissimus</i> <i>var. gelifactum</i>	1	1
— <i>convolutus</i> <i>var. minutus</i>	8	2
— <i>falcatus</i> <i>varr.</i>	2	4.5
<i>Pediastrum Boryanum</i>	5.5	5
<i>Tetrastrum staurogeniaeforme</i>	12.75	7.25
<i>Coelastrum microporum</i>	4	2
<i>Dictyosphaerium pulchellum</i>	3.5	1
<i>Oocystis parva</i>	7	4
<i>Micractinium pusillum</i>	4	2.5
<i>Scenedesmus armatus</i> <i>var. Chodati</i>	49	54
<i>Closterium subulatum</i>	1	1.5

By obligatorily periodical organisms are meant organisms which every year attain a more or less distinct maximum and then disappear. Typical instances: *Micractinium pusillum* (see text-fig. 23) and the *Anabaena*-species (see text-fig. 13).

The facultatively periodical organisms only attain a maximum at intervals of several years. In the lake of Frederiksborg castle the following species are facultatively periodical: *Volvox globator*, which was noticed in great quantities in 1894 (June, 15th—July, 7th) by C. WESENBERG-LUND (1904, p. 92). The water was coloured green by the alga; a cup of water contained the alga by thousands. In the following year the alga had a maximum in June—July, but during the last 10 years it has not been met with in the lake. During the present investigation I never succeeded in seeing one single specimen. Further *Chlamydomonas Braunii* (see text-fig. 14), *Stephanodiscus Hantzschii* var. *pusillus* (see text-fig. 17) and *Synedra acus* var. *delicatissima* (see text-fig. 26). Less marked are *Ankistrodesmus falcatus* var. *acicularis* (see text-fig. 13), *Trachelomonas volvocina* f. *minuta* (see text-fig. 20) and *Cyclotella comta* (see p. 286).

To the perennial organisms, which, though present all the year round, may still have a very distinct maximum, belong e. g. *Trachelomonas volvocina* and *Pediastrum Boryanum* (see text-fig. 22). Further the two most important species of the lake: *Microcystis aeruginosa* (see text-fig. 12) and *Scenedesmus armatus* var. *Chodatii* must be classed within this group.

E. WEHRLE (1927) has investigated the algal vegetation (mainly the Chlorophyceae) at Freiburg in Breisgau and determined the H-ion concentration corresponding to each locality. For each species the p_H interval was determined, the limits of which are indicated by the extreme p_H values in which the species occurred. The highest p_H value measured by WEHRLE in the investigated territory was 8.2. In eutrophic lakelets and ponds it is often found that in early summer, when the assimilation of carbonic acid begins to increase strongly, p_H rises to 9.1—9.2. In the spring of 1927 I measured p_H in the lake of Frederiksborg castle and found a rather sudden rise during the month of May from 8.3 to 9.1—9.2. Now it is clear that the organisms mentioned here, the vegetation period of which lasts until May, can exist at a p_H value of 8.3, while those which extend the vegetative period into the summer or are confined exclusively to this period, have $p_H = 9.1—9.2$ as the temporary extreme value. As an example *Pandorina morum* has thus an unbroken p_H interval from 5.2 (according to WEHRLE) to 9.2.

It is well known that not only do different species constitute the plankton of the various seasons, also the number of species changes throughout the year. The table below shows the number of organisms (species and varieties) constituting the phytoplankton of the different seasons of the years 1925 and 1926.

Conditions in the year 1926 are shown graphically in fig. 11. Here the continuous curve shows the quantitative development of the phytoplankton, the dotted curve shows the number of organisms constituting the phytoplankton at the different

Table showing the number of organisms constituting the phytoplankton
in 1925 and 1926.

Apr. 2nd, 1925.....	26 species	Feb. 5th, 1926.....	27 species
— 7th, —	30 —	— 27th, —	24 —
— 18th, —	30 —	Mar. 13th, —	27 —
— 28th, —	32 —	— 26th, —	27 —
May 5th, —	33 —	Apr. 9th, —	30 —
— 12th, —	22 —	— 24th, —	33 —
— 25th, —	25 —	May 7th, —	31 —
Jun. 6th, —	28 —	— 23rd, —	24 —
— 11th, —	26 —	Jun. 7th, —	25 —
— 25th, —	31 —	— 22nd, —	29 —
Jul. 8th, —	33 —	Jul. 9th, —	32 —
— 15th, —	32 —	— 23rd, —	33 —
— 20th, —	32 —	Aug. 19th, —	27 —
Aug. 19th, —	27 —	Sep. 7th, —	20 —
Sep. 14th, —	20 —	— 23rd, —	18 —
— 29th, —	12 —	Oct. 12th, —	14 —
Oct. 9th, —	16 —	Nov. 13th, —	21 —
— 21st, —	18 —		
— 31st, —	19 —		
Nov. 23rd, —	26 —		

seasons. The curve illustrating the quantitative proportions is more thoroughly dealt with on p. 243. The dotted curve has two equally large maxima (33 species): one at the end of April and one at the end of July: the intermediate minimum (24 species) occurs at the end of May. It reaches its absolute minimum in October (14 species). As there are no samples from December 1925 and from January 1926, nothing can be said about the conditions within this period. The somewhat irregular course of the curve in February—March (24—27 species) is most likely due to oscillations of temperature about zero, when the lake at times was covered with ice and sometimes free from ice (see p. 240).

The two curves in text-fig. 11 apparently run independently of each other. A scrutiny shows the following characteristic facts: the maxima of the dotted curve occur at an earlier point of time than those of the continuous curve, and shortly after the continuous curve has reached its absolute maximum, the dotted curve reaches its absolute minimum.

The spring maximum of the continuous curve is mainly formed by *Scenedesmus armatus* var. *Chodati*, while the maximum of late summer is almost exclusively due to the strong development of *Microcystis aeruginosa*. Then it is natural to connect the strong development of these two species with the reduction in the number of species in May and October. It is difficult to say anything definite of the exact causes of such a reduction, but probably an organism like *Microcystis aeruginosa* contributes to limiting the number of species e. g. by its evil-

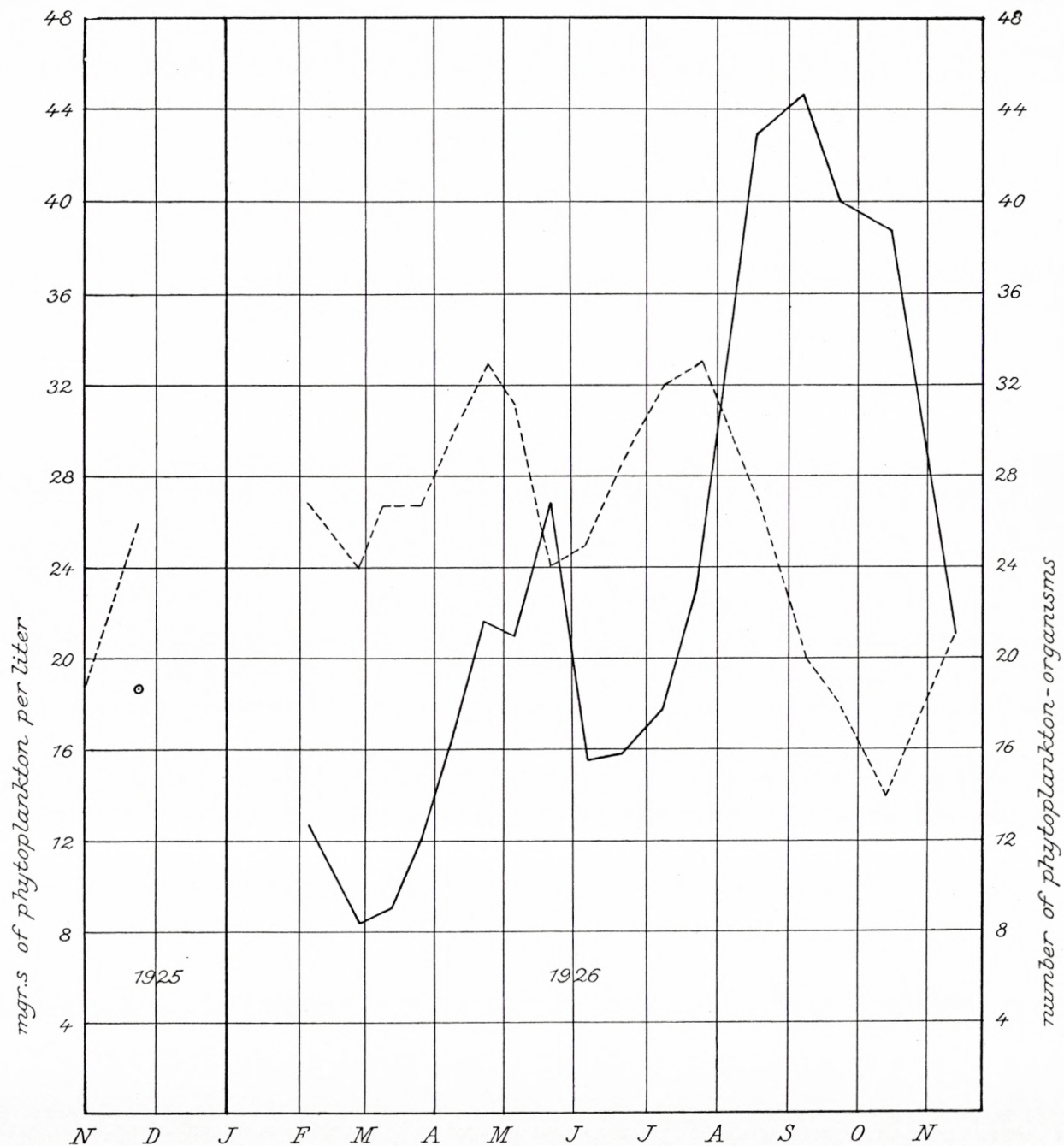


Fig. 11. The continuous curve shows the number of mgr.s of phytoplankton per liter, the dotted curve shows the number of organisms constituting the phytoplankton.

smelling excretions and by its altering of the conditions of light (because it forms water bloom).

So the production of phytoplankton in the lake of Frederiksborg castle in 1926 was five to six times as great in late summer (August—September) as at the end of the winter (February—March). The abundance of species was just as great in spring (April) as in mid-summer (July); it was smallest in October.

The double maximum in the quantitative development of the phytoplankton is well-known (see e. g. APSTEIN 1896, BIRGE and JUDAY 1922). Similar circumstances are met with in the plankton of the sea (see e. g. CLEVE 1905, JACOBSEN and PAULSEN 1912). In this connection it need only be mentioned that CLEVE found the volume of the plankton in the Kattegat to be greatest in April and in October—November, and that the abundance of species was greatest in April—May and in November.

As a result of the present investigation it must be emphasised that several of the organisms mentioned in the systematic-biological account have two-topped bio-curves. For these organisms C. H. OSTENFELD has introduced the designation “*diacmic*”, while organisms the curve of which has one top only are called “*monacmic*”. As instances of diacmic plankton-forms may be mentioned *Tetrastrum staurogeniaeforme* (see text-fig. 15) and *Pteromonas angulosa* (see text-fig. 21); as to *Phacotus lenticularis* (text-fig. 20) see p. 296, and *Stephanodiscus dubius* (text-fig. 12) see p. 286. As instances of monacmic plankton-forms may be mentioned *Anabaena incrassata* and *Anabaena flos aquae* together with *Ankistrodesmus falcatus* var. *acicularis* (see text-fig. 13); further *Micractinium pusillum* (see text-fig. 23) and *Closterium subulatum* (see text-fig. 27).

Now it turns out that the maxima of the diacmic species in many cases occur in April—May and in July—August. The former coincides with the spring maximum of the production of the phytoplankton as a whole, the latter with the beginning of its late summer maximum. The later part of the latter, however, is nearly exclusively due to the enormous development of *Microcystis aeruginosa*. As mentioned before, the spring maximum is mainly caused by *Scenedesmus armatus* var. *Chodati*. Besides this predominating form several diacmic species contribute to the spring maximum of the quantitative development of the phytoplankton, e. g. *Tetrastrum staurogeniaeforme*, *Dictyosphaerium pulchellum* (in 1925), *Pteromonas angulosa*, *Stephanodiscus dubius*, *Pandorina morum* (in 1925), *Actinastrum Hantzschii*, *Kirchneriella contorta* (in 1926), and *Ankistrodesmus falcatus* var. *acicularis* forma; the same is the case with certain monacmic species, as e. g. *Synedra acus* var. *delicatissima*, *Cyclotella comta* (in 1927), *Stephanodiscus Hantzschii* var. *pusilla*, *Chlamydomonas Braunii* (in 1925), *Cryptomonas ovata* (in 1925), *Micractinium pusillum* (in 1925), and *Closterium subulatum*.

The maximum of the monacmic species as a rule occurs in April—May (instances of such species have just been given above) or in July—August. Of monacmic mid-summer species may be mentioned: *Anabaena incrassata*, *Anabaena flos aquae*, *Pteromonas aculeata*, *Gomphosphaeria lacustris*, and *Microcystis firma*. Other

monacmic species, however, as e. g. *Coelastrum microporum*, *Trachelomonas volvocina* forma *minuta*, and *Ankistrodesmus falcatus* var. *acicularis* attain their greatest development at other times than those mentioned above; the first in June and the two last-mentioned in March.

Now in order to give a short characterisation of the plankton-flora of the lake of Frederiksborg castle the following may be said: there is an enormous development of blue-green algae (especially *Microcystis aeruginosa*) in the autumn and a very rich flora of unicellular green algae; of the latter group *Scenedesmus armatus* var. *Chodati* plays the most prominent part. Add to this another point, viz. a richer development of the Diatom-flora than could be expected in a lake of so small a depth. In such a lake one should suppose that only *Asterionella gracillima* and *Stephanodiscus Hantzschii* var. *pusillus* could occur in great quantities, but the investigation has shown that, besides these two genuine plankton-forms, the plankton-diatoms *Melosira italica* subsp. *subarctica* and *Stephanodiscus dubius* play a great part. Further, *Synedra acus* var. *delicatissima*, which — as a plankton-organism — has till now only been found in larger lakes (C. WESENBURG-LUND, 1904 p. 72), attained a rather considerable development in the spring of 1926. *Fragilaria crotonensis* and *Melosira granulata* with its variety *angustissima*, which also reach a considerable development in our larger lakes, are also found in the lake of Frederiksborg castle, but they only attain a very inconsiderable development.

Further the plankton is negatively characterised by its scarcity of *Dinobryon* and the absence of *Ceratium hirundinella*. Otherwise *Dinobryon* does not avoid contaminated lakelets and ponds, and in fact some very few colonies have been noticed in the lake at spring-time, but strange to say the genus attained only an exceedingly insignificant development. *Ceratium hirundinella* might more probably be expected to avoid the contaminated lakelets and ponds. As in the case of *Dinobryon* it is hardly the quite considerable quantity of lime (see p. 237) which excludes it from the lake of Frederiksborg castle, for on other occasions I have found both genera richly developed in water which was far more abundant in lime. Finally it is remarkable that a species like *Botryococcus Braunii* is completely absent.

In shallow lakes like that of Frederiksborg castle a mixing of the layers of water often takes place. With this fact it agrees well that the qualitative composition of the phytoplankton is the same at the surface as at depths of 1, 2, and 3 meters. Altogether 146 samples were investigated but I never succeeded in making out any difference between the four samples from the same day. The only exception is *Phacotus lenticularis*, which apparently ascends to the surface. The summer-samples from the surface and from a depth of 1 meter contain *Phacotus lenticularis* in considerable quantities, while it is much less frequent in the two other samples, especially in the 3 meter sample (see also p. 298).

Systematic-Biological Account.

Cyanophyceae.

Chroococcaceae.

Microcystis Kütz.

1. *Microcystis aeruginosa* Kütz.

Text-fig. 12.

In the inlets of the lake, which are protected from the wind, the water is already in June sometimes quite green with *Microcystis*-colonies, and when the weather is calm, a distinct forming of water bloom often occurs; but in the middle of the lake the conditions are quite different; here *Microcystis* does not become predominant until August or September and is prevalent until November; during this time the whole lake is of a light verdigris colour. Though *Microcystis aeruginosa* is so very common in the lake, I never found thalli of such a size as I noticed in the year 1924 in the Søgaard Sø in South Jutland. At the margins of the lake, among the Phragmites-stems, some light verdigris-coloured gelatinous lumps were found, some of which were about as big as a hazel nut. These thalli, made up of *Microcystis aeruginosa*-colonies which have united, were of a very soft consistence, yet they stuck together when taken out of the water.

In 1925 *Microcystis aeruginosa* attained a greater development than in the year 1926 which was colder. C. WESENBERG-LUND states its maximum in larger Danish lakes to be in July—August, somewhat earlier than the highest temperature of the water or nearly simultaneously with it. The lake of Frederiksborg castle differs from this, the species not reaching its maximum until the close of the warm period of the lake in the years 1925 and 1926 (see text-fig. 2 on p. 240). In 1925 it reached its highest development after the middle of August. This development lasted throughout September and then it decreased during October. In 1926 it did not reach its maximum until the end of September, and as the number of individuals, as in the year before, decreased during October, the maximum was of a considerably shorter duration than in 1925.

The species is perennial and typically monacmic. It is always present in quite small but rather constant quantities in the winter- and spring-samples.

2. *Microcystis firma* Rab.

Text-fig. 12.

This small species, the cells of which have pseudovacuoles, and are 1—2.5 μ in diameter, apparently occurs in varying quantities in the plankton; in late summer, however, it attains a distinct maximum. This takes place before *Microcystis aeruginosa* reaches its far more conspicuous maximum. In 1925 its greatest devel-

opment began in July—August, but it was still present in rather considerable quantities throughout the autumn. In 1926 the maximum occurred at the end of August.

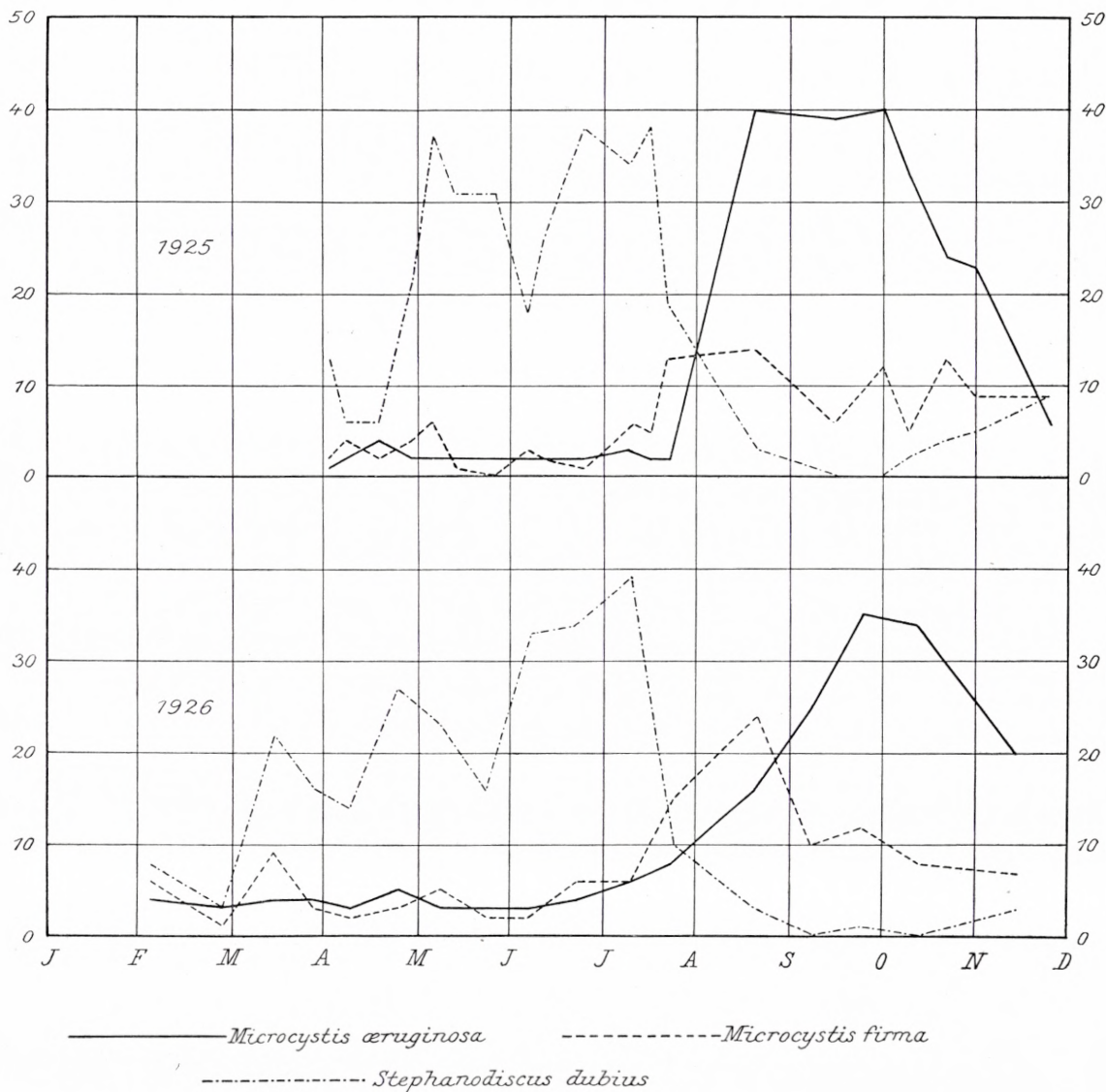


Fig. 12.

Chroococcus Nägeli.

3. *Chroococcus limneticus* Lemm.

Pl. VI, fig. 48.

Like the following species, this one does not play any part in the composition of the plankton, as it has been observed but few times (Jun., 25th, 1925; Aug. 19th, 1926).

The cells were of a deep blue-green colour, and with special teguments they were 7—13 μ broad, and 6—8 μ without special teguments. After C. WESENBERG-LUND (1904, p. 34) it possibly has its maximum in the winter, which is exceptional within the Cyanophyceae.

4. *Chroococcus minimus* Lemm.

Pl. III, fig. 46.

Several specimens of this minute species were observed in February 1926. The cells, 2—3 μ in diameter, were situated in distinct groups of 4 or 8 in a brownish mucus. The colonies were round or oblong, some of them even very elongated.

Gomphosphaeria Kütz.

5. *Gomphosphaeria lacustris* Chodat.

Pl. IV, fig. 23. Text-fig. 19.

In August 1927 I had the opportunity of studying this interesting plankton-organism more closely, as it occurred in rather considerable quantities in the plankton of Tissø, one of the comparatively large Danish lakes. The inner mucus of the colonies showed a distinct branching structure, which was visible in most cases, because the cells were situated rather dispersedly in the periphery of the colony. In the lake of Frederiksborg castle, however, the cells were situated very close to each other, fig. 23 showing one of the less compact colonies. The cells are as a rule pyriform and somewhat longer than broad (1.5—2.5 $\mu \times$ 3.0—4.0 μ), but there are colonies with almost spherical cells. When the latter are closely situated in the mucus, it is very difficult to decide whether it is *Coelosphaerium Kützingianum* Näg. or *Gomphosphaeria lacustris* Chodat.

In the year 1925, which was considerably warmer than the following year, its vegetative period lasted from May to November, and it reached its maximum at the end of July. In 1926 the vegetative period only lasted from June to September; here, too, its maximum development took place at the end of July.

Coelosphaerium Nägeli.

6. *Coelosphaerium Nägelianum* Unger.

Pl. VI, fig. 47.

This characteristic species with pseudovacuoles is very rarely met with in the lake of Frederiksborg castle. The cells were 2—3.5 μ in breadth, 4—7 μ in length. Possibly the hydrogen ion concentration is too low, or the contamination of the water is too great, so that it cannot reach any considerable development. At any rate it can reach a very great development in lakes where p_H oscillates about the value of 7.

Nostocaceae.

Anabaena Bory.7. *Anabaena flos aquae* Breb.?

Pl. V, fig. 11. Text-fig. 13.

The cells are as a rule spherical, now a little shorter, now a little longer than broad. They measure 6—7 μ in breadth, 5—8 μ in length. Heterocysts 8—9 μ in diameter. A typical mass of spores of *Anabaena flos aquae* has been observed; its spores were too narrow for it to belong to the *Anabaena Hassallii* Wittr. In the lake of Frederiksborg castle, however, I never observed the typical gelatinous spheres of *Anabaena flos aquae* with the characteristic trichome loops round a compact aggregation of spores. So the above determination is not quite satisfactory. Strange to say there has been no very great development of this species in the years 1925, 1926, and 1927.

As is common within the *Anabaena*-genus this species has a short vegetative period. It appears at the end of June or the beginning of July and reaches its maximum a little later than the middle of July; then it disappears during September.

8. *Anabaena incrassata* n. sp.

Pl. V, fig. 12—20. Text-fig. 13.

Trichomes single, without gelatinous sheaths, irregularly curved or forming a loose spiral, in most cases with only one spire, free-floating. Vegetative cells quadrangular, 3—4 μ broad, 3—9 μ long, with pseudovacuoles. Heterocysts round, 6 μ in diameter, or oval, 6 μ in breadth, 7—8 μ in length, with or without gelatinous coat. Spores single or two in series, very rarely adjoining a heterocyst, as a rule slightly curved; but straight as well as strongly arcuate spores were observed. Contents granulous, spore wall smooth and colourless, thickened at the end of the spore. Breadth 6—8 μ , length 18—45 μ .

Hab. in the lake of Frederiksborg castle, Denmark, free-floating.

It was only after long deliberations that I found it appropriate to consider this form as a new species. It comes very near to *Anabaena cylindrica* Lemm. and *Anabaena subcylindrica* Borge. The present species differs from both of them in the following way:

1. Presence of pseudovacuoles.
2. The spores are nearly always separated from the heterocysts and often have thickened end-walls.
3. The trichomes do not form thallus, but are found singly; they are strongly curved or more or less spirally twisted, without mucus.

From *Anabaena cylindrica* Lemm. it also differs by the greater length of cells and spores, and then the spores occur singly or at most 2 in series. From

Anabaena subcylindrica the present species differs by the shorter spores and by the fact that the spores are not always isolated, but sometimes occur in series of two.

Spores of more than $35\ \mu$ in length are rare, the average size being about $25\ \mu$. In some cases the middle of the spores is thinner than the ends.

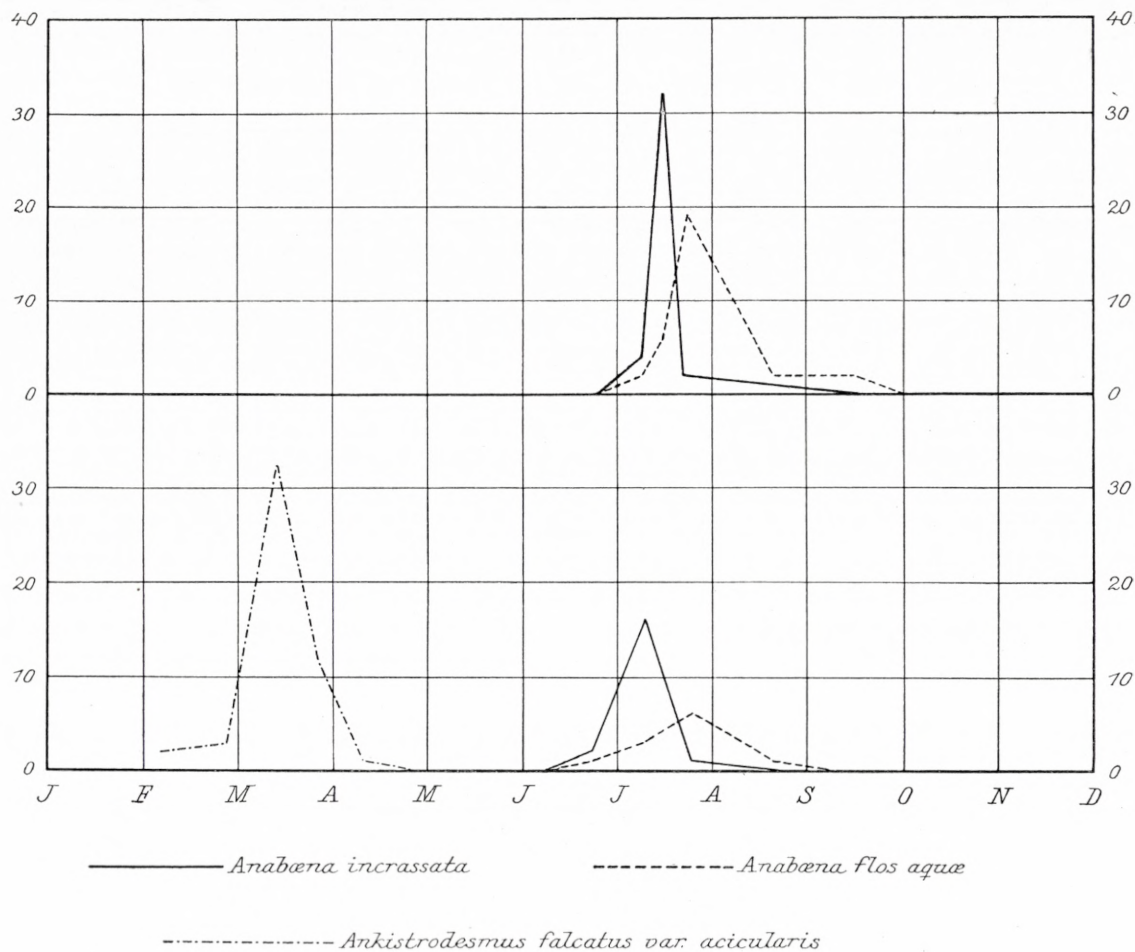


Fig. 13.

In 1927 (July 21st) all the heterocysts had gelatinous coats (see Pl. V, fig. 12), which was not the case in 1925 nor in 1926.

In the warm year 1925 it reached a high development on July 15th, or rather, a short time before. At the time mentioned great numbers of free spores were present in the plankton. Already on July 20th the species was very rare. In 1926 its development was far more insignificant; in this year, too, it reached its maximum in July.

The curve of *Anabaena incrassata* shows a very steep rise and fall. The period of its maximum development is very short, even shorter than that of *Anabaena flos aquae*. Both *Anabaena*-species are good examples of monacmic organisms. The germination of the spores seems to take place in April. The spore figured on Pl. V, fig. 13 was found in a sample from April 18th, 1925. At the investigation in May, 1927, it turned out that a couple of trichomes of *Anabaena incrassata* were found at this early period.

Oscillatoriaceae.

Oscillatoria Vaucher.

9. *Oscillatoria Agardhii* Gomont.

Text-fig. 26.

Many things speak in favour of the opinion that *Lyngbya cryptovaginata* Schkorbatoff (which I only know from Pascher's Süßwasserflora, Cyanophyceae) is identical with this species. The only thing in which *Lyngbya cryptovaginata* differs from the present species, is the slightly narrowed trichomes, the presence of sheaths, and the occurrence in water containing hydric sulphide. At the present investigation it turned out that the forming of sheaths may be very distinct in *Oscillatoria Agardhii*, especially during the *Microcystis*-maximum in the autumn, and these specimens have slightly narrowed trichomes; but as a rule the trichomes have no sheaths. The end cell is either rounded or a little thickened (much as in *Lyngbya major*) or slightly conically thickened (much as in *Phormidium autumnale*). Diameter trich. 5—5.5 μ .

Of all the plankton-forms to be found in the lake of Frederiksborg castle, *Oscillatoria Agardhii* is probably the one which has the greatest power of floating. Even in formaline water it is able to keep floating for several months. Both the living and the dead trichomes place themselves vertically when the water of the glass is quiet. This particular power of floating is the cause why it does not attain any great frequency in the samples of 1925 and 1926, because it is likely that not all the trichomes have been deposited together with the plankton. By filtration through a nitrocellulose membrane this species was pointed out in May 1927 in considerably greater quantities than in the May samples of the two preceding years.

In 1925 when its vegetative period was comparatively short it attained an insignificant maximum in August. In 1926 it was present throughout the autumn and here reached an insignificant maximum in October. However, on Aug. 15th 1927 it was present in such quantities that it gave the plankton a peculiar stamp.

10. *Oscillatoria* sp.

Pl. V, fig. 21.

The trichome very flexible, not constricted, thickness at the middle 5 μ , uniformly tapering towards the end where the trichome was 3 μ thick; it was of a

considerable length, was irregularly curved, and of a pale blue-green colour. The cells were 7–14 μ long, without pseudovacuoles and granules, cross-walls distinct; in the middle of the trichome were found the shortest cells (7 μ), but also here cells of 10–13 μ in length occurred. Terminal cell not narrowing, distinctly incurved, not capitate. Only the terminal cell of the trichome was incurved.

In spite of the fact that only one trichome was observed (both ends showed

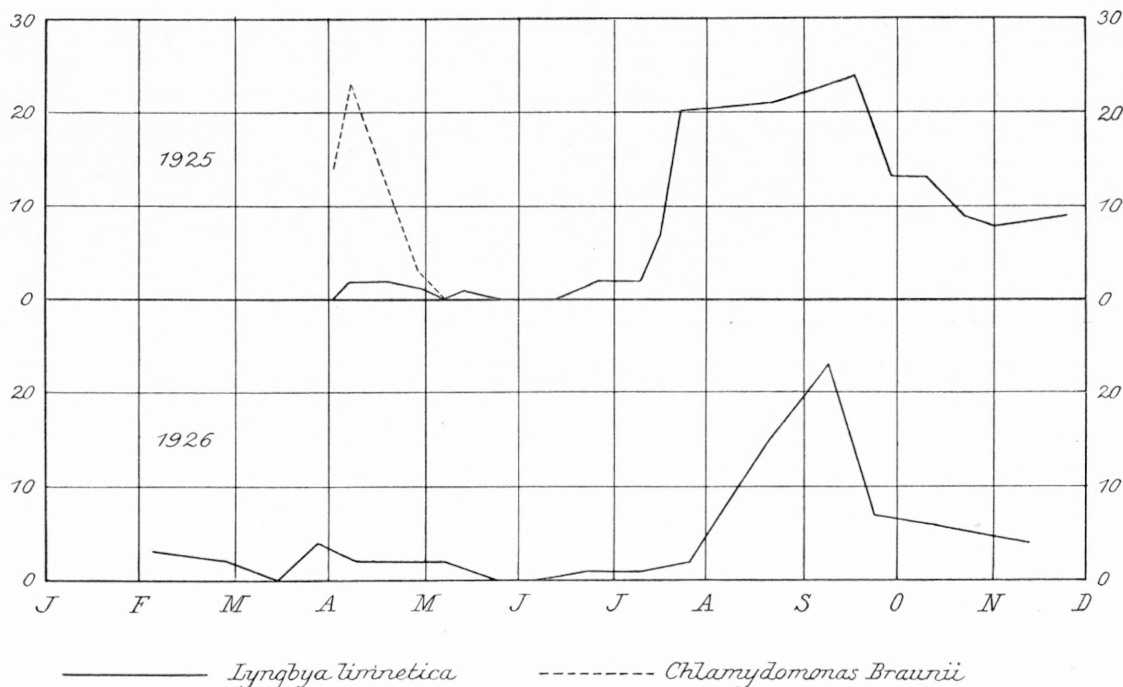


Fig. 14.

the incurvation) the differences (which are emphasised in the diagnosis) from *Oscillatoria Cortiana* Gomont are so great that the specimen cannot be identified with this species. Perhaps the species is an undescribed one. The material is, however, insufficient as a basis for the description of a new species. The alga was observed in April 1925.

Lyngbya Agardh.

11. *Lyngbya limnetica* Lemm.

Text-fig. 14.

This species, to which *Lyngbya lacustris* Lemm. must be reckoned, plays a rather prominent part in the lake of Frederiksborg castle. It seems to disappear during the early summer minimum of the phytoplankton as a whole, and is present

only in small quantities in the plankton of winter and spring. In 1925 it began to develop considerably already in July. It was rather common in the plankton far into September, at which time the maximum occurred. Then it decreased slowly during the autumn. In 1926 its development was hardly so great, but also in this year it attained its maximum in September. Breadth of cells 1.5μ , length $1-2.5 \mu$.

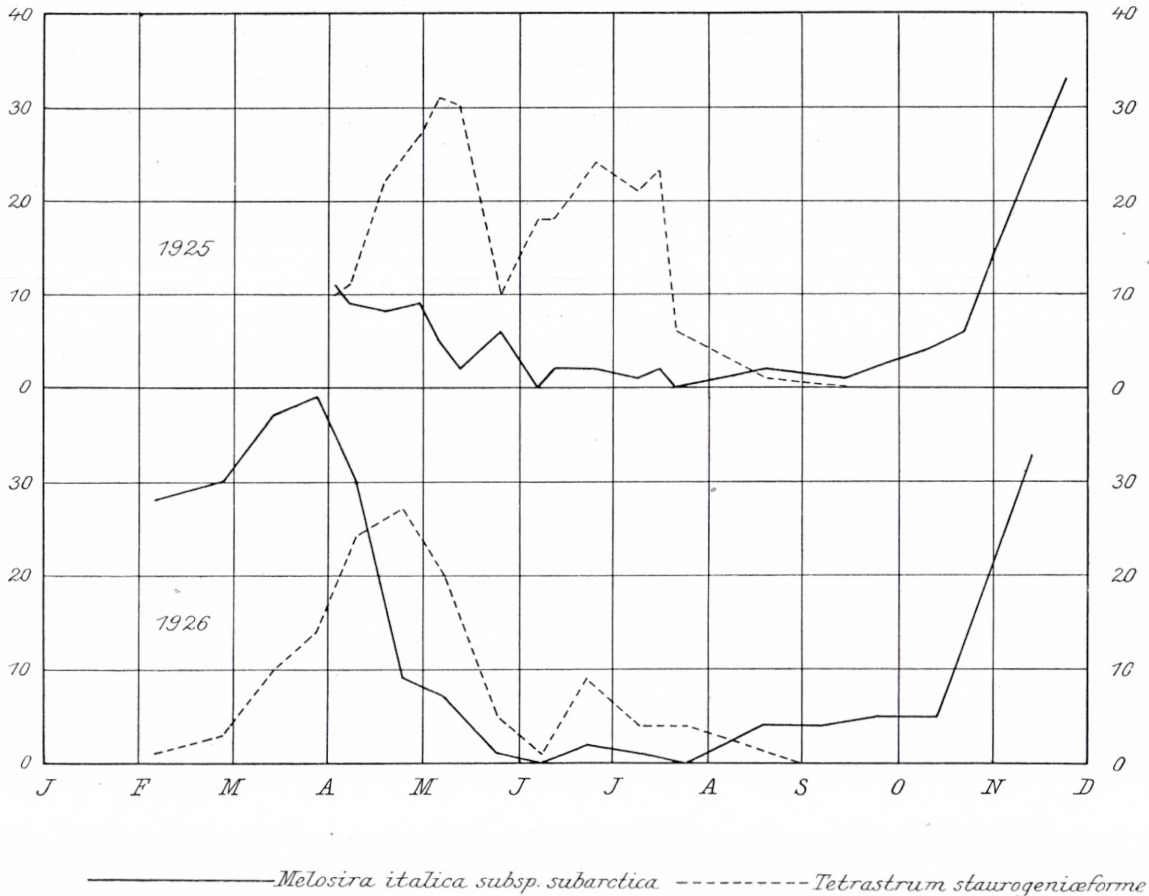


Fig. 15.

Diatomaceae.

Melosirinae.

Melosira Ag.

12. *Melosira italica* Kg. subsp. *subarctica* Müller forma *recta* Müller.

Text-fig. 15 and 16 b.

The present specimens agree well with the diagnosis of Müller. The number of pores and rows of pores is 18—20 in 10μ in the individuals of the lake of

Frederiksborg castle. Müller gives 18 in $10\ \mu$. As to the proportions the species varies very little, considerably less than *Melosira granulata*. Breadth $7-9\ \mu$, height $5-6\ \mu$. It shows a distinct pleomorphism.

This Diatom is a typical cold-water form. In 1926 it reached its considerable maximum at the end of March. Then it decreased more and more during April, but was still present in the plankton in very small quantities until November, when it again began to be common. In 1925 the collections did not begin until April, 2nd, so it is impossible to say anything of its development during the spring of that year. In 1927 it was common in the plankton from March, but from the beginning of April the quantity began to decrease strongly. In other words the species attains its maximum development when the temperature is below 6°C . If the temperature rises above 6°C . the number of individuals decreases strongly. The conditions when the lake is covered with ice are not known, as we have no collections from December and January.

With the exception of *Asterionella gracillima* and *Stephanodiscus Hantzschii* var. *pusillus* the plankton-diatoms are confined to larger lakes. Therefore it is rather peculiar that *Melosira italica* subsp. *subarctica* should attain such a strong development in the lake of Frederiksborg castle, which at most can be characterised as a small lake. It is also significant that *Melosira granulata* and its variety *angustissima*, which are typical lake-forms, play such a small part in the lake of Frederiksborg castle. In the Søgaard Sø in South Jutland *Melosira granulata* var. *angustissima* was common in the *Microcystis*-plankton of mid-summer.

13. *Melosira granulata* Ralfs.

Text-fig. 16 a.

It is present in its typical form together with var. *angustissima* Müller. Both forms show a distinct pleomorphism. The walls of the terminal cells are thick, with coarse pores and the rows of pores parallel with the perivalvular axis. The rest of the cells, those with coarse pores as well as those with delicate ones, have spirally twisted rows of pores. The specimen figured measures $9\ \mu$ in breadth, $16-17\ \mu$ in height; $8-9$ pores in $10\ \mu$.

The species, which is wide-spread in larger lakes, does not by far attain the same development as the preceding species in the lake of Frederiksborg castle. It is found in small and variable quantities at the different seasons, with the exception of the period from August to October when the number of individuals gets more constant. This slightly pronounced maximum is for the most part due to the fact that var.

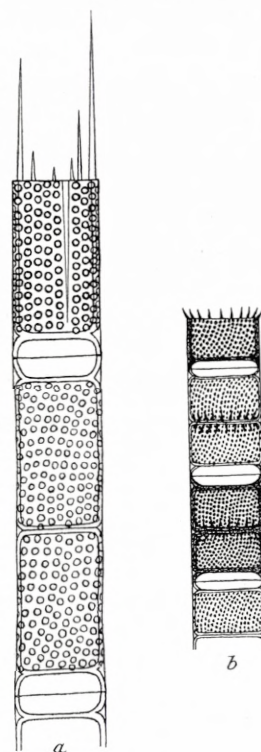


Fig. 16. a: *Melosira granulata* Ralfs, b: *Melosira italica* Kg. subsp. *subarctica* Müller, $1300\times$.

angustissima is more common than at other seasons. Transition-forms between the main species and the variety mentioned have been observed. C. WESENBERG-LUND (1904, p. 64) states the maximum of *Melosira granulata* to be in September—October, which agrees well with the facts of the lake of Frederiksborg castle.

Coscinodiscinae.

Cyclotella Kütz.

14. *Cyclotella comta* Kg.

This species is facultatively periodical in the lake of Frederiksborg castle. Both in 1925 and in 1926 it was very rare, while it had a distinct maximum at the end of April 1927, after which time it quickly decreased in number during the month of May. C. WESENBERG-LUND states its maximum to be in April—May.

15. *Cyclotella Meneghiniana* Kg. var. *plana* Fricke.

Pl. IV, fig. 25.

Occurs in very small quantities and plays no particular part in the composition of the plankton.

Stephanodiscus Ehrb.

16. *Stephanodiscus dubius* (Fricke) Hustedt.

Hustedt 1927, p. 367, fig. 192. — Pl. IV, fig. 24, Text-fig. 12.

This small diatom is one of the most conspicuous organisms in the lake of Frederiksborg castle (s. p. 271). Beside *Asterionella gracillima* only this species together with *Melosira italica* subsp. *subarctica* is able to give the plankton a peculiar stamp at certain seasons. Text-fig. 12 shows three maxima in the development of 1926. The first one, however, was determined by one observation only, the other two by several. So in the present case it cannot be said with certainty whether the species is triacmic or not, but at any rate it is diaemic; this is shown by the curves both of 1925 and 1926. Strange to say the greatest maximum occurs in the middle of the summer, in June—July, while the other maximum occurs in April—May.

Roughly it may be laid down as a rule that the maximum of the plankton-diatoms occurs in the cold season, especially in the spring, but here *Stephanodiscus dubius* stands rather by itself as it also reached a great development during the warmest season — the temperature of the water was then 18°—21.5° C. — and to such a degree that it really characterised the plankton. Similar conditions are displayed by *Rhizolenia longiseta* in our lakes according to the investigations of C. WESENBERG-LUND, as “it occurred abundantly in Almindsø near Silkeborg on Aug. 3rd 1901 (temp. 18°)”.

As to the structure it is to be noticed that the length of the small rectangular edge fields may vary somewhat. The diameter of the cells was 11—19 μ . Dr. FR. HUSTEDT has been so kind as to confirm my determination for which I tender my best thanks.

17. *Stephanodiscus Astraea* Grun. forma?

Pl. IV, fig. 26.

This is an extremely rare form in the lake of Frederiksborg castle; only the specimen figured was observed, and so the above determination is doubtful. Diameter of the cell 14μ ; 4—5 spines in 10μ , and 11—12 rows of pores in 10μ .

18. *Stephanodiscus Hantzschii* Grunow.

Text-fig. 17.

It reaches its maximum development in spring, and the maximum seems to be the greater the smaller the maximum of its variety is. In 1925 its maximum was perhaps considerable smaller than in 1926, but it is difficult to decide, as the samples from 1925 do not go farther back than April. In 1926 it was nearly perennial and had a pronounced maximum in April.

6—7 spines and 13—16 rows of pores in 10μ ; diameter 17μ , height 11μ .

var. *pusillus* Grunow.

Pl. IV, fig. 27—35, Text-fig. 17.

This characteristic variety, which, in the lake of Frederiksborg castle, is connected with the main species by transition-forms, will probably turn out to be very common in our eutrophic lakelets and ponds. Its frustules are so thin that they will scarcely bear being boiled in concentrated sulphuric acid or heated on a cover-glass. The cells form chains with usually 4 individuals, but chains with up to 10 individuals have been observed. The relation between the length and breadth of the cells is very variable, as the cells in some cases are shorter than broad and in other cases twice as long as they are broad; measures: length 7— 13μ , breadth 7— 14μ . The length of the bristles is up to 47μ . Fig. 35, which has been drawn from living material, shows the parietal chromatophores, which are mainly found at the end of the cells.

This variety is of a marked facultative periodicity, attaining a very considerable maximum in April 1925, while only a few specimens were observed in 1926. In 1927 it was not very common on March 12th, and during April it was extremely rare. It seems as if *Stephanodiscus Hantzschii* in certain years appears mainly as var. *pusillus*, while this variety does not reach any development in other years.

Fragilarieae.

Fragilaria Grunow.19. *Fragilaria crotonensis* Kitton.

It plays a very inferior part in the composition of the plankton; only a few specimens were observed on April 3rd, 1927. C. WESENBERG-LUND (1904, p. 70) has pointed out this plankton-diatom in our larger lakes. It is diamic when the

summer temperature of the lake rises much above 16° C. In cold summers, however, the two maxima are reduced to one.

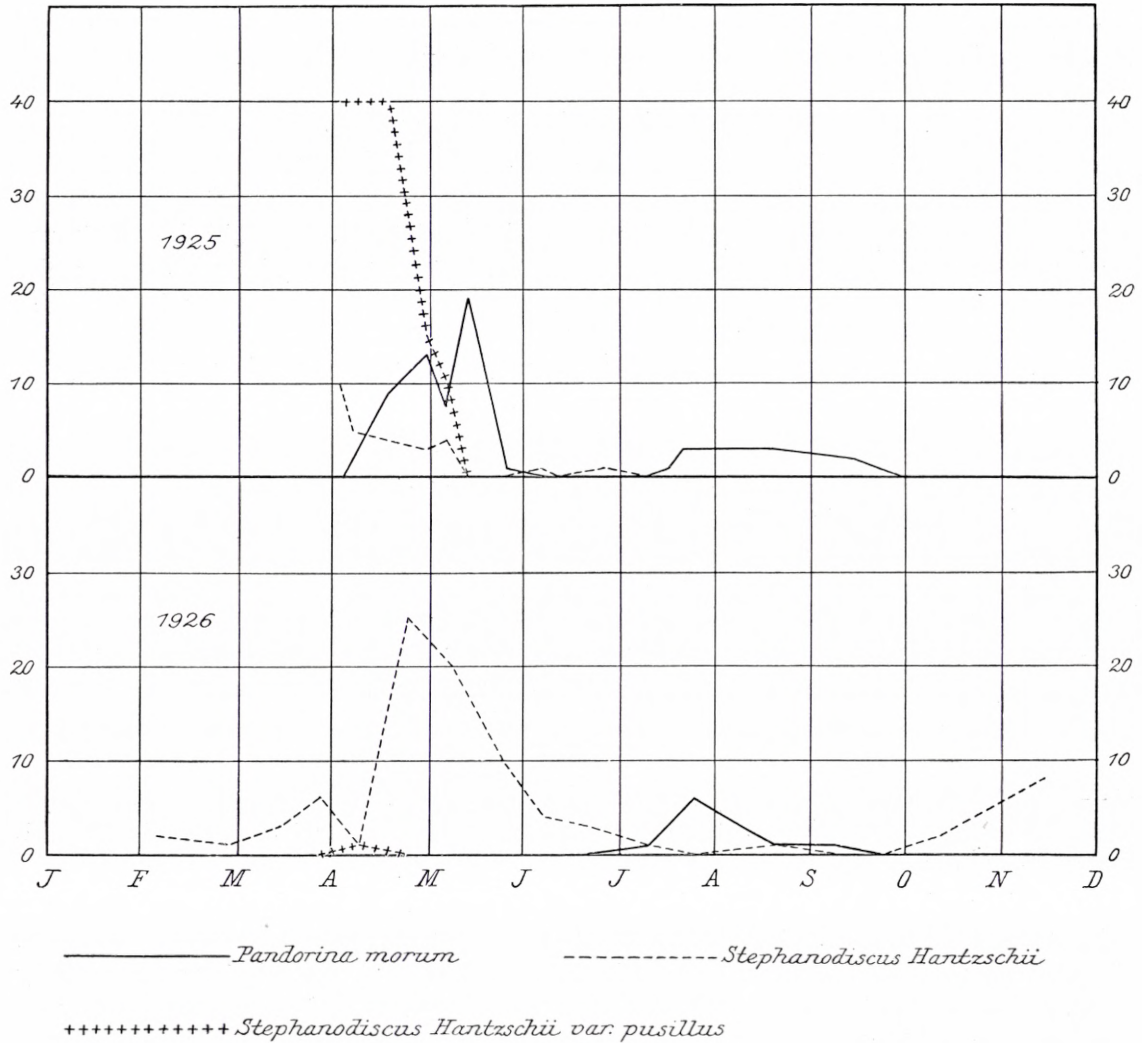


Fig. 17.

Synedra Ehrb.

20. *Synedra acus* Grunow var. *delicatissima* Grunow.

Van Heurck 1884, Pl. 39, fig. 7. — Text-fig. 18 and 26.

All the cells had a central hyaline space and measured 3.5–4.0 μ in breadth and 114–135 μ in length, which is somewhat more than stated by VAN HEURCK (50–100 μ in length). VAN HEURCK further states that there are about 13 striae in

10 μ ; the specimens from the lake of Frederiksborg castle had 14—15 striae in 10 μ . The cells were often more or less curved.

In his great investigation (1904, p. 72) C. WESENBERG-LUND did not find this Diatom in ponds; on the other hand, it is very common in our larger lakes where it reaches its maximum development in April—May. Also ZACHARIAS (1896, p. 57) says that its greatest development occurs in April—May. In the lake of Frederiksborg castle the species attained a rather marked maximum on May 7th, 1926, and then disappeared from the plankton at the beginning of June. In 1925 it was not observed. In 1927 it was present in very small quantities in April and May. The species is monacmic and must be characterised as facultatively periodical.

Asterionella Hassal.

21. *Asterionella gracillima* Heiberg.

Pl. V, fig. 27.

C. WESENBERG-LUND states (1904, p. 74) that it attained an enormous maximum in April—May 1898 in the lake of Frederiksborg castle. The colonies were 4-cellular, which agrees well with the present investigation; only very few 8-cellular colonies were seen by me. C. WESENBERG-LUND has noticed that the 4-rayed colonies only attain their maximum in May. Judging from the material in question (from 1926—1927) the species seems to reach its maximum in March. I do not know if it was present in considerable quantities in 1925, as the investigations did not begin until April 2nd, at which time only very few specimens were seen. In 1926 it reached an insignificant maximum (19+) on March 26th and then disappeared completely during April. In 1927 it attained a distinct maximum (38+) on March 12th, yet it was in no way predominant; *Scenedesmus armatus* var. *Chodati* was quite as common; in this year, too, it disappeared completely during the month of April. Thus, in the years 1925, 1926 and 1927 *Asterionella gracillima* disappeared completely during the month of April, which is by no means always the case as it may often be found in our small lakes and turf-pits till late in the summer.

The species must be classed within the group of organisms which in this paper are described as obligatorily periodical, though it cannot be set up as a good type of this group. Further it has been shown that the species is diacmic, i. e. by C. WESENBERG-LUND (1904, p. 74) and by APSTEIN (1896, p. 141). It is very wide-spread and highly indifferent to different p_H -values (according to my experience its p_H -interval is from 4.2—8.3) and to different concentrations of humic substances. High content of the latter act as a restrictive factor on the richness in species of a

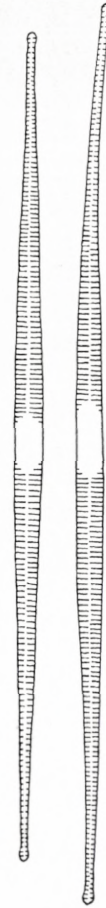


Fig. 18.
Synedra acus
Grun., var.
delicatissima
Grun., 907 \times .

plankton-flora. *Asterionella gracillima* is among the species which can stand high concentrations of humic substances.

The size of the cells during the maximum on March 12th, 1927 was 2—3.5 μ in breadth, but only 27—37 μ in length. VAN HEURCK (1881, Text, p. 154) states the length to be 70—100 μ . In the lake of Frederiksborg castle the colonies (in 1925—27) were thus 4-rayed and had very short and comparatively thick cells.

Silicoflagellatae.

Distephanus Stöhr.

23. **Distephanus erux** Haeckel.

Pl. VI, fig. 59.

It is a wonder to me how this marine Silicoflagellate has got into the fresh water of the lake of Frederiksborg castle. Possibly some offal of fish has been thrown into the lake and so caused its presence. The species was observed in several fragments or a few whole specimens in each of the Diatom-slides (not in the other slides, see p. 267) and is thus present in very small quantities in all the samples. The outlines of the specimens were irregular; this fact suggests a dissolution of the testae. Its silicium testae have apparently been whirled up in the water by the wind.

Length 124 μ , breadth 80 μ .

Flagellatae.

Mallomonadaceae.

Mallomonas Perty.

22. **Mallomonas akrokomos** Ruttner.

Pl. IV, fig. 14—15.

Hitherto this flagellate was only known from the Lunzer See; PASCHER (1913, p. 36) thinks that the species is most likely alpine. After it has now been found also in the lake of Frederiksborg castle, it must be characterised as a cold-water form, as it was observed in very few specimens (one of which contained a cyst) on March 12th, 1927 (temp. 5° C).

Length (without bristle) 26—33 μ , breadth 6—7 μ ; cyst 7×9 μ ; bristles 13—16 μ long.

24. **Mallomonas acaroides** Perty.

This wide-spread pond- and lake-form like the preceding one is extremely rare in the lake of Frederiksborg castle. Only a few specimens were observed in the samples from July.

Euhymenomonadaceae.

Synura Ehrb.

25. *Synura uvella* Ehrb.

Among the flagellates this is one of the most typical spring-forms. It is remarkable that it was not found in the lake in the spring of 1926. On March 12th, 1927, however, it was present in few but well-developed colonies. It is thus facultatively periodical in the lake of Frederiksborg castle.

Lepochromonadineae.

Dinobryon Ehrb.

26. *Dinobryon sociale* Ehrb.

As no well-developed colonies were observed, the determination is not quite certain. Length of cells 35—45 μ , breadth 7—9 μ . Only some very few specimens were observed in the samples from April 1925.

27. *Dinobryon divergens* Imhof.

A couple of poorly developed colonies were observed on May 4th, 1927.

Cryptomonadaceae.

Cryptomonas Ehrb.

28. *Cryptomonas ovata* Ehrb.

Pl. V, fig. 22—24. Text-fig. 19.

As I have not seen how far down the "gorge" ("Schlund") stretched, the above determination is not quite certain. The size: 24—60 μ in length, 15—23 μ in breadth, does not, however, agree with that of *C. erosa* Ehrb., which has considerably smaller cells; also the shape of the cells is more like that of *C. ovata*. The largest specimens often had almost parallel side-walls.

This monacmic species is a spring form, as it reached its rather considerable maximum in March or April and disappeared during May or June.

Euglenaceae.

Phacus Dujardin.

29. *Phacus pyrum* Stein.

Pl. IV, fig. 20—22.

This characteristic and easily recognisable species was observed in some few specimens in April—May 1925 and 1926.

Length 37—43 μ , breadth 19—20 μ .

Trachelomonas Ehrb.**30. Trachelomonas volvocina Ehrb.**

Pl. V, fig. 10. Text-fig. 22.

Cells spherical, smooth or with very delicate pores, which can only be seen in optical transverse section. The diameter is 9–17 μ . The cell-wall is of a deep and pure brown colour. Round the opening of the cilia the test is thickened.

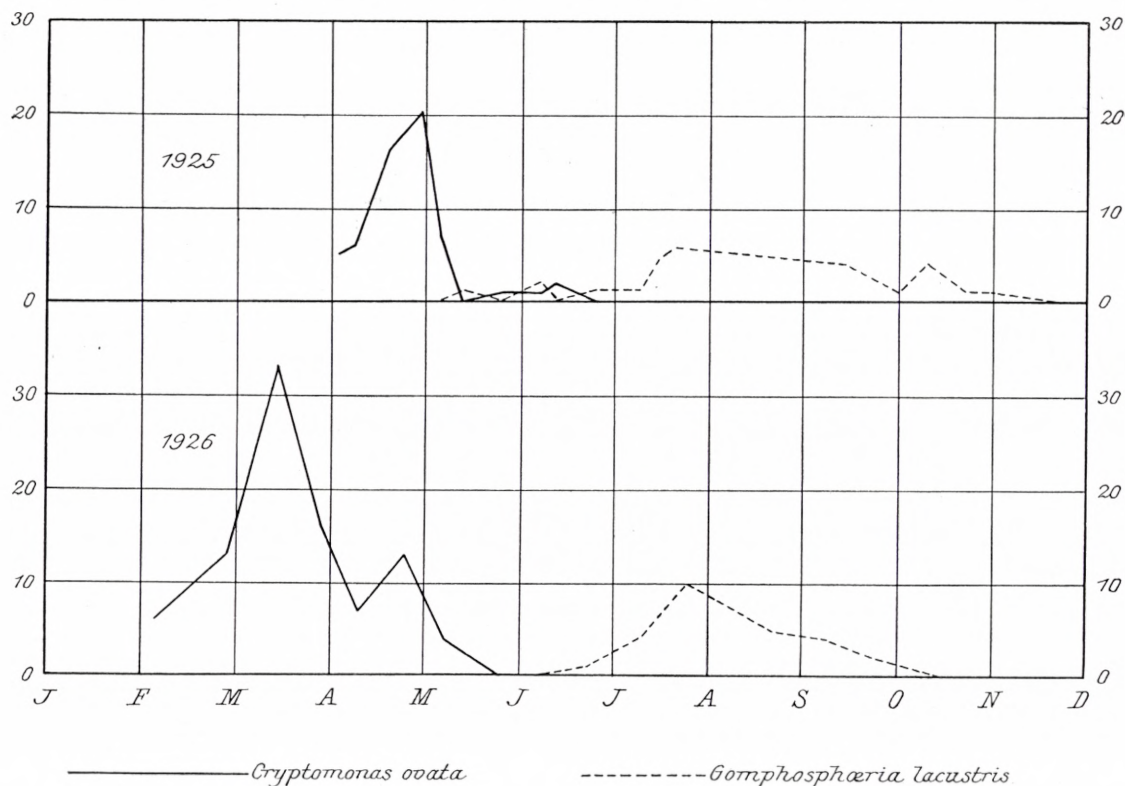


Fig. 19.

The species plays a quite inferior part in the composition of the plankton. In 1925 (from April 2nd) it was perennial, but very rare. In 1926 it was somewhat commoner in February; then it was present in very small quantities until July 9th, after which date it appeared no more during that year. In 1927, from March 12th, it was very sparingly present in the samples. The maximum of the species probably occurs in winter or early spring in the lake of Frederiksborg castle.

forma minuta Fritsch.

Pl. III, fig. 42. Text-fig. 20.

This minute species has been described by Fritsch (1918, p. 485, 603, fig. 43 F), who found it in a South African pond. He states the diameter to be 5–6 μ and

mentions a small pore opposite the opening of the cilia. This pore could also be observed in the present individuals, which were brown, 5—7 μ in diameter, and circular or oval. I never succeeded in pointing out a cilium by means of gentian violet, nor were several chromatophores observed; so it is by no means certain if it is really a *Trachelomonas*.

This form is a typical winter-form, which in 1926 attained a considerable maximum at the end of March (temp. 5° C.), but it was also common in February; it disappeared during April. In 1927 it was extremely rare in the sample from March 12th and later samples from the same year. Nothing can be said of its occurrence in 1925, as the samples only date back to April 2nd. The species is monacmic and seems to be facultatively periodical.

31. *Trachelomonas hispida* Stein var.

Pl. V, fig. 3—8.

This species is very variable in the lake of Frederiksborg castle. The cells were mostly of a pale brown colour with a touch of green; they were oblong, 16—28 μ in length, 14.5—25 μ in breadth (the most common measures are 20—24 $\mu \times$ 17—20 μ). There were most uniform transitions between specimens with very delicate pores (in some specimens the pores were found only at the opposite end of the opening of the cilia) and such as had coarse pores. Also specimens with both sorts of pores were observed (*Trachelomonas hispida* Stein var. *bipunctata* Skvortzow) i. e.: coarser, more dispersed pores among delicate, more closely situated pores. Several specimens with teeth round the opening of the cilia were observed (var. *punctulosa* Skvortzow and var. *papillata* Skvortzow); on the other hand cells with collar and teeth are the rarest (var. *spinulosa* Skvortzow and var. *spinupunctulosa* Skvortzow). Also cells with very delicate spines were observed.

In his richly illustrated paper on the genus *Trachelomonas*, SKVORTZOW (1925) distinguishes between a number of varieties of *Tr. hispida* Stein beside the varieties set up by LEMMERMANN et al. Having seen how much the present species varies, especially with regard to the more delicate structures of the test and, less markedly, with regard to the forming of collar and papillae, I do not think that all these varieties of *Trachelomonas hispida* can be upheld.

The figures below show some measurements of the relation between the cilium and length of the cell; the cilium has been measured by means of a thin thread placed on the drawing along the irregular curves of the cilia and then stretched out:

2.4—2.4—2.5—2.8—3.0—3.2—3.4—3.8.

This relation thus varies considerably. *Trachelomonas hispida* Stein var. occurs as a perennial organism in the lake of Frederiksborg castle, where it is of very small importance. It seems to thrive a little better in early spring than at other seasons.

32. *Trachelomonas Kellogii* Skvortzow var. *effigurata* Skvortzow.

Pl. V, fig. 9.

Only one specimen was observed, on June 7th, 1926.

33. *Trachelomonas* sp.

Pl. V, fig. 1—2.

Cells spherical, 27—28 μ in diameter, irregularly set with coarse verrucae, the number of which seems to vary somewhat; opening of cilium large, 8 μ in diameter; cell-wall colourless.

This is perhaps a new species, at any rate it is not figured in SKVORTZOW'S systematic survey (1925); but as only 2 specimens were seen and the protoplast and cilium are unknown to me, the basis for the description as a new species is too slight. It is not even possible to give an estimate of the season at which this species occurs, as it was found in March and October.

Peranemaceae.

Heteronema Stein.

34. *Heteronema* sp.?

Pl. IV, fig. 18—19.

As only the two specimens figured from preserved material were observed, a more precise determination cannot be given; it seems that the cells are not dorsiventrally flattened. The swimming cilium is of about the same length as the cell or a little longer, the trailing cilium 44—56 μ in length (not considering its windings). Cells 24—28 μ long, 11 μ broad.

The species was only seen in September 1926.

Dinoflagellatae.

Gymnodiniaceae.

Gymnodinium Stein.

35. *Gymnodinium inversum* n. sp.

Pl. V, fig. 28—36.

Cells slightly dorsiventrally flattened, 20—27 μ thick, 28—36 μ long, 23—28 μ broad. Hypovalva rounded and in the greater part of the individuals larger than epivalva, most frequently in length but some times also in breadth. The transversal furrow indistinctly limited, the longitudinal furrow does not continue, or at any rate

continues very little on epivalva, while it stretches far down on hypovalva. Chromatophores brownish, numerous and radiately situated.

Hab. in the lake of Frederiksborg castle, Denmark; limnetic.

The species comes near to *Gymnodinium rufescens* (Penard) Lemm. and *Gymnodinium viride* Penard but differs from both of them, hypovalva being larger than epivalva, which is also the case with *Gymnodinium musei* Danysz.

The species described was not very common in the plankton from March 12th, 1927 — the only time when it was observed with certainty. The temperature was 5.5° C. So many individuals were observed, however, that it was possible to get a rather reliable estimate of the range of variability.

Glenodiniaceae.

Glenodinium Stein.

36. *Glenodinium pulvisculus* Stein.

Pl. III, fig. 47—52.

This species, which mainly occurs together with *Peridinium aciculiferum* Lemm., is rather variable with regard to the relation between length and breadth. The cells are often shorter than broad and in extreme cases may remind one of var. *depressum* Virieux, which occurs in Victoria Nyanza. Breadth 12—20 μ , length 14—19 μ .

The species is present in greater quantities than *Peridinium aciculiferum* Lemm. and is found in early spring; perhaps its quantity is greatest in December—January, but from these months there are no samples. At the beginning of May, when the temperature rises above 10° C., it disappears.

Peridiniaceae.

Peridinium Ehrb.

37. *Peridinium aciculiferum* Lemm.

This characteristic and easily recognisable cold-water form is rather rare in the lake of Frederiksborg castle. Sometimes it appears already at the end of November and apparently reaches its maximum development shortly after the ice breaks up. In the winter and spring of 1926 — the collection of samples began on Febr. 2nd — it was very rare and became more and more rare until the end of March, when it disappeared (at a temperature of 5° C.). In 1927 several specimens were observed on March 12th (temp. 5.5° C.). To judge from the present material the species at any rate disappears when the temperature rises above 8° C.

Length of cells 42—43 μ , breadth 30—31 μ .

Volvocales.

Chlamydomonadaceae.

Carteria Diesing.

38. *Carteria* sp.?

Pl. III, fig. 41.

The cell was heart-shaped with a bell-shaped chromatophore; the length was $11.5\ \mu$, the breadth $9\ \mu$. Only one specimen was seen in the sample from Febr. 5th, 1926.

Chlamydomonas Ehrb.

39. *Chlamydomonas Braunii* Gorosch.

Pl. IV, fig. 7—11. Text-fig. 14.

The species, which is easily recognisable by its crescent-shaped pyrenoid, is most likely monacmic and is of a pronounced facultative periodicity, as it only developed in the spring of 1925 when it attained a maximum on April 7th, and then disappeared at the beginning of May. Neither in 1926 nor in 1927 was it found again.

It measured $18\text{--}24\ \mu$ in length, $17\text{--}20\ \mu$ in breadth.

Phacotus Perty.

40. *Phacotus lenticularis* Stein.

Pl. VI, fig. 37—41. Text-fig. 20.

Beside the typical specimens, which were $16\text{--}19\ \mu$ in diameter and $9\ \mu$ thick, I have seen forms that come near to *Phacotus Lendneri* Chodat, the testae of which have a reticular structure; however, the present specimens looked as if they were thickly set with needles which went in all directions. These individuals, occurring here and there among *Phacotus lenticularis* itself, measured $14\text{--}15\ \mu$ in diameter. Only rarely did I observe individuals with a dentated outstanding membrane as figured in fig. 37. The thickness of the wall varied; a few individuals had very thick testae.

The species is a typical mid-summer form. Already in March it may appear, but only in small quantities; it reaches its maximum development in June—July. Both in 1925 and in 1926 it attained two maxima, one in June, the other in July. Thus the species was diacmic in these two years, but in quite another way than the rest of the organisms of the phytoplankton in the lake of Frederiksborg castle, for its first maximum did not occur in May but in June, at a time when the phytoplankton as a whole showed a relative minimum in a quantitative respect (comp. fig. 20 with fig. 11). Thus the species did not contribute or at any rate contributed very little to the spring maximum in the quantitative development of

the phytoplankton. The two maxima most likely arose by the reaction of the species to those changes of temperature which in both years occurred during the summer. In fig. 20 the temperature curve is also marked out. It is seen that in 1925

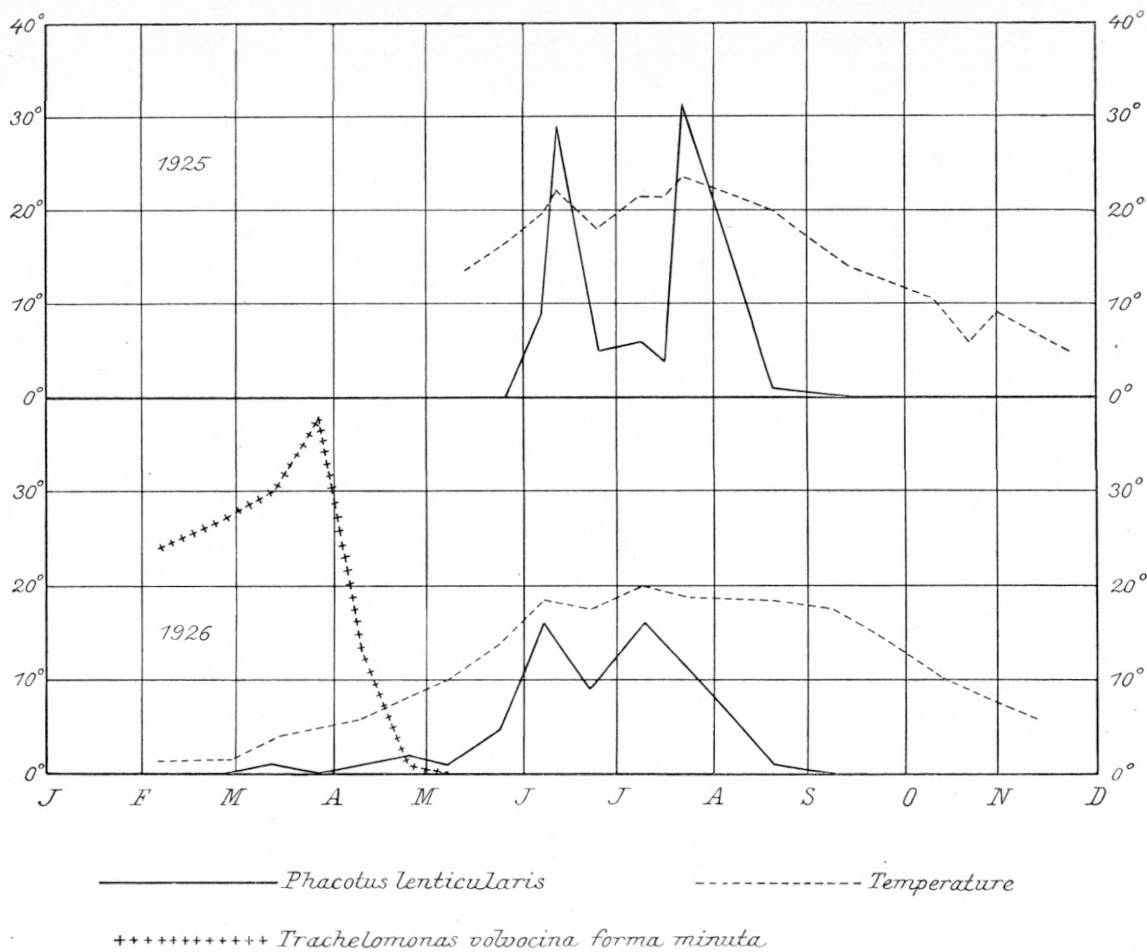


Fig. 20.

Phacotus lenticularis reaches its first maximum at a temperature of 22° C. (June 11th), the second at a temperature of 23.8° C. (July 20th); in the meantime (temperatures 18°—21.5° C.) it had a relative minimum. In 1926 the circumstances were rather similar, but the development was not so great, probably on account of lower temperatures. By the way it is the only plankton-organism in the lake of Frederiksborg castle which prefers particular layers of the water to others; during its maximum development it is most frequent at the surface where temperature and intensity of light are greatest, but considerably rarer at depths of 2 and 3 metres.

Table showing relative frequency of *Phacotus* at different depths.

	0 m.	1 m.	2 m.	3 m.
June 11th, 1925	8 + (23°)	8 + (23°)	7 + (22°)	5 + (20.5°)
July 20th, 1925	10 + (25°)	10 + (25°)	7 + (24°)	4 + (21°)
June 7th, 1926	7 + (20.5°)	5 + (20.5°)	3 + (19°)	1 + (16.5°)
July 9th, 1926	8 + (20.5°)	4 + (20.5°)	4 + (20.5°)	0 (19.5°)

Pteromonas Seligo.

41. *Pteromonas angulosa* Lemm.

Pl. III, fig. 7—15. Text-fig. 21.

The present specimens differ a little from those figured by G. S. WEST (1916, page 7, fig. 5). Fig. 11 shows the testae as they appear in side view; in vertical view (fig. 10, 12) the projecting membrane appears curved. The cells, all of which had one pyrenoid, were 12—18 μ long, 12—17 μ broad, and 7 μ thick. My figures show the difference in the breadth of the projecting membrane and some phases of the division; fig. 15 shows the 4 daughter-cells leaving the wall of the mother-cell fully developed. The division-stages were observed at the end of June 1926.

Biologically the species shows a pronounced spring maximum; in early summer it disappears from the plankton and then develops once more in the middle of the summer. Consequently the species is diamic as against the following species, which curiously enough is monamic.

42. *Pteromonas aculeata* Lemm.

Pl. III, fig. 16—24. Text-fig. 21.

The specimens from the lake of Frederiksborg castle agree well with LEMMERMANN's figures (1900, p. 94, t. 3, fig. 11 *a-c*); the cilia only were of the same length as the cell or somewhat shorter. In vertical view the projecting membrane appears curved; but in side view it is not so curved as shown by LEMMERMANN's figures. 4 pyrenoids are always present; further the species differs from *Pteromonas angulosa* Lemm. by its larger size: length 24—34 μ , breadth 19—24 μ , thickness 8.5—12 μ . In this species I have observed the forming of spores (see fig. 21); the diameter of the spore was 9 μ .

In distinction from the preceding species this one does not participate in the spring maximum of the phytoplankton, its vegetative period being confined to the middle of the summer. Both in 1925 and in 1926 it attained its maximum devel-

opment at the end of July. In comparison with the preceding species its development occurs at a later time.

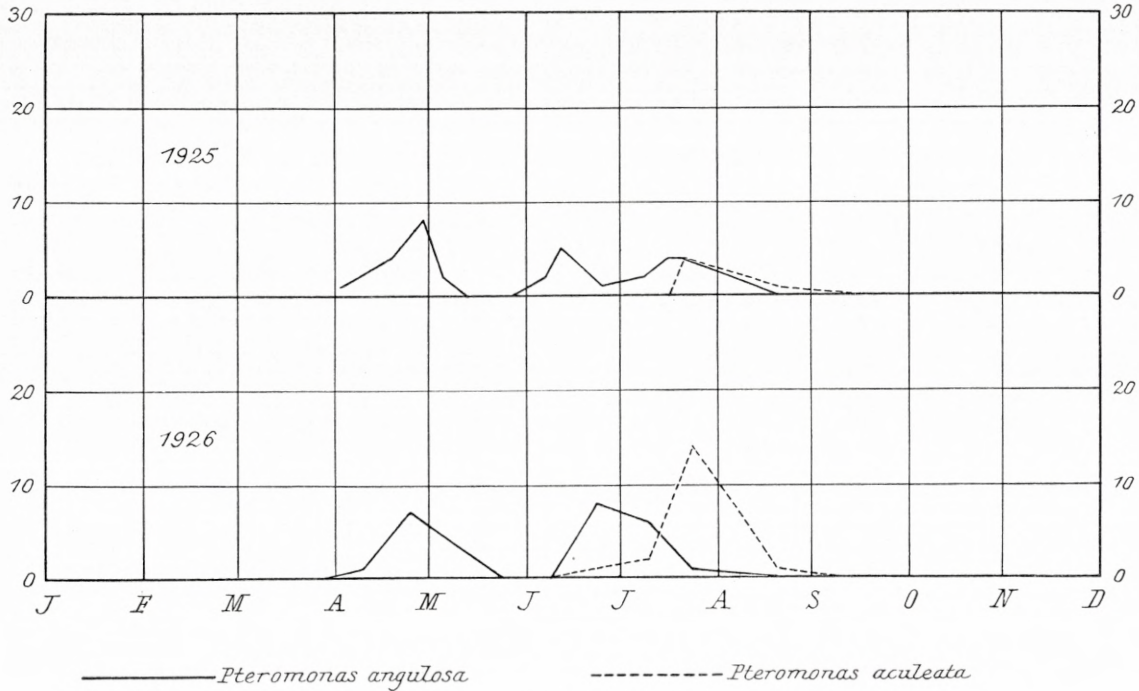


Fig. 21.

Volvocaceae.

Pandorina Bory.

43. *Pandorina morum* Bory.

Text-fig. 17.

It had both a spring- and a summer-maximum in 1925 when it reached a rather considerable development in May. The summer maximum occurred in July. In 1926 and 1927 it only attained a maximum in the summer. The species was thus diaemic in 1925, but monaemic in 1926 and 1927.

Chlorophyceae.

Hydrodictyaceae.

Pediastrum Meyen.

44. *Pediastrum Boryanum* Menegh.

Text-fig. 22.

In his systematic survey of the *Pediastrum*-species NITARDY (1914) distinguishes between *P. Boryanum* Menegh. and *P. pertusum* Kg. According to my experience of the

material in question this distinction can hardly be upheld, as there occur all sorts of transition-forms between the coenobia, which would formerly have been called *P. duplex* Meyen var. *clathratum* A. Braun and a typical *P. Boryanum* Menegh. with the cells closely united.

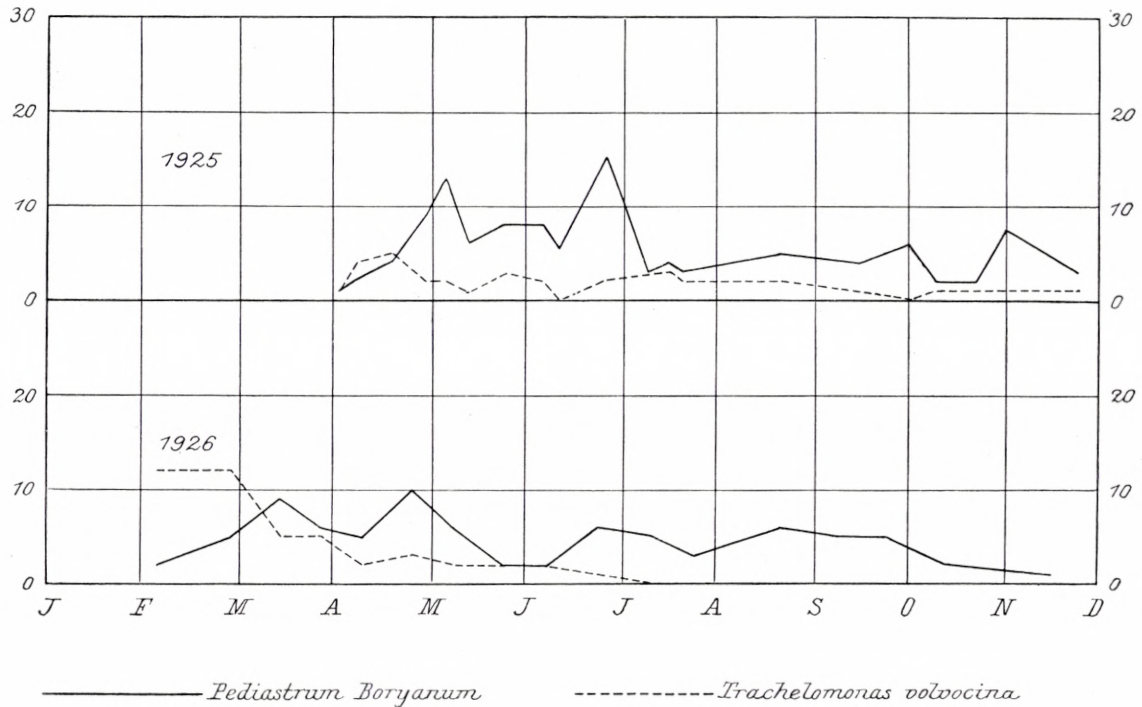


Fig. 22.

The species is perennial and often found in greatly varying quantities in the plankton.

45. *Pediatrum incisum* Nitardy.

This wide-spread species is rarely met with in the lake of Frederiksborg castle. It appears in May and disappears in July or August but is always extremely rare.

Oocystaceae.

Micractinium Fresenius.

46. *Micractinium pusillum* Fresenius.

Text-fig. 23.

The specimens in question cannot be identified with *Errerella bornhemiensis* Conrad, as the chromatophore contained a pyrenoid. C. WESENBERG-LUND (1904, p. 94) found it (*Richteriella botryoides* Lemm.) in the summer samples from two large

Danish lakes. In ponds it is a typical winter- or spring-form according to my experience; only the latter is apparently the case in the lake of Frederiksborg castle, the conspicuous maxima occurring on May 5th (1925) and on March 26th (1926).

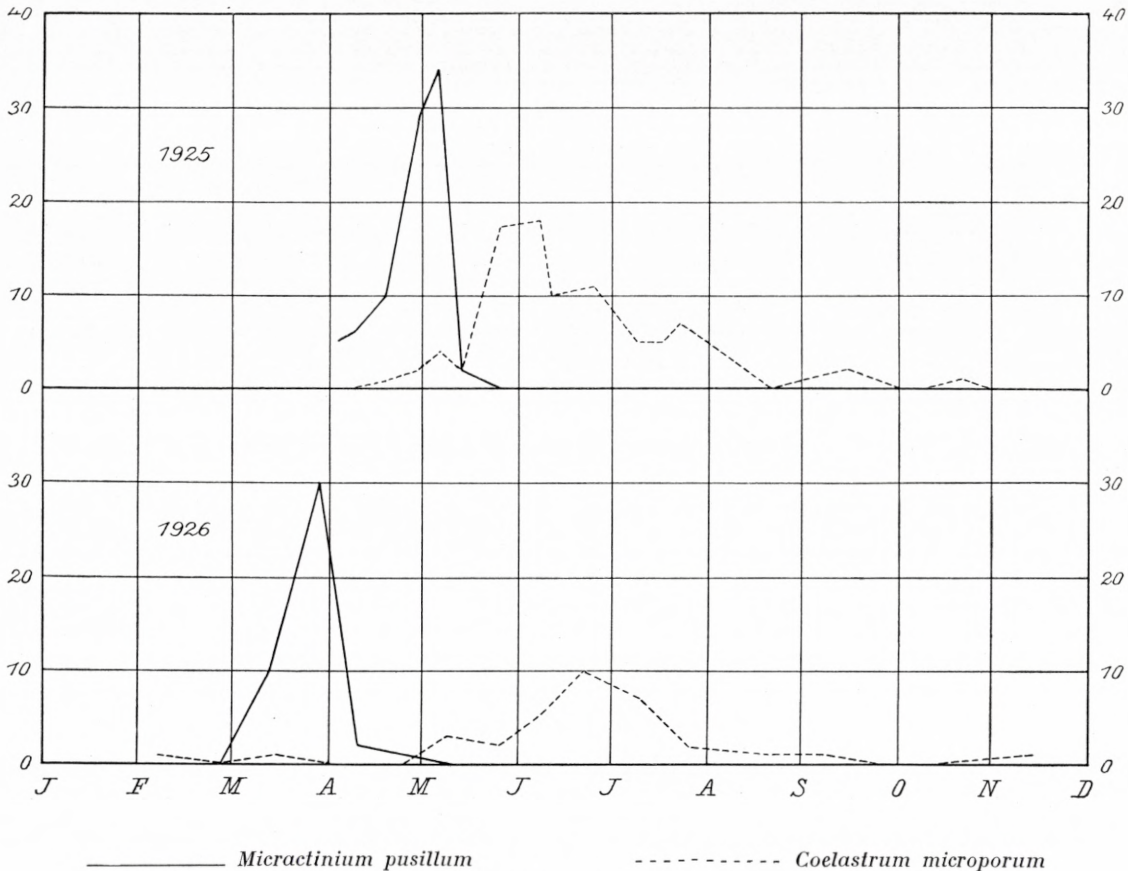


Fig. 23.

I have found it elsewhere in January — immediately after the melting of the ice — in rather considerable quantities. This species will no doubt turn out to be exceedingly frequent in eutrophic ponds.

Lagerheimia Chodat.

47. *Lagerheimia wratislaviensis* Schroeder.

Pl. III, fig. 39—40.

The four bristles of the cells were not hair-shaped but about $1\ \mu$ thick, brownish and short, nearly of the same length as the cells or a little longer; length of cells

13.5—14 μ , breadth 8—10 μ . G. M. SMITH (1922, p. 5) also describes specimens with bristles of a brownish colour from a pond near Stockholm.

The species was observed in very few specimens in April and May 1925.

48. *Lagerheimia quadriseta* Lemm.

A few specimens were observed on April 2nd, 1927.

49. *Lagerheimia longiseta* Printz.

Pl. III, fig. 1—6.

6—9, as a rule 7, bristles at each pole; the length of these bristles varies much, as they may be from 1—3 times as long as the cell. 2—4 chromatophores without a pyrenoid in each cell. Length of cells 15—19 μ , breadth 8—11 μ .

On Pl. V, fig. 26 a *Lagerheimia*-species is figured, which may possibly be classified as *Lagerheimia citriformis* (Snow) Smith. Pl. III, fig. 43—45 shows another *Lagerheimia*-species, the cells of which have only 4 bristles and are 11—18 μ in length, 5.5—13 μ in breadth; this species possibly comes near to *L. longiseta*. The material, however, is too scarce for a certain determination.

The vegetative period of this species seems to be in April—June; the greatest number of specimens were observed in May; like the two preceding species of *Lagerheimia* it is, however, extremely rare in the lake of Frederiksborg castle.

Oocystis Nägeli.

50. *Oocystis parva* W. & G. S. West.

Pl. VI, fig. 26—34. Text-fig. 24.

During the spring of 1927 I studied the living plankton of the lake, which was of importance especially in order to get a more thorough knowledge of the inner structure of certain organisms. It then became apparent, that each of the *Oocystis*-cells contains 1—4 chromatophores without distinct pyrenoids; further two or three small droplets of oil were as a rule found at either end of the cell. Breadth of the cells 4—9 μ , length 8.5—13 μ , size of the colonies 11.5—34 μ .

I have been in great doubt as to whether the specimens should be identified with *Oocystis parva* West or with *Oocystis pusilla* Hansg. (see PRINTZ, 1913, p. 181). In fact these two species are so nearly related that it would perhaps be most correct to unite them. As to the inner structure of the cells it is the same in both species, but according to the descriptions the form of the cells is different, the cells of *O. parva* being broadly fusiform and a little asymmetrical, while the cells of *O. pusilla* are rounded at the ends. However, all transitions between these two shapes of cells were observed in the present material. The other characteristic of *O. parva*, that of the mother-cell-wall having two polar thickenings, is not always

conspicuous because this thickening is sometimes very little developed. By far the greater part of the specimens observed could, however, with certainty be identified with *Oocystis parva* West.

The species is likely to be perennial. It reaches its maximum development within the period May—July.

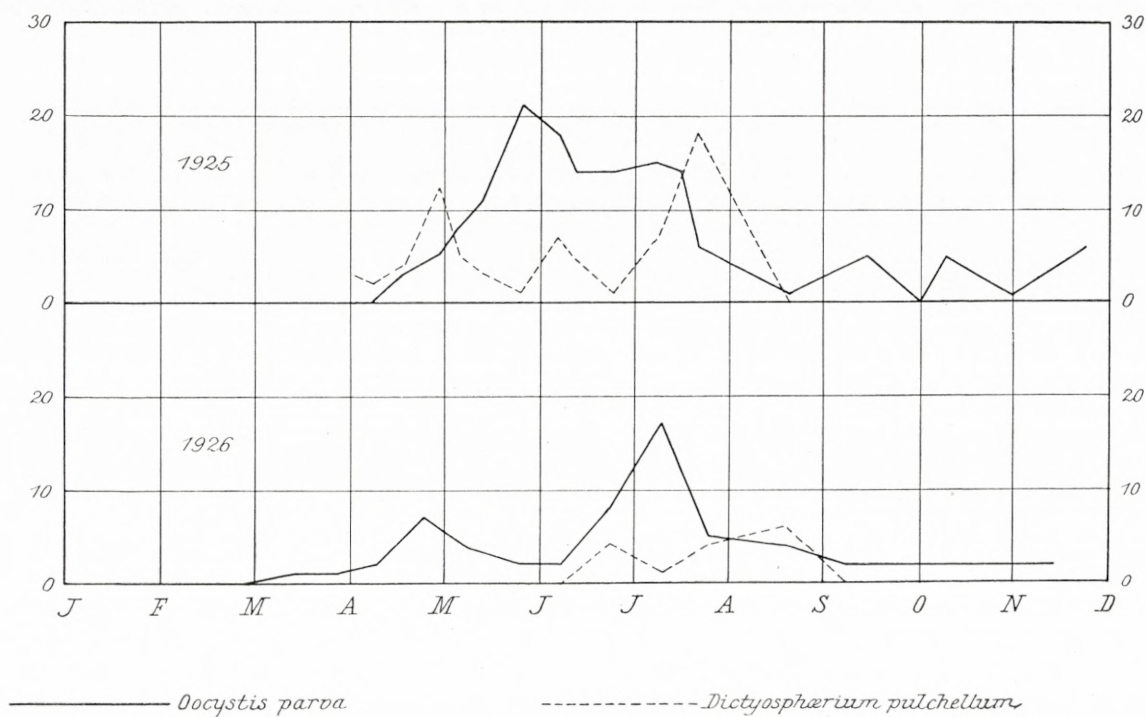


Fig. 24.

Kirchneriella Schmidle.

51. *Kirchneriella obesa* Schmidle.

Pl. VI, fig. 45—46.

Only observed a few times in the spring, e. g. on April 2nd, 1927, when it was extremely rare.

Length of cells $10\ \mu$, breadth $6-7\ \mu$.

52. *Kirchneriella contorta* Bohlin.

Pl. V, fig. 40, and Pl. VI, fig. 42—44.

This species, the cells of which measure $1.5-2\ \mu$ in breadth, $7-8\ \mu$ in length (in diameter), is present in greater quantities than the preceding species. In 1925 its development was not very considerable; it attained its greatest frequency (8+) at the end of July. In 1926 the species, however, also attained a spring maximum,

during which it reached a relative frequency of 19+ (April 9th); the mid-summer maximum was then quite insignificant.

On Pl. V, fig. 40 I have figured some specimens which come near to *Selenastrum capricornutum* Printz (1914, p. 92, tab. VII, fig. 195). The cells, which were partly solitary and partly lying two or four together, were spirally twisted, but the spiral was not situated in one plane; they measured 1—2 μ in breadth and 5—7 μ in diameter. The cells, however, did not touch each other on the dorsal sides, which is a specific character of the genus *Selenastrum*, but were irregularly placed in relation to each other. They were never enveloped in mucous investments. Further all transitions are found between acute, spiral cells and rounded, more or less circularly curved cells. Neither the determination as *Kirchneriella contorta* nor that as *Selenastrum capricornutum* is thus satisfying.

Tetraedron Kütz.

53. *Tetraedron muticum* Hansgirg.

Pl. V, fig. 37.

It is most common in April—May, but like all the other *Tetraedron*-species it plays a quite inferior part in the lake of Frederiksborg castle. In 1925, when on the whole it was more common than in 1926, it was present in the greatest quantity on May 12th.

54. *Tetraedron minimum* Hansgirg.

Pl. IV, fig. 16—17.

The specimens are as a rule 9—10 μ in size, rarely up to 15 μ ; the largest individuals show a distinct punctuation of the cell-wall. The cells had one pyrenoid. It is present as a perennial organism and reaches its greatest development in the middle of the summer.

55. *Tetraedron arthrodesmiforme* G. S. West.

Pl. V, fig. 39.

J. WOŁOSZYŃSKA has set up quite a number of varieties and forms of this species from Africa (1914, p. 203). The present specimens come nearest to var. *contorta* Wolosz. or *Tetraedron victoriae* Wolosz., forms which are perhaps identical with *Tetraedron arthrodesmiforme* West. They had veritable spines at the four ends of the cell, and the two semicell-like parts were twisted in proportion to each other. Size 15 μ without spines. The species was only observed a few times in 1925 within the period May—July.

56. *Tetraedron caudatum* Hansgirg.

Pl. V, fig. 38.

The most common form was var. *incisum* Lagerh.; also var. *punctatum* Lagerh. was observed. Diameter of cells 17—23 μ . Several times I observed a mother-cell

with one smaller cell within (fig. 38). It is not easy to decide whether this small cell may be considered as a daughter-cell left behind, or if it is a sort of rejuvenescence of the cell without division.

This species also reaches its maximum development in May—July; but it does not seem to be perennial as both in 1925 and 1926 it did not appear until the end of April.

57. *Tetraedron Schmidlei* Lemm. var. *eurycanthum* Lemm.

Pl. IV, fig. 12—13.

With this remarkable species, which apart from the proportions of size bears a considerable resemblance to *Borgea planctonica* Smith (1922, p. 2), I think it possible to identify the organisms shown in fig. 12—13. Breadth without spines 7—8 μ , with spines 21—22 μ . This form was observed only a few times, viz. on May 5th, 1925 and on May 7th, 1926.

58. *Tetraedron limneticum* Borge var. *simplex* Schröder.

Pl. VI, fig. 35—36.

The figures show two extreme forms of this variety; it bears a certain resemblance to *Tetraedron hastatum* Hansg. var. *palatinum* Lemm. Size 48—50 μ , the middle part 10—13 μ broad. Several specimens were observed in June—July in both years, but still it is extremely rare in the lake of Frederiksborg castle.

Coelastraceae.

Dictyosphaerium Nägeli.

59. *Dictyosphaerium pulchellum* Wood.

Pl. VI, fig. 60—64.

This species often shows a peculiar and regular structure of the gelatinous envelope. In material fixed in formaline these structures are very indistinct. Figs. 61 and 63 were drawn from living specimens. Fig. 63 highly resembles *Dictyosphaerium tetrachotomum* Printz (1914, p. 24, tab. I, figs. 5—6), a species which is based entirely upon the tetrachotomously branching threads of mucus. Size of cells of the specimens from the lake of Frederiksborg castle 4—8 μ in diameter.

This easily recognisable green alga is not exclusively confined to ponds, but may also be found in our larger lakes. C. WESENBERG-LUND mentions (1904, p. 93) a great maximum in Esrom Sø on Sept. 30th, 1901. In the lake of Frederiksborg castle it seems to reach its maximum either in July or August, but its occurrence varies somewhat from year to year. In 1925 it reached a distinct spring maximum at the end of April. At the end of July it once more attained a rather considerable development and then disappeared during August. In 1926 strange to say the spring maximum failed to appear, and the species did not make its appearance until

June and had a quite insignificant maximum in August. Then it disappeared at the beginning of September.

Scenedesmus Meyen.

60. *Scenedesmus dimorphus* Kg.

Pl. VI, fig. 49—50.

This organism is very rare, but perennial in the lake in question. At the beginning of April 1927, however, it was present in somewhat greater quantities, but still in no way characterising the plankton.

61. *Scenedesmus armatus* Chodat.

Pl. VI, fig. 51—58. Text-fig. 25.

G. M. SMITH (1916) gives the following measures for var. *Chodati* Smith: $3.5-5 \mu \times 11-15 \mu$. The present specimens measure $2.5-4 \mu \times 8-11 \mu$, but in the spring (March—April) coenobia are found, the cells of which measure up to 10μ in breadth and up to 37μ in length (fig. 56), which shows that there is a rather considerable range of variation in the proportions of the variety. Var. *subalternans* Smith (fig. 54 and 57) is found in very small quantities beside the other variety; its cells are more or less pyriform and measure $9-10 \mu$ in length and $5-6 \mu$ in breadth.

It is a rather exceptional case that a species like this is common in the plankton all the year round. In 1926 it reached the relative frequency c (40+) in all the samples; in the samples from April 9th—June 7th (incl.) it attained cc with a maximum ccc on April 24th. In 1925 it was rather rare in the samples from the beginning of April, but increased during the month, so that it had attained the relative frequency c (40+) at the end of April. Its greatest development occurred at the end of May (relative frequency cc). From May 25th to July 15th, it was present with a frequency of cc and the rest of the year with a frequency of c. It is noticeable that it thrived well during the enormous *Microcystis aeruginosa*-maximum.

In the tabular survey on p. 271 the relative annual average of the species is calculated at 49 and 54, values which by far exceed the annual averages of all the other organisms, which never surpass 20. These two values for *Scenedesmus armatus* var. *Chodati* are not too great; as to their calculation see p. 269.

The species was present as 2-, 4-, and 8-cellular coenobia. Now it turns out that at a certain season either the 2-cellular or the 4-cellular coenobia are predominant. The minimum development of the 2-cellular coenobia occurs in June or May, while their maximum development occurs in September or October, nearly simultaneously with the maximum of *Microcystis aeruginosa*; at this time they may constitute up to 78% of all the coenobia. The 4-cellular coenobia, however, are most common in the spring, in April or May, when the species as a whole has its maximum, while their minimum development occurs in September or October. At

the end of May 1925 not less than 96 % of all the coenobia were 4-cellular. The 8-cellular coenobia play a quite inferior part; the highest number observed here is 13 % (at the end of April 1925).

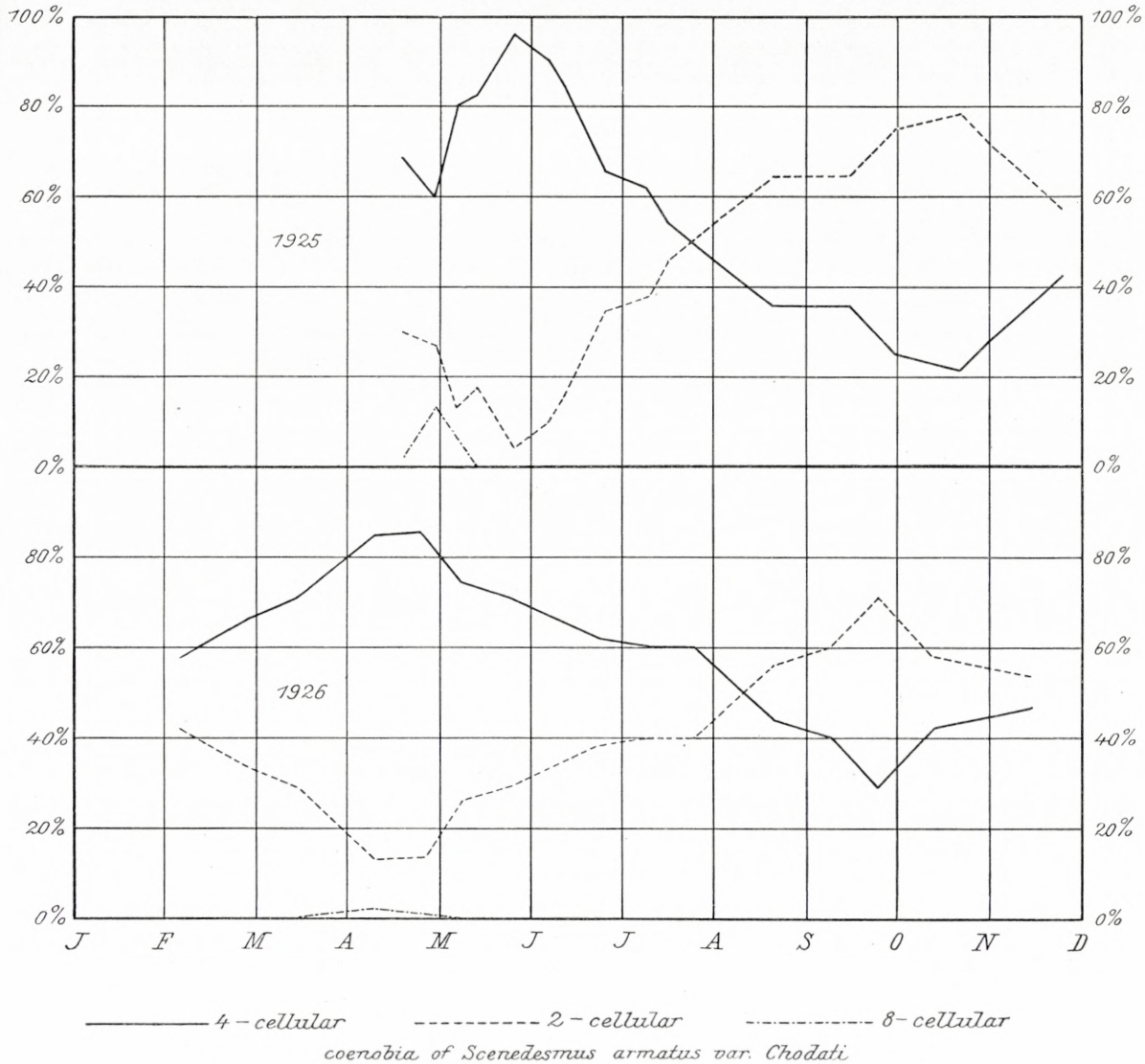


Fig. 25.

62. *Scenedesmus arcuatus* Lemm.

Pl. V, fig. 41—43.

This species, which is rare in the lake of Frederiksborg castle, is a typical summer form. In 1925 its vegetative period extended from the end of May to Sep-

tember; most specimens were observed in June and July. In 1926 the species was confined to the month of July. Length of cells 12—16 μ , breadth 4.5—7 μ .

Actinastrum Lagerheim.

63. Actinastrum Hantzschii Lagerh.

Pl. IV, fig. 1—6.

This easily recognisable green alga is present both as a spring- and a summer-form. The spring-form, present in several specimens in April 1925, has slender and slightly curved cells, which are 25—34 μ long, 3—7 μ broad; whereas the cells of the summer-form are short and straight, 13—18 μ long, 3—5 μ broad. While the cells of the summer-form are 3—4.5 times as long as they are broad, the cells of the spring-form are 3.7—10 times as long as they are broad. Syncoenobia are not common, but were seen both in the spring- and the summer-form.

An interesting circumstance — and as far as I know not previously observed — is the forming of resting-spores. They are only found in the cells of the spring-form. The spores, which are always furnished with a small oil body at the end facing the base of the mother-cell, are oval, sometimes a little edged, 5.5—7.5 μ broad, 8—10.5 μ long. Fig. 1 shows a coenobium composed of one cell with a resting-spore, three degenerated cells, and two cells in full growth and division. This circumstance may perhaps be explained by the supposition that the coenobium has been exposed to very changeable external conditions.

In 1925 the vegetative period of the spring-form extend from April to May (both incl.) with a very insignificant maximum at the middle of April. The vegetative period of the summer-form began at the end of June and continued into August with an insignificant maximum on July 20th. In 1926 the spring-form was much rarer than in 1925 and only present at the end of March; the vegetative period of the summer-form, however, occurred within the same time as in 1925 and its maximum took place on July 23rd.

It seems unlikely to me that the summer-form should arise from the resting-spores of the spring-form, as the latent period of the resting-spores could then be only 1—2 months. Supposing, however, that the latent period is considerably longer, probably nearly a year, we are dealing with two not only morphologically but also biologically different forms of *Actinastrum Hantzschii* Lagerheim.

Tetrastrum Chodat.

64. Tetrastrum apiculatum Schmidle.

A few specimens were observed in the spring- and summer-samples.

65. *Tetrastrum staurogeniaeforme* Lemm.

Text-fig. 15.

This small diacmic species, the cells of which have a pyrenoid, exhibits the peculiarity in its life-cycle that the spring-maximum in April or May is greater than the summer maximum in June or July. This was especially obvious in 1926. In 1925 its development was rather considerable in the middle of the summer. Apart from the all-dominating *Scenedesmus armatus* var. *Chodati* it is the Chlorophyceae which plays the greatest part in the lake of Frederiksborg castle (see table on p. 271).

Coelastrum Nägeli.66. *Coelastrum microporum* Nägeli.

Text-fig. 23.

The species, which is perennial, attains its maximum at the end of May or in June. This maximum, which was not very great, was more considerable in the warm year of 1925 than in the cooler year of 1926. Like *Dictyosphaerium pulchellum* it is not exclusively confined to ponds, but, according to C. WESENBERG-LUND, reached a great maximum in the Viborg Sø in June—July, 1902.

Ankistrodesmus Corda.67. *Ankistrodesmus falcatus* Ralfs.

Pl. VI, fig. 14—16.

This species appears in several forms, which are sometimes very difficult to separate from each other. The comparatively thick specimens, which measure 70—130 μ in length, 3—6 μ in breadth, are identified with the main species. The latter was extremely rare in 1925, but in 1926 and 1927 several specimens were observed in April—May, especially on April 2nd, 1927. Fig. 15 shows a specimen forming a spore; this specimen was observed on July 20th, 1927.

Var. *spirilliformis* G. S. West. (Pl. VI, fig. 17) was only observed in very few specimens in April 1925, 1926, and 1927 and in June 1925. Length 36 μ , breadth 1.5 μ .

Var. *acicularis* G. S. West. (Pl. VI, fig. 22—25) is present in its typical form. Length of cells 60—80 μ , breadth 1.5—1.75 μ . The chromatophore does not continue into the hyaline and extremely delicate points of the cell. The chloroplast is interrupted in the middle of the cell and often fragmented as in *Ankistrodesmus fractus* (W. & G. S. West) Brunthaler, which seems to be a dubious species. Like this species the present individuals are often slightly curved, so that the hyaline apices are a little recurvate. This variety, which is the only one of the species and varieties of

Ankistrodesmus that plays a prominent part in the lake of Frederiksborg castle, is perhaps facultatively periodical, reaching a rather considerable maximum on March

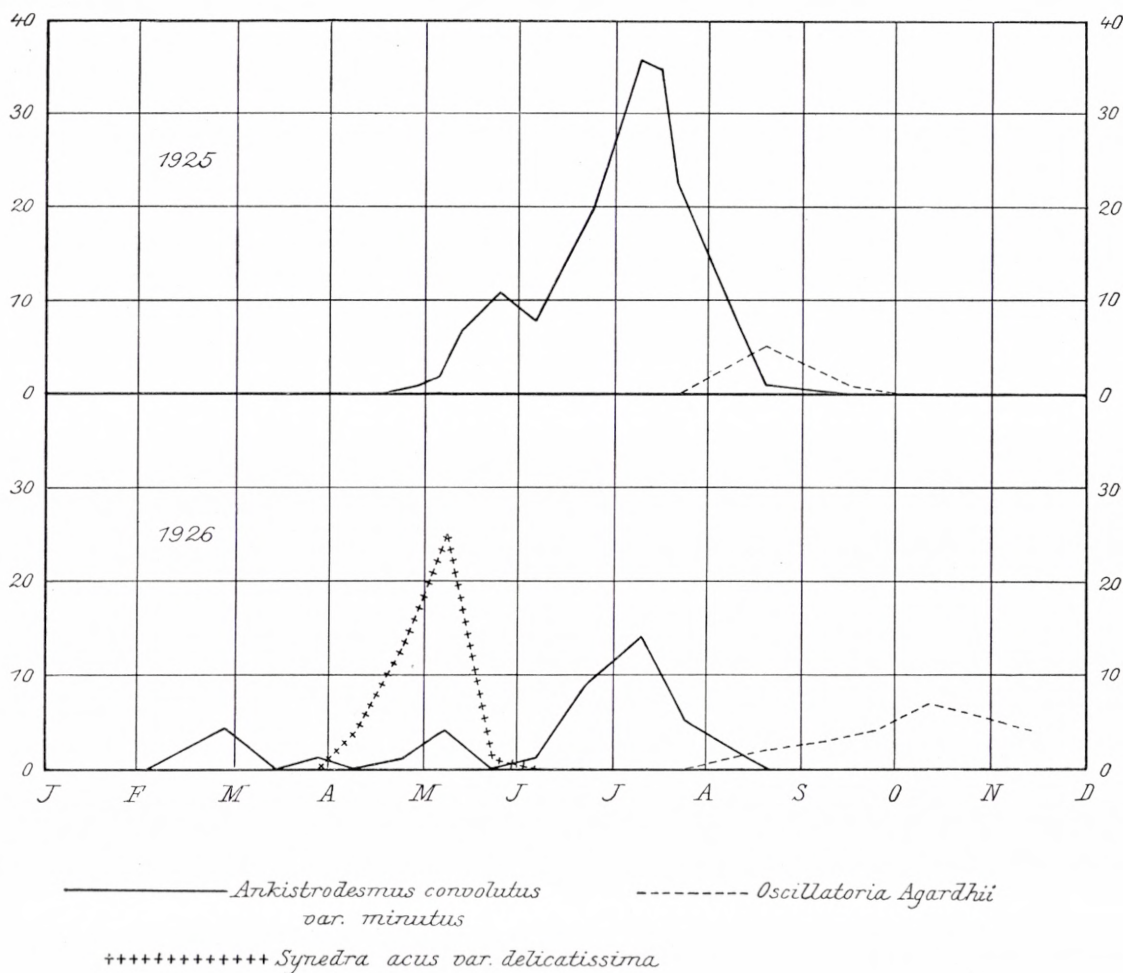


Fig. 26.

13th, 1926. Then it disappeared at the beginning of April. In 1927 it was not present in the plankton from March and April. Text-fig. 13.

Figs. 18—21 on Pl. VI are nearly related to var. *acicularis* West but differ by the absence of the long hyaline and slightly recurvate apices. This form appeared in April and decreased at the end of May. It increased once more in June and attained a quite inconsiderable maximum in July, at the end of which month it disappeared from the plankton. The cells measured $1.5-2\ \mu$ in breadth and $86-138\ \mu$ in length.

68. *Ankistrodesmus convolutus* Corda var. *minutus* Rab.

Pl. V, fig. 25. Text-fig. 26.

This small, easily recognisable species, the cells of which were 10—12 μ long, 4—5 μ broad, attained its maximum development in the middle of the summer (July). In 1925 its development was very considerable, more pronounced than in 1926; this is perhaps due to the lower summer temperatures of 1926. The curves in fig. 26 show that the species may be found in the winter and throughout the spring; it disappears from the plankton in August or September and is thus obligately periodical.

69. *Ankistrodesmus Falcula* Brunnth.?

Pl. VI, fig. 11—13.

According to the description of the species the cells are nearly ellipsoid or lanceolate in the middle, which is not in agreement with the present specimens. Size: 4—9 μ in breadth, 23—31 μ in diameter. The cells were falcate or slightly spiral as illustrated by the figures. Figs. 12—13 show the densely situated, new-formed cells surrounded by the membrane of the mother-cell.

The species has its vegetative period within the months of April to July but is always extremely rare.

70. *Ankistrodesmus longissimus* Wille var. *gelifactum* Chodat.

Pl. VI, fig. 1—10.

During my study of the living plankton in the spring of 1927 I had the opportunity of ascertaining that one or two chromatophores, each with its pyrenoid, were present in all the cells. In preserved material as a rule no pyrenoids were visible, not even after staining. The specimens from the lake of Frederiksborg castle are nearly related to *Ankistrodesmus lacustris* Ostefeld, in the cells of which pyrenoids are, however, lacking. The proportions of *Ankistrodesmus longissimus* var. *gelifactum* are unknown to me. The colonies of the present specimens are 17—37 μ broad, 23—53 μ long; the cells are 3—5 μ broad and 11—20 μ long.

This form is never present in considerable quantities in the spring; its proper vegetative period occurs in the middle of the summer with an almost imperceptible maximum at the end of July. It may, however, be found in very small quantities throughout the autumn until November, at which time it disappears not to reappear until April or May in the next year. Thus the species is not perennial.

Desmidiaceae.

This group, which contains many genuine plankton-forms, is of no great importance in the lake of Frederiksborg castle. Of the following four organisms *Closterium subulatum* is the only one which is fairly common in the plankton. The cause is most likely the considerable contamination of the water.

Closterium Nitzsch.

As I was not quite able to determine the systematic position of the two *Closterium*-species in question, some drawings were sent to Dr. O. BORGE in Stockholm, who was so kind as to express his opinion of it. I tender my best thanks to Dr. Borge.

71. *Closterium polymorphum* n. sp.

Pl. III, fig. 25—33. Text-fig. 27.

Cells slender, 14—49 times longer than broad, strongly arcuate (at most 163° of an arc) or irregularly curved or nearly straight with slightly incurved apices. As a rule each semicell contains 2 (less commonly 4) pyrenoids. Cell-wall colourless and not striated. Cells $2.5\text{--}5\ \mu$ broad, distance between apices $62\text{--}122\ \mu$.

Hab. in the lake of Frederiksborg castle, Denmark, limnetic.

This species, which, as shown in the following, is very variable is a typical summer- and autumn-form. Its vegetative period lasts from July to October (both incl.), and it is present in small but constant quantities within this time. From July to the beginning of September all the cells were regularly and strongly arcuate and 14—21 times longer than broad. At the end of September, however, they were often irregularly arcuate or even straight at one end, so that they apparently got still longer than broad (27—28 times). At the end of October several specimens were almost straight and up to 49 times longer than broad, as the thickness of the cell had decreased to $2.5\ \mu$, and the length at the same time had really become greater than that of the summer specimens. Further these long specimens often contained 4 pyrenoids in each semicell, while the summer specimens invariably had 2 pyrenoids.

72. *Closterium subulatum* Breb.

Pl. III, fig. 34—38. Text-fig. 27.

The specimens in question are nearly related to this species; the only difference is that the cells are more slender, being 18—30 (as a rule 24—25) times longer than broad. The inner margin is straight or very slightly tumid, and 2—6 (as a rule 3—4) pyrenoids are present in each semicell. The specimens are much like *Closterium pseudospirotaenium* Lemm. var. *typicum* Lemm., which is referred by Lütkemüller (in litt. ad Nordstedt ^{28/3} 1913) to *Closterium subulatum* Breb. (according to Dr. BORGE's statement). In the small table below the nearly related species are put together.

species	length: breadth	measures	inner margin	pyrenoids
C. acutum	20—33	$3.8\text{--}6\ \mu \times 132\text{--}146\ \mu$	not tumid	4—5
C. subulatum	17—20	$6\text{--}12.5\ \mu \times 102\text{--}180\ \mu$	slightly tumid	3—4
C. pseudospirotaenium	23—25	$10\text{--}11\ \mu \times 230\text{--}270\ \mu$	slightly tumid	4
Present species	18—30	$5\text{--}8\ \mu \times 107\text{--}185\ \mu$	not tumid	2—6

According to WEHRLE the p_H -interval of *C. acutum* is from 4.1—6.2, while the species in question was found at a p_H value of 8.3.

As illustrated in the table, the measures of the specimens from the lake of Frederiksborg castle are: 5—8 μ in breadth and 107—185 μ in length.

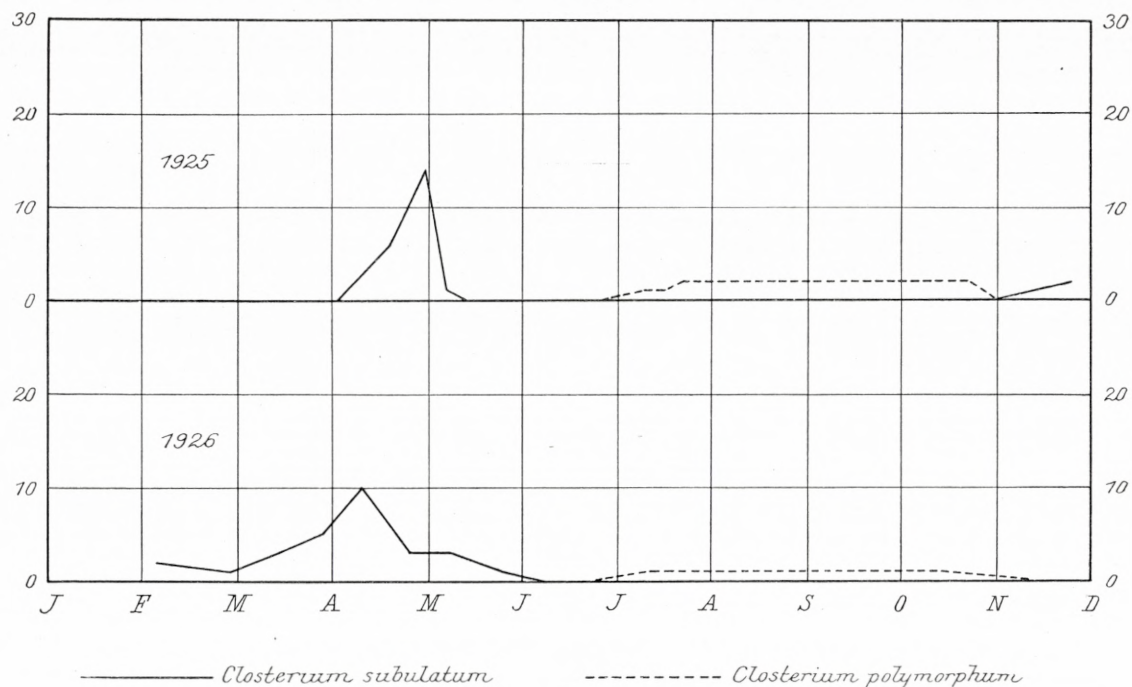


Fig. 27.

The species is a typical spring form and reaches its greatest development, which by the way is not very considerable, in April. During May it disappears and reappears at the end of November or a little later. In 1926, from which year the series of samples and measurements of temperatures is most complete, it attained its maximum at a temperature of 6° C. and disappeared when the temperature rose above 14° C. Like the preceding species this one is monacmic.

Staurastrum Meyen.

73. *Staurastrum paradoxum* Meyen.

Both 2- and 3-horned individuals were observed in the plankton. Its vegetative period is within the period from April to August, but is very rare during this time and a maximum did not occur.

74. *Staurastrum tetracerum* Ralfs.

This species is still more sparingly represented than *Staurastrum paradoxum* Meyen. It occurs in extremely small quantities in the plankton from May to September.

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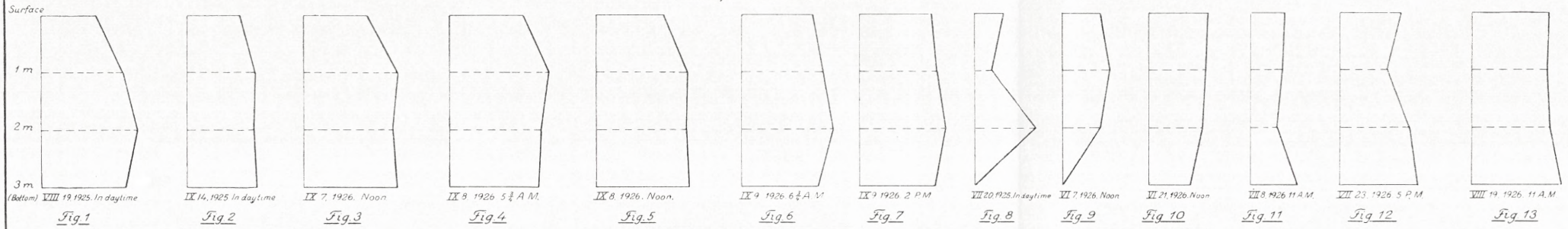
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EXPLANATION OF PLATES

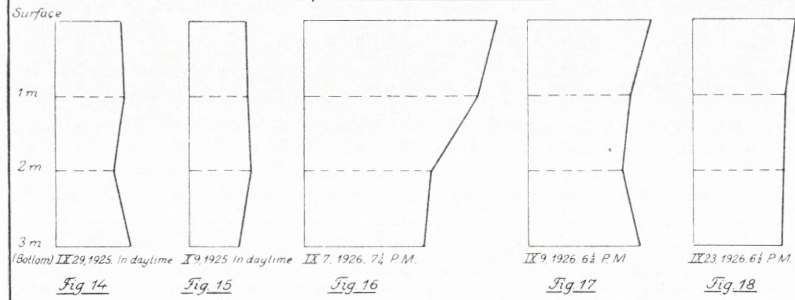
Plate I.

Spherical curves showing the vertical distribution of the Entomostraca in the lake of Frederiksborg castle. The distance of the curves from the ordinate is equal to the radius of the sphere whose volume corresponds to the number of individuals existing on the depth in question; with regard to the method employed to illustrate by means of spherical curves, the reader is referred to the explanation on p. 236.

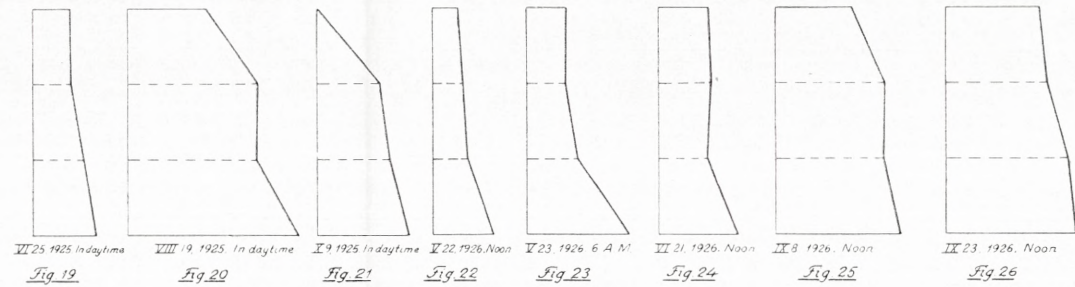
Daphnia cucullata



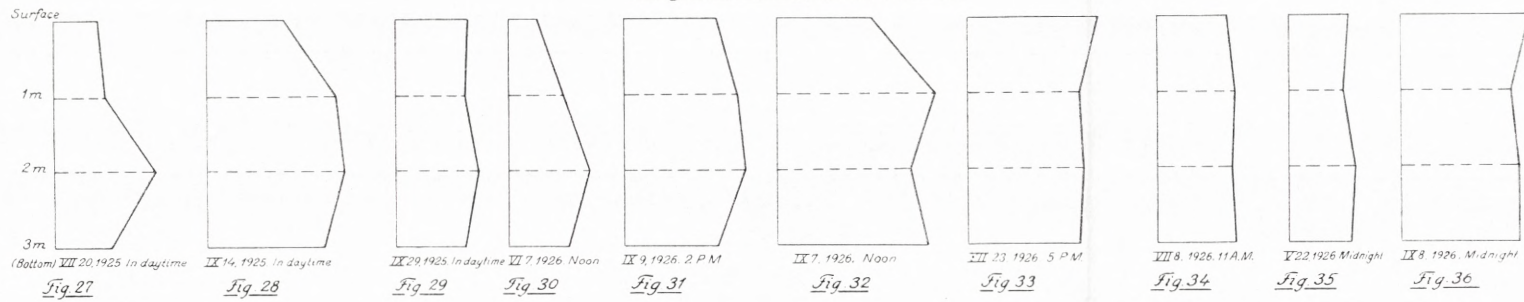
Daphnia cucullata



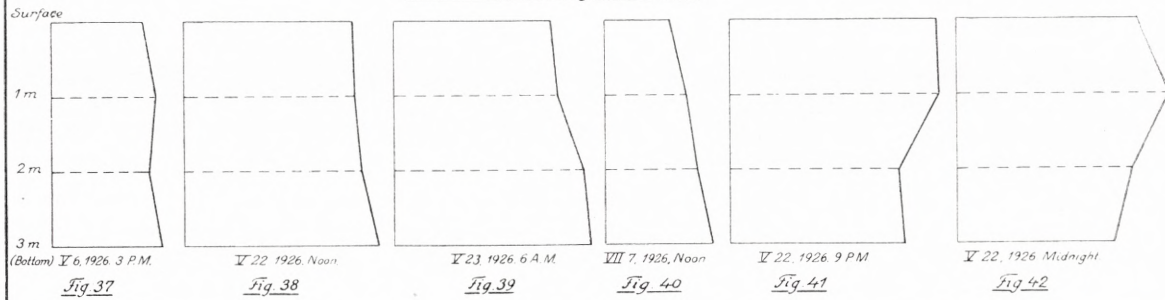
Chydorus sphaericus



Chydorus sphaericus



Bosmina longirostris



Cyclops strenuus

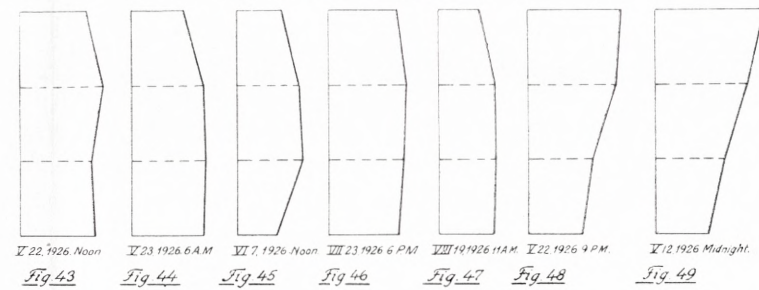


Plate II.

Curves showing the number of individuals at the surface and at the bottom of the lake of Frederiksborg castle at different hours of the day and night.

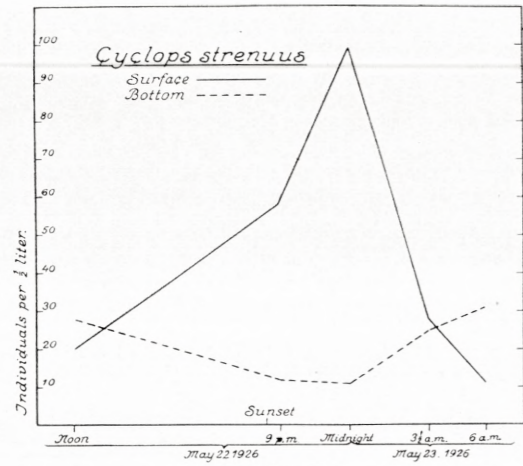


Fig. 1.

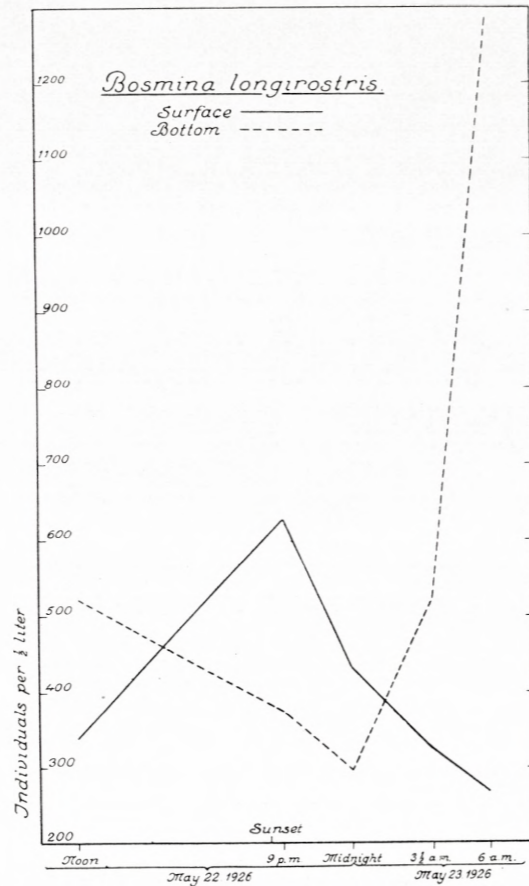


Fig. 3.

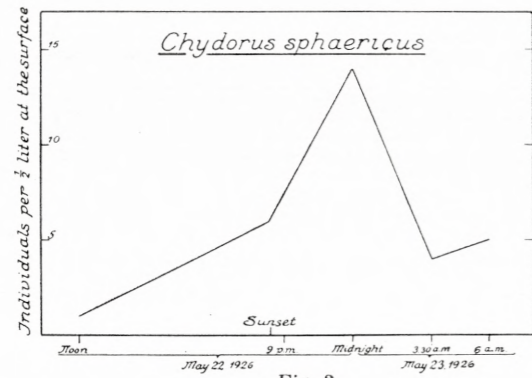


Fig. 2.

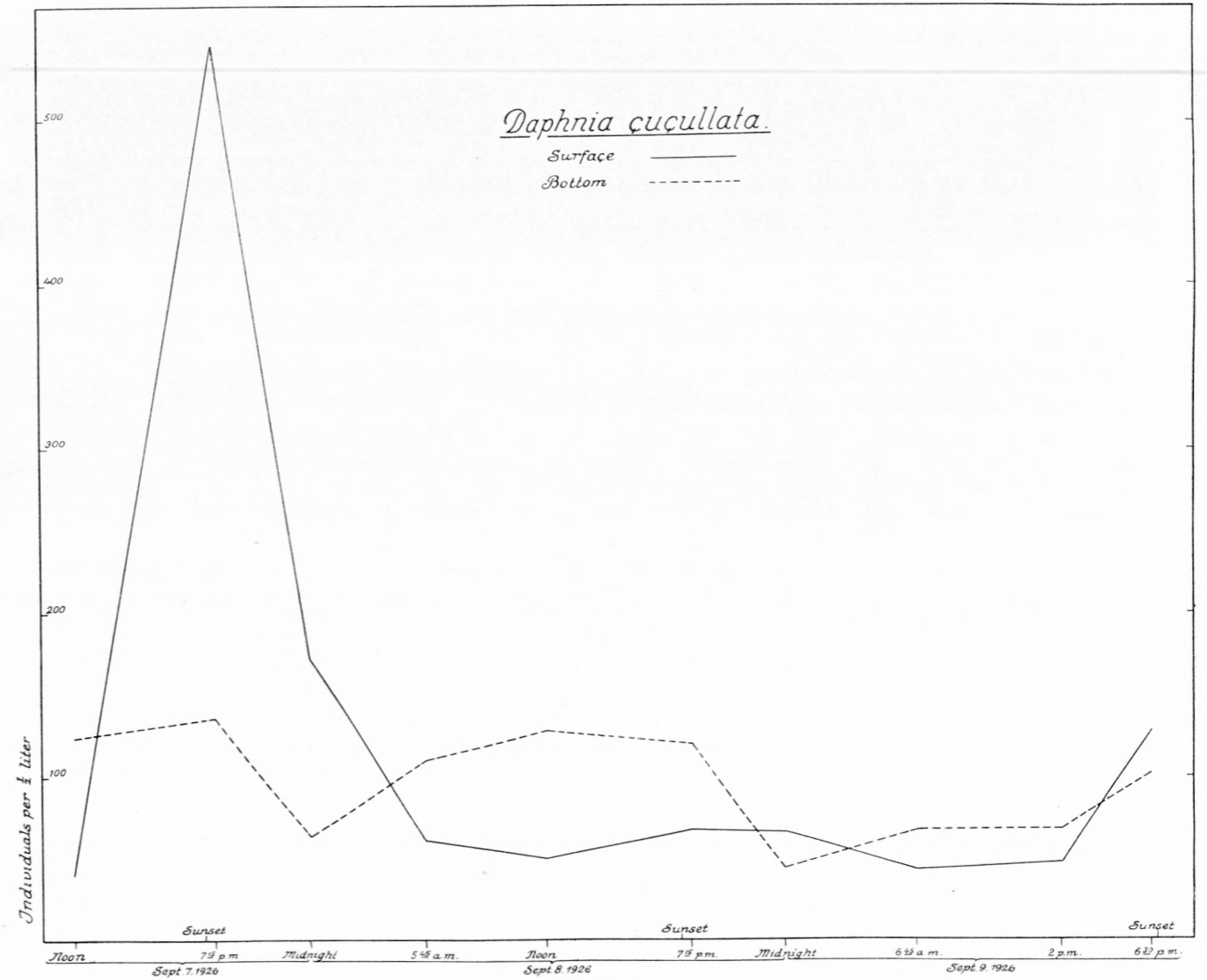


Fig. 4.

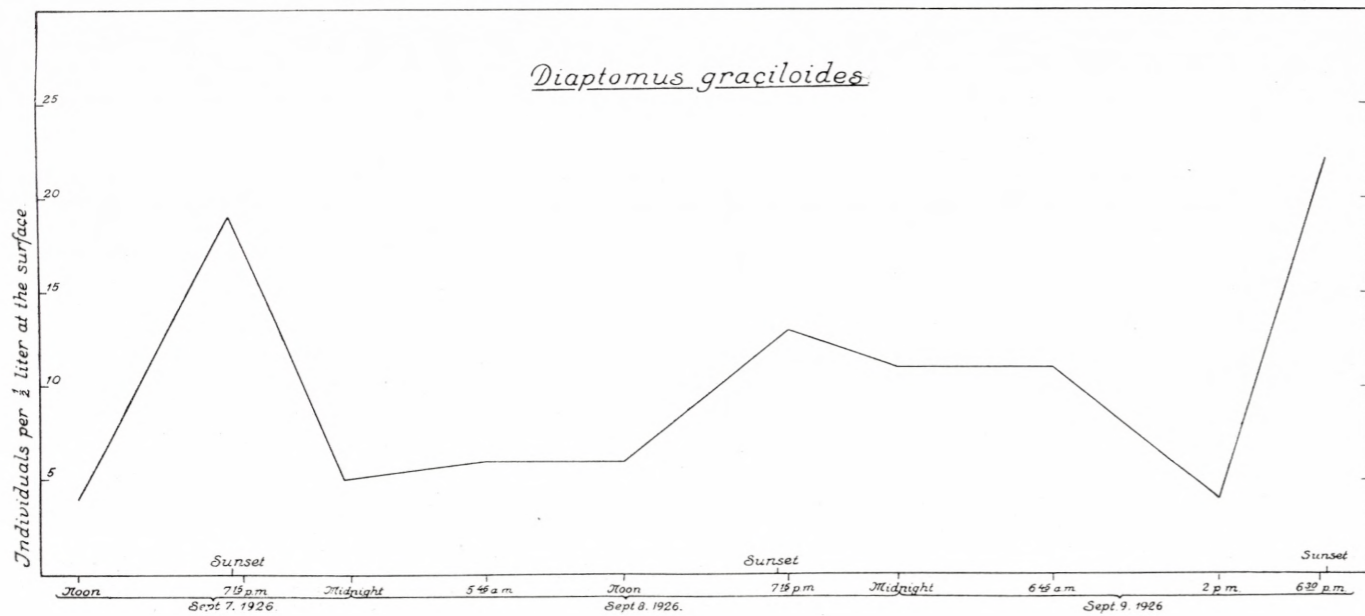


Fig. 5.

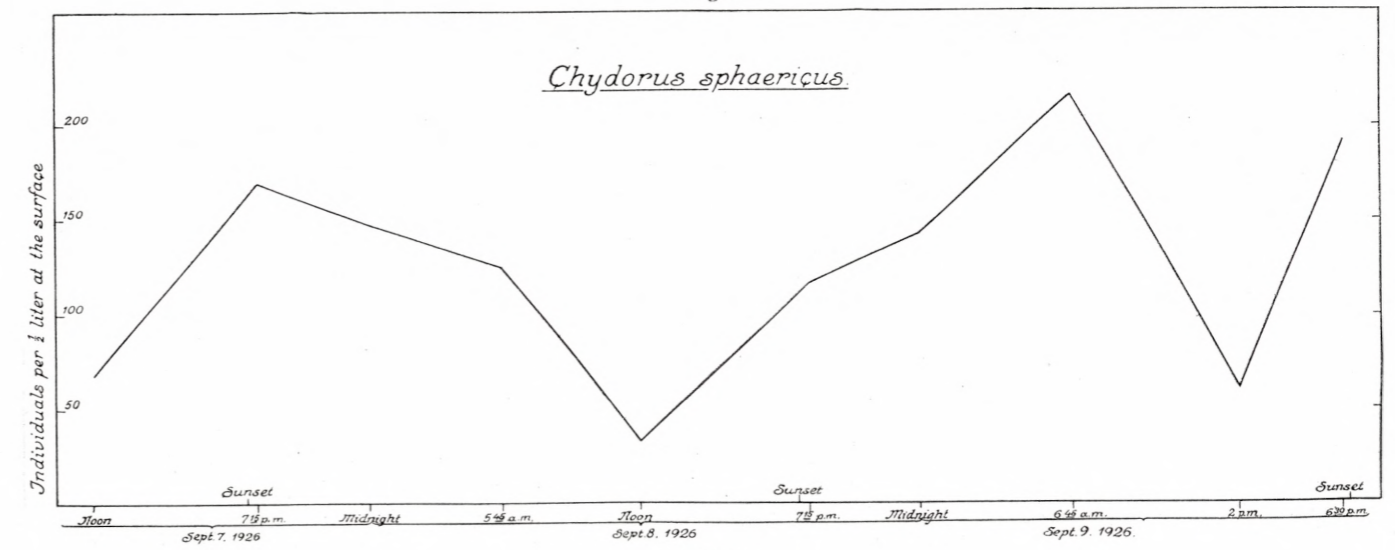


Fig. 6.

Plate III.

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figs. 1— 6: <i>Lagerheimia longiseta</i> Printz; 3 and 4 are drawn from living material, 375 ×; 1—2, 5—6: 606 ×	302
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fig. 42: <i>Trachelomonas volvocina</i> Ehrb. forma <i>minula</i> Fritsch, 606 ×	292
figs. 43—45: <i>Lagerheimia longiseta</i> Printz? 606 ×	302
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figs. 47—52: <i>Glenodinium pulvisculus</i> Stein; 47—49, 51: 500 ×; 50, 52: 606 ×	295

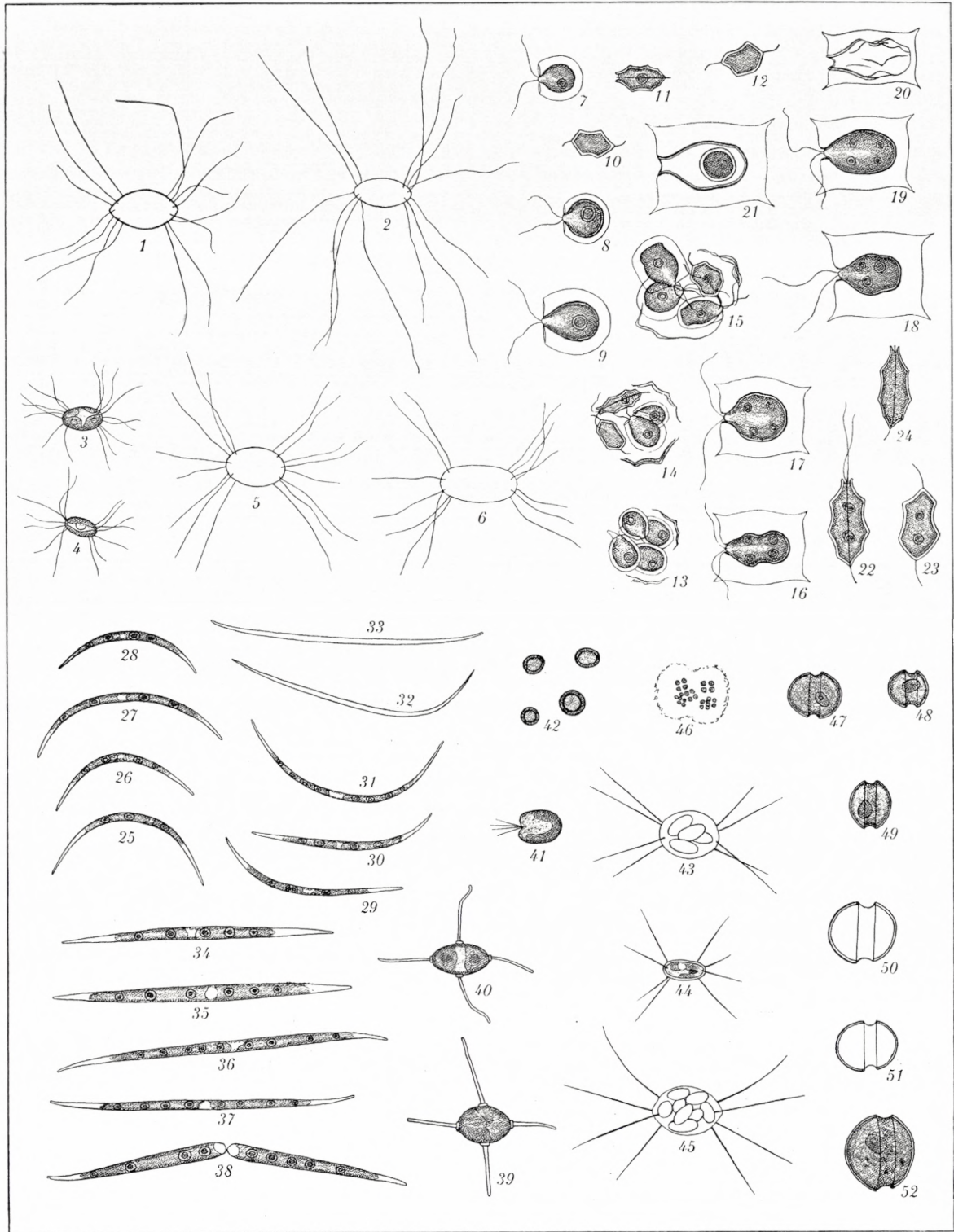


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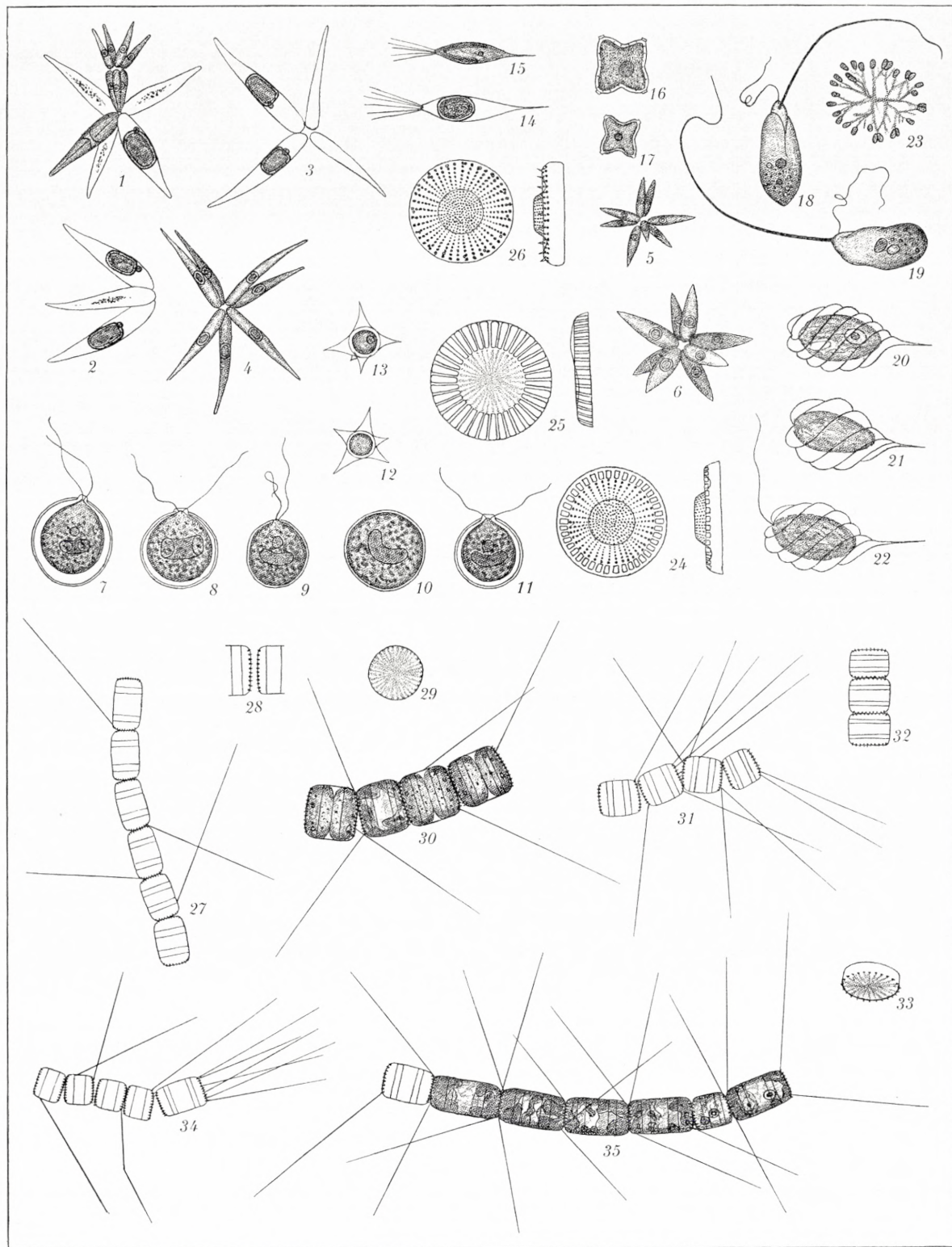


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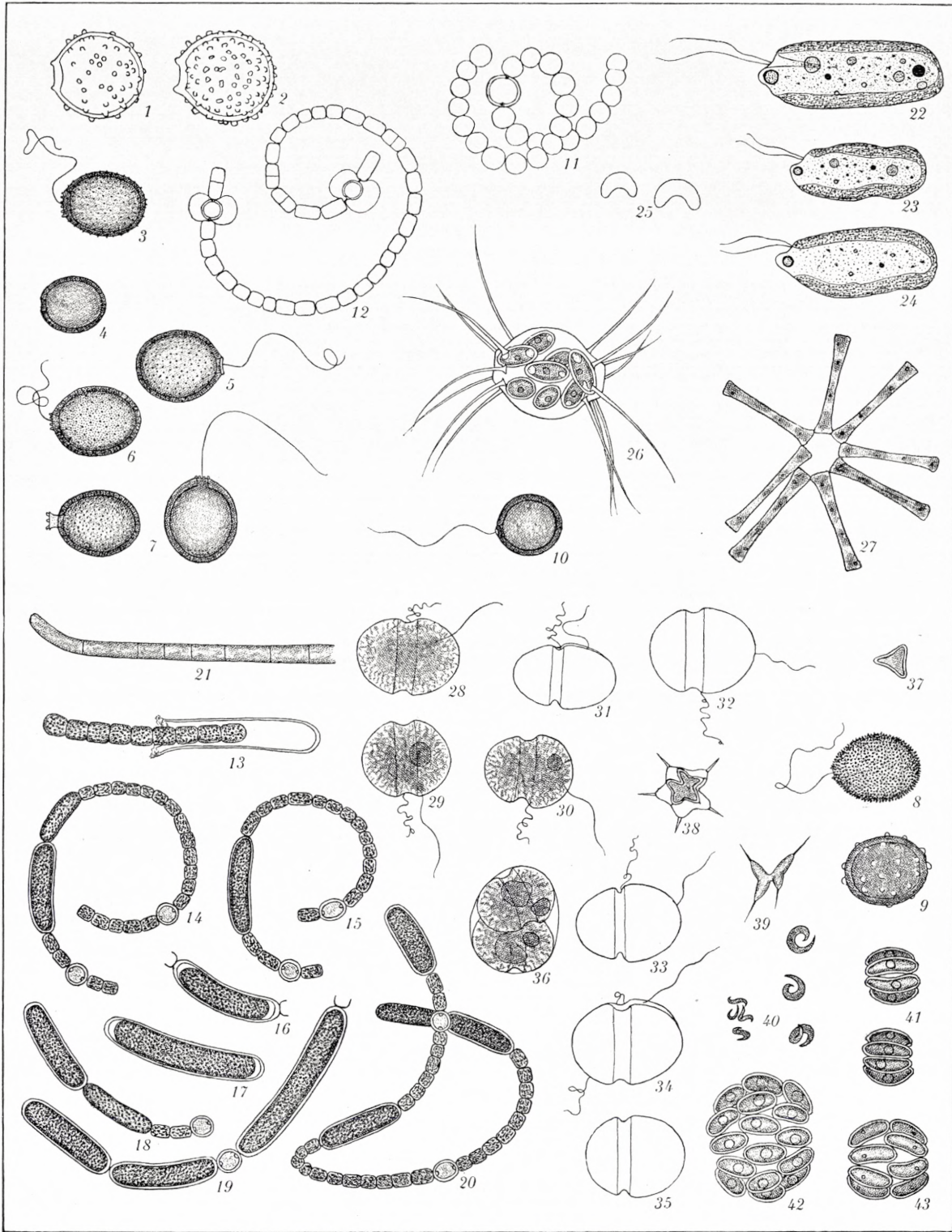
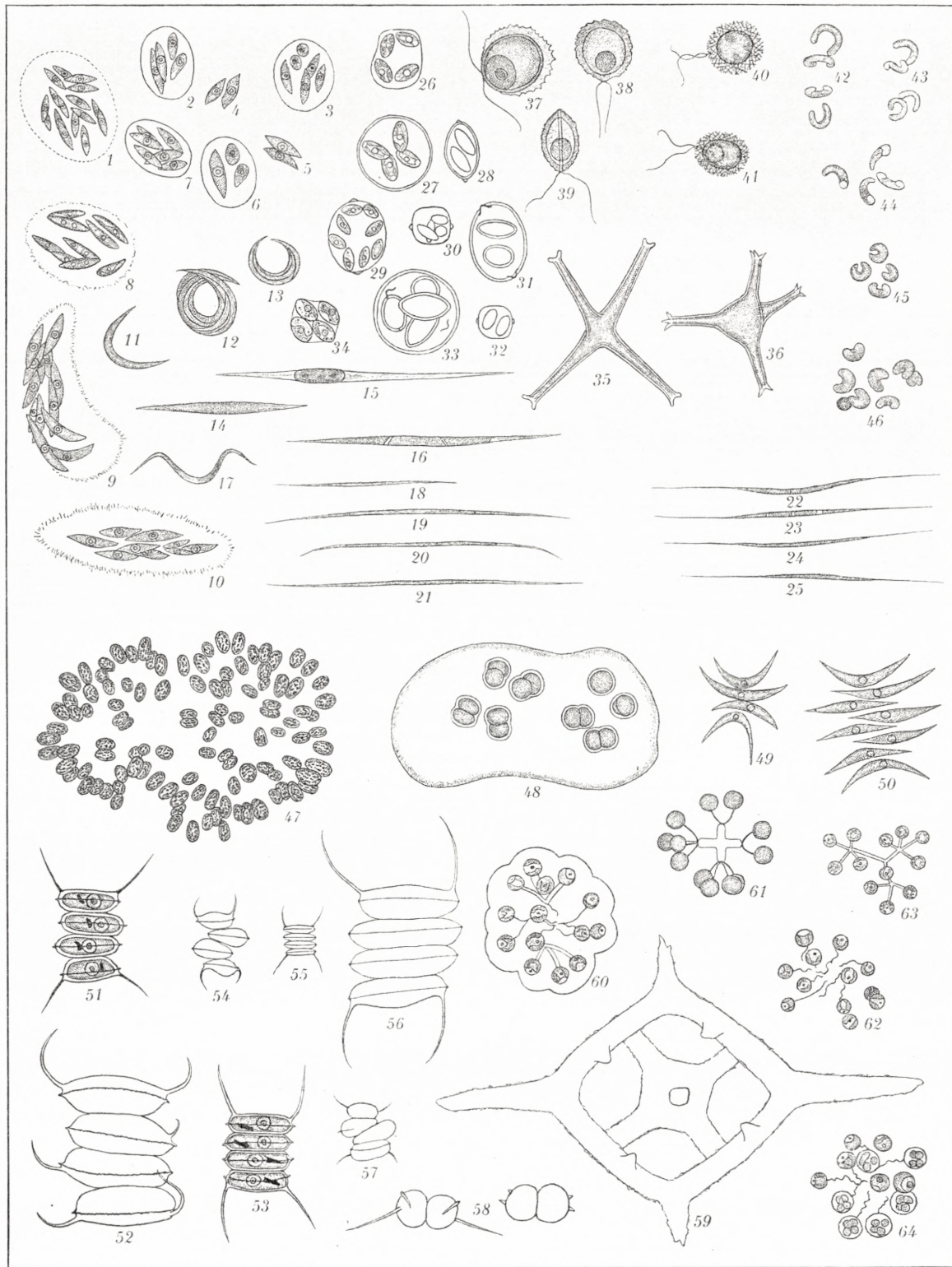


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2. Hansen-Ostenfeld, Carl: De danske Farvandes Plankton i Aarene 1898—1901. Phytoplankton og Protozoer. 2. Protozoer; Organismer med usikker Stilling; Parasiter i Phytoplanktoner. Med 4 Figurgrupper og 7 Tabeller i Teksten. Avec un résumé en français. 1916	2.	75.
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