DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB
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HYDROBIOLOGICAL STUDIES ON SOME DANISH PONDS AND LAKES

PART II: THE QUOTIENT HYPOTHESIS AND SOME NEW OR LITTLE KNOWN PHYTOPLANKTON ORGANISMS

BY

GUNNAR NYGAARD

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
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1. Introduction.

The first part of this treatise was published in the "Archiv für Hydrobiologie" in 1938. It contained a detailed chemical treatment of a number of highly different Danish ponds, especially the annual variation in some of the dissolved substances. Further an elaborate account was given of the fluctuations of the plankton quantities through 1—4 years of sample collectings in each of the ponds. Both oligotrophic lakes and ponds (of the acidotrophic as well as the dystrophic phase) and eutrophic lakes and ponds (also of the mixotrophic phase) were represented in this selection. Finally the saprotrophic type of pond was erroneously set up as a new type (p. 621). As for instance REINHOLD WEIMANN in his instructive paper of 1942 (p. 508) has referred to me as the originator of this type, it should be mentioned here that R. MAUCHA set up the type in 1931 (p. 92), a fact of which I was ignorant at the time.

It is difficult to say who has first set up the "biological lake types," every author building on the results of previous investigators. THIENEMANN (1913—14), for instance, by working on the lakes of Eifel built on BIRGE & JUDAY's important results (1911—12) from lakes in Wisconsin and New York. When NAUMANN in 1917 set up his lake types of poor or rich nutrition, he was able to found on E. TEILING's significant paper of 1916, a paper that was written in Swedish and is perhaps therefore little known, but its argument for the classification of the lakes is similar to that given by NAUMANN (TEILING 1916, p. 509).

In the present paper some new or interesting phytoplankton species of the material from eastern Funen from 1925—30, northeastern Seeland from 1929—31 and Jutland from 1925—46 are dealt with. Several new localities, particularly in North Sleswick (the Sønderborg district) have been visited; a list of them is found on p. 219. A few of the new species, which are supposed to be distributed in this country, have been described and pictured in "Dansk Plante-Plankton" (1945, p. 52). Of course some of these species will also be subjected to a closer study here, which was not possible in an exoteric paper.

I have made a point of characterising the species considered as accurately as possible and so I have not only accounted for their morphology and systematic position, but also for the periodicity, sociology and ecology to the full of the extent permitted by the material.

Under periodicity *i. a.* the limits of temperature and pH are given within which the species was found. In the present paper organisms that have been found only at temperatures between 0 and 7° C. are termed "oligothermic," between 8 and 15° C. "mesothermic" and form 16° C. upwards "polythermic." Furthermore the values of temperature and pH are given which, judging from the material, seem to be particularly favourable to the development of the species in question.

How is it possible, then, to characterise the individual species sociologically? In this paper I have partly given the associations in which the species occurs and partly mentioned the constant associates.

The value of the constant associates depends on our present and future knowledge of their ecology. Species that occur in less than 75 % of the samples containing the species to be characterised are normally not considered worthy of the term "constant associate." In fact the degrees of frequency of the constant associates, considered as associates, are presumably higher than stated in this paper. If a constantly associating species is generally represented by very few individuals in the plankton samples, is it much easier to overlook this species than a constant associate that plays a prominent rôle in the locality considered.

It must be acknowledged that the setting up of the associations is mostly based on an estimate of the relative degree of abundance of the plankton organisms, and always so when nothing else is stated. In order to simplify the long names of associations the Latin-Greek names of the dominants and sub-dominants are, if possible, reduced to the first two letters of the names of genus, species, variety and form. In several cases it has been necessary to use 3, occasionally even 4 or 5 letters in order to avoid confusion:

*Os*cillatoria *li*mnetica	= *Os li*
*Mic*ra*c*tinium *pu*sillum	= *Mia pu*
*Mi*crocystis *ae*ruginosa	= *Mio ae*
*Chla*mydomonas *bi*cocca	= *Chla bi*
*Chlo*rogonium *ma*ximum	= *Chlo ma*
*Chrom*ulina *fl*avicans	= *Chrm fl*
*Chroo*coccus *li*mneticus	= *Chroc li*
*Chroom*onas *a*cuta	= *Chrom ac*
*Chry*sococcus *ru*fescens	= *Chry ru*

A list of these abbreviations is found on p. 225.

In his paper from 1945 (p. 18), where he thoroughly and critically reviews certain sides of the sociology of the plankton, Sv. Thunmark proposes a special method ("Methode der exakten Deckungsgradbestimmung") for the determination of the species that dominates in a net sample of plankton. As regards the total volume of the species the method, which after all is subjective because an estimate of the thickness of the organisms measured is introduced after a measuring of their relative area, is better

than W. H. PEARSALL's method, by which a total of 500—2000 plankton organisms are counted, after which it is calculated how many $^0/_0$ of individuals is reached by every single species. However, if we start a great and time-wasting counting, the only really satisfactory result in my opinion is achieved in the following way: by means of the Kolkwitz chamber or in some other way we determine the number of individuals of each individual species per 1 ml or 1 litre. In order to find the volume of the cells of each species from 1 ml or 1 litre we must base our calculations on direct measurings of the spherical, cylindrical, spindle-shaped, ellipsoidical, etc. cells. If the cells have no "mathematical" shape as in the case of for instance *Ceratium hirundinella*, we may find the volume by making, on the basis of some drawings, a wax model of an average cell in for instance a 1000 times linear magnification and a wax cube of 1 μ^3 in the same linear magnification (= 1 mm^3). The ratio between the weights of the model and the cube will then be the volume of the cell. In all these measurings we must of course use the usual statistical formulas. A special problem is the gelatinous envelope of the organisms, which in many cases can be seen only when the plankton is inserted into Chinese ink.

Another way in which to find the volume of for instance *Ceratium hirundinella* is to make a pure culture of the species. After drawings, slides or photomicrographs of the species have been made it is possible by means of the Kolkwitz chamber to determine how many individuals are found in for instance 10 litres of the culture medium. If this known number of individuals is filtered off and weighed in an adequate state of moistness, we shall be able to find the mean weight of a *Ceratium* cell. After experimentally finding the saline solution in which the *Ceratium* cells are just able to remain suspended we may put the specific gravity of the cells equal to that of the saline solution if due regard is paid to the osmotic effect of the fluid. We are then able to determine the volume of an average cell from the weight and the specific gravity. If the dominant of an association is understood to be the species of which the individuals from 1 ml or litre reach the highest total weight of dry matter, the known number of *Ceratium* individuals, which have been filtered off, must be dried to constant weight and the weight of one cell then determined.

It appears from Fig. 2 in THUNMARK's paper of 1945 how difficult it may be to determine the dominant on an estimate. In the explanation of the figure it is told that *Anabaena circinalis* is the dominant and that quantitively it is much superior to *Tabellaria fenestrata* (besides 2 *Fragilaria crotonensis* colonies about 4 *Asterionella* colonies are visible). If we put the diameter of the *Anabaena* cells in the figure at 1 mm, their total area is

$$\text{abt. } 1240 \times 3.1 \times {}^1/_4 \text{ mm}^2 = \text{abt. } 961 \text{ mm}^2.$$

If we put the breadth of the *Tabellaria* cells in the figure at 1 mm and the length at 11 mm, their total area is

$$\text{abt. } 113 \times 11 \text{ mm}^2 = \text{abt. } 1234 \text{ mm}^2!$$

As the thichness of the *Tabellaria* cells is not very different from that of the *Anabaena* cells, it is misleading to write like this in the explanation of the figure and to make Fig. 2 an instance of the easiness with which it is often possible to solve the problem of the dominant by an estimate (1945, p. 22). The discrepancy between the figure and the text may be due to THUNMARK's possible use of this method of area determination on the water-bloom from Lake Ryven, by which he established that *Anabaena* is really the dominant.

It has often proved difficult to find the dominant in the Danish net samples of plankton. In these cases the method applied was the same as that used by PEARSALL (1925, p. 56) with the exception that only 100—200 individuals or colonies were counted and the numerically superior organism was considered dominant. It was normally marked down as c, cc or ccc (c =common, cc = very common, ccc = abundant) according to its numerical strength in proportion to the other species counted, its being a colony form or a single cell, and its relative proportion of size. The frequensies of the other species were marked down as c+, +, r+, r, rr or rrr according to the numbers reached by them in the counting (+ = rather common, r = infrequent, rr = rare, rrr = sporadic).

All these relative frequencies do not tell us very much about the absolute frequency. When *Uroglena americana* in Madum Sø reaches the frequency cc (or ccc) on May 23th, 1929, this covers an absolute frequency of 0.48 colony per 1 ml, but when *Uroglena volvox* in Badstue-Ødam reaches ccc on May 16th, 1930, these ccc cover an absolute frequency of 694 colonies per 1 ml.

There is no doubt that the samples of net plankton only occasionally are absolutely representative of the world of pelagic organisms in the water, both in a qualitative and especially in a quantitative respect. BIRGE & JUDAY's minute and very frequent examinations (1922, Tables 43—44) of the net plankton and the nannoplankton of the eutrophic Lake Mendota show very convincingly that in 1915—17 the quantity of nannoplankton was never less than twice the quantity of net plankton and sometimes even rose to 45 times as much. Even in the summer months the quantities of nannoplankton were often 10 times larger than those of net plankton and would even rise to 34 times as much, as for instance on July 24th—28th, 1916: 116 mg of net plankton per 1 m^3 against 3951 mg of nannoplankton per 1 m^3. Some of the Swedish lakes, examined by THUNMARK (1945), may be quite similar. As far as I know there is unfortunately no corresponding examination of an oligotrophic lake, but there are symptoms that conditions here are perhaps different (cp. NAUMANN 1927, p. 18—19). In order to avoid misunderstandings it should be mentioned that the term "nannoplankton" in my paper of 1938 and in the present paper of course also includes the organisms of the net plankton, which are sedimented (or filtered off through filter paper) together with the nanno-forms. The composition in Store Gribsø will serve as an example of the difference that may exist between samples of netplankton and nannoplankton from a dystrophic lake.

Store Gribsø, 18. VI. 1929:

	nannoplankton	net plankton
Ceratium hirundinella	..	rrr
Closterium Kützingii	..	rrr
Cryptomonas ovata	ccc	rrr
Mallomonas caudata	+	c
Mallomonas tessellata	rrr	..
Peridinium Willei	rr	rr

2. The Phytoplankton Quotients.

a. Definitions.

THUNMARK (1945, p. 55) has proposed to use the ratio of Chlorococcales to Desmids for the characterisation of a phytoplankton community. The author further shows that this ratio (in the following termed the "chlorophycean quotient") is eloquently expressive of the trophic degree of the lake in question. Though this ratio within the same locality in the course of one or two months may vary between 5.4 and 14.0 (Lake Trummen), Table 1 in THUNMARK's paper shows that in oligotrophic Swedish lakes the quotient ranges between 0.2 and 0.5, in slightly eutrophic Swedish lakes between 1.0 and 3.0 and in highly eutrophic Swedish lakes between 2.6 and 14.0.

Unfortunately Table 1 in PEARSALL's paper from 1925, which minutely deals with the sociology of the phytoplankton in the lakes of the English Lake District, does not illustrate the composition of the plankton of the individual samples. Therefore it is not possible to determine THUNMARK's chlorophycean quotient for these lakes, of which for instance Wastwater and Ennerdale are presumably poorer in nutritive substances than the Swedish oligotrophic lakes of the Fiolen type. It is true that PEARSALL in his significant paper of 1932 gives the composition of the individual samples, but this is only for the more important algae.

W. H. PEARSALL (1932, p. 252) has shown that generally speaking the ratio of Desmids to green colonial forms falls when the $\frac{N}{P}$ ratio rises, but on the whole he uses this quotient with great caution. While PEARSALL includes *Tetrasporales* in his term "green colonial froms" and uses the numbers of individuals (expressed in percentages of the total number of organisms of the sample) of the Desmids and green colonial forms, THUNMARK exclusively employs the numbers of species of *Chlorococcales* and *Desmidieae*.

We will now try to characterise the trophic degree of some chosen Danish lakes and ponds by the following quotients, which are based exclusively on the numbers of species of taxonomic groups:

$$\text{The myxophycean quotient} = \frac{Myxophyceae}{Desmidieae}$$

$$\text{The chlorophycean quotient} = \frac{Chlorococcales}{Desmidieae} \text{ (THUNMARK 1945)}$$

$$\text{The diatom quotient} = \frac{Centrales}{Pennales}$$

$$\text{The euglenine quotient} = \frac{Euglenineae}{Myxophyceae + Chlorococcales}$$

$$\text{The compound quotient} = \frac{Myxophyceae+Chlorococcales+Centrales+Euglenineae}{Desmidieae}$$

It is well-known that especially *Euglenineae*, but also *Myxophyceae* and the great majority of *Chlorococcales* and *Centrales* are taxonomic groups with an eutrophic tendency, *Desmids*, however, with an oligotrophic tendency. *Pennales* and certain *Chlorococcales* are more or less eurytrophically disposed (cp. for instance PEARSALL 1925, pp. 64—65; BERG & NYGAARD 1929, p. 289; FR. HUSTEDT 1930; THUNMARK 1945, p. 54).

It must be emphasized here that there are exceptions to these rules. Even the highly food-craving group of *Euglenineae* contains eurytrophic species like *Euglena proxima* and *Trachelomonas intermedia*. Among the *Myxophyceae Coelosphaerium Kützingianum* is very adaptive: it may be found in acid heath lakes on fluvioglacial deposits. Within the Diatoms even species like *Cymatopleura elliptica*, *Cymatopleura solea* and *Synedra acus* var. *angustissima*, which all belong to *Pennales*, are undoubtedly just as "eutrophic" as for instance the *Melosira* species, which belong to *Centrales*. On the other hand the alpine lakes of Europe contain *Cyclotella* species (*Centrales*) that are probably more "oligotrophic" than for instance *Tabellaria fenestrata* (*Pennales*). Even among the Desmids we know "eutrophic" forms like for instance *Cosmarium depressum* var. *planctonicum*, *Closterium gracile* and *Staurastrum tetracerum* var. *validum*. Within the *Chlorococcales* TEILING (1916, p. 510) established the oligotrophic (or eurytrophic) tendency of a number of species.

In my opinion, therefore, the quotients proposed by THUNMARK and me should be considered provisional because the aim must be to work up an E:O-quotient where E denotes the number of ecologically well-studied plankton species of an "eutrophic," O the number of ecologically well-known plankton species of an "oligotrophic" tendency. It remains an open question whether the quantitative factor should be introduced into this E:O-quotient.

By far the most extensive development of *Myxophyceae*, *Chlorococcales* and *Desmidieae* takes place within the period May—September whereas *Centrales* and *Pennales* also develop during the cold season. Therefore the importance attached to the myxophycean, chlorophycean, euglenine and compound quotients should be confined to the period May—September or even the months of June—August whereas the diatom quotient may be of indicative value at any season.

The Desmid species in several cases being bigger than the *Chlorococcales* species, which escape more easily through the pores of the tow-net, we would expect beforehand to find a somewhat higher chlorophycean quotient for the nannoplankton than for the net plankton when both are taken under exactly the same conditions. This is indeed the case as will appear from Table III:

Lille Gribsø,	28. VI.	1929:	1.25	for	nannoplankton,	0.3	for	net	plankton
Blankeborg I,	17. VIII.	1927:	1.7	—	—	1.25	—	—	—
Blankeborg I,	18. VIII.	1928:	1.8	—	—	0.6	—	—	—
Frederiksborg Slotssø,	11. VI.	1929:	4.25	—	—	2	—	—	—
Blankeborg II,	28. VIII.	1928:	11	—	—	6	—	—	—
Vandingsdam,	28. VI.	1929:	25	—	—	14	—	—	—

Of course this fact must also—though to a much less degree—influence the compound quotient for both net plankton and nannoplankton.

If we want to characterise a phytoplankton community, this may be done briefly by giving the dominant and its absolute frequency and perhaps the sub-dominant(s) that reach at least half the absolute frequency of the dominant; further the total number of species and the 5 phytoplankton quotients in such a way, be it understood, that the numbers of species of the taxonomic groups can be seen. As examples may be mentioned:

Madum Sø, May 23rd, 1929: *Ura am*-association (0.48 colonies per ml), 6 species; myxophycean quotient $\frac{0}{2}$, chlorophycean quotient $\frac{0}{2}$, diatom quotient $\frac{0}{0}$, euglenine quotient $\frac{0}{0}$, compound quotient $\frac{0}{2}$.

Hampen Sø, September 23rd, 1929: *Ta fe-Ana Ha ma*-association (1.5 colonies and 1.2 trichomes per ml), 33 species; myxophycean quotient $\frac{4}{13}$, chlorophycean quotient $\frac{5}{13}$, diatom quotient $\frac{0}{2}$, euglenine quotient $\frac{0}{9}$, compound quotient $\frac{9}{13}$.

Tissø, August 10th, 1927: *Ly li*-association (195 trichomes per ml) with *Os Ag* as sub-dominant, 55 species; myxophycean quotient $\frac{16}{8}$, chlorophycean quotient $\frac{17}{8}$, diatom quotient $\frac{6}{2}$, euglenine quotient $\frac{1}{33}$, compound quotient $\frac{40}{8}$.

Lynge Vandingsdam, August 6th, 1947: *Eug ob*-association (23300 cells per ml), 33 species; myxophycean quotient $\frac{0}{0}$, chlorophycean quotient $\frac{7}{0}$, diatom quotient $\frac{1}{2}$, euglenine quotient $\frac{21}{7}$, compound quotient $\frac{29}{0}$.

b. Classification of the lakes.

The lakes in question are not classified as dystrophic lakes (Thienemann 1921), oligotrophic lakes (Teiling 1916, Naumann 1921), eutrophic lakes (Naumann 1921, Teiling 1916) and mixotrophic lakes (Järnefelt 1925) as proposed

by Åberg & Rohde (1942, p. 232). At normal thermic conditions and exposition to wind the size of the production of plankton should be the primary basis of classification, and a distinction is made only between oligotrophic and eutrophic lakes with their sub-phases.

This is because the notion of oligotrophy is by no means unvarying: Donat (1926b, p. 51) distinguishes 2 types of oligotrophic waters, the geomorphologically oligotrophic type (= Thienemann's "harmonisch oligotropher Seetypus") and the physiologically oligotrophic type. According to Iversen (1929, p. 304) the latter type, which is also called the Lobelia-Isoëtes type, in this country occurs in 2 phases: the very acid phase (Madum Sø) and the alternately slightly acid — alkaline phase (Hampen Sø).

In northern Europe clear and intact heath lakes situated on fluvioglacial sand or on deposits of moraine sand and with well-developed Lobelia-Isoëtes vegetations are frequently very acid. When Donat stresses that *Myriophyllum alterniflorum* is lacking in his typical example of a physiologically oligotrophic lake (Höllenpinnowsee in Pomerania), this would seem to indicate that this typical Lobelia-Isoëtes lake is very acid. According to Donat this physiologically oligotrophic type of lake regularly contains quite a number of pelagic Desmids; indeed this Desmid plankton is occasionally said to abound in species. As will appear from Table I and from the list of species on p. 256—62 it is true that the Danish lake Madum Sø sometimes contains up to 15 Desmids in one plankton sample, but the quantitatively dominant species are the Flagellates *Dinobryon cylindricum* var. *palustre* and *Uroglena americana*. For such "disharmonic" lakes as for instance Höllenpinnowsee and Madum Sø with pH constantly below 5.5 we ought to retain the characteristic term acidotrophic (Naumann 1932), indicating a subtype of the oligotrophic type.

Lohammar (1938, p. 243) says about the acidotrophic water type, "Man kann aber die Frage aufwerfen, ob es in Nordeuropa überhaupt Seen mit so saurem Wasser gibt, dass die Produktion von der Azidität beherrscht wird." However, Steemann Nielsen's investigations (1944 and 1945) on the photosynthesis at different pH values and varying concentrations of free carbon dioxide, bicarbonate ion and carbonate ion show that if pH is below 4 there can be no bicarbonate ions in the water because the high hydrogen ion concentration will then prevent the dissociation of carbonic acid. To certain aquatic plants bicarbonate ions seem to be a much better source of carbon than the free carbon dioxide when the concentrations are low. There are many indications that also the amount of free carbon dioxide is very small in clear, highly acid heath lakes. Although our knowledge of the photo-synthesis and the ecology of the individual limnophytes and phytoplankton species is limited, there is no doubt that indirectly pH is able to influence the production to a considerable degree. Basing on K. Münster Ström's (1931) and Ruttner's (1931) views W. Ohle (1934, p. 436) is of opinion that the free carbon dioxide can be used for the classification of the lakes. With Steemann Nielsen's results in mind it must be supposed that the amount

of free carbon dioxide, bicarbonate ion and carbonate ion is a factor of at least the same value for the classification as the oxygen.

WEIMANN (1942, p. 492) maintains that actually harmonically oligotrophic ponds are found on pure sandy substratum and as an example he mentions Pechofen Teich in Silesia. About its vegetation it is only said that Equisetum is the predominant plant near the margins, and curiously enough WEIMANN does not mention one Desmid for the oligotrophic ponds in the otherwise very instructive survey of plankton in his paper of 1942. In a previous paper (1939, p. 671) the May value of pH for Pechofen Teich is stated to be 6.9.

It is hardly likely that this neutral, clear type of heath lake is identical with the harmonically oligotrophic water type on a pre-Cambrian substratum (cliff lakes in Scandinavia and Great Britain). One would think beforehand that the decomposition of the pre-Cambrian minerals would make possible a more comprehensive representation of salts than the poor sediments of SiO_2 that constitute by far the greater part of sandy deposits.

On account of the character of the substratum (mostly sand) the Danish Lobelia-Isoëtes lakes Hampen Sø and Kalgaard Sø with their pH variation about the neutral point and their clear water bear a close relationship to the oligotrophic type. Their average depth being considerably lower than THIENEMANN's morphometric value of 18.5 m, these lakes are not harmonically oligotrophic in THIENEMANN's sense.

LOHAMMAR (1938, p. 239) is of opinion that LUNDBECK's distinction between the primarily oligotrophic lake, which is situated on a poor substratum and is therefore poor in nutrition, and the secondarily oligotrophic, deep lake on a soil that is rich in nutrition, the nutritive matters of which, however, are distributed in a very large volume of water, is rather irrelevant: examinations of the lakes of Wisconsin have shown that seepage lakes are mostly much poorer in inorganic and organic matter than drainage lakes. LOHAMMAR maintains that the content of nutrition in the lake is determined by the inlets or rather by the quality of the surroundings. Lakes in poor tracts will therefore be poor in nutrition, lakes in fertile tracts rich in nutrition, no matter whether all these lakes be shallow or deep. As shown before (NYGAARD 1944, p. 36) the truth is no doubt that in lakes with inlets and outlets the inlet is a more important factor for the trophic degree than the morphometry of the lake; if the lake has no inlet, however, it is not always certain that the quality of the surroundings is the dominant factor in comparison to the shape and depth of the basin of the lake. On account of the comparatively high temperatures and the consequential intenser decomposition during the summer season the epilimnion of the shallow lake must always contain larger amounts of recently extricated nutritive matters than the colder epilimnion of the deep lake, all other things equal. Two morphologically different lakes without inlets and outlets and situated in surroundings of the same quality must therefore be considered able to show a different production.

c. Lakes.

In Table I the trophic degree is determined partly by an estimate of the higher or lower transparency of the water, partly, in certain lakes, by a statement of the absolute frequency of the dominants. The numbers of individuals were counted in 5 ml (Tissø), 100 ml (Store Gribsø, Madum Sø and Furesø) or 275 ml (Hampen Sø). The few chemical analyses (NYGAARD 1938, p. 684) may also afford some data for the valuation of the trophic degree though it must be admitted that two heterogeneous lakes as for instance Hampen Sø and Furesø in the winter months mentioned are not very different as regards nitrate (and also phosphate and ammonia). The lake Tissø on the other hand was remarkably rich in nitrate in the winter of 1931, and this was also true of its bottom water in the summer of 1929.

As regards the total number of species of the net plankton the oligotrophic lakes of the dystrophic phase are conspicuous by their remarkably low numbers of plankton organisms, which range between 5 and 8! The plankton of the other lakes that are oligotrophic is somewhat richer in species (6—33 species) while the eutrophic lakes may be very rich in species (18—76) likewise as the lakes of the mixotrophic phase (31—57 species). FRITSCH's statement (1931, p. 235) that the plankton of oligotrophic waters is in general richer in species than that of eutrophic waters accordingly does not apply to Danish lakes. The discrepancy is no doubt explained by the fact that we have no harmonically oligotrophic lakes in this country. It must further be mentioned that the number of phytoplankton species in net samples from Danish lakes only occasionally exceeds 50.

A closer contemplation of the quotients given in Table I will show that the myxophycean quotient ranges between 0 and 3.0, the chlorophycean quotient (apart from the value 9 in Hulsø which may just as well be considered a pond as a lake) between 0 and 3.5, the diatom quotient between 0 and 3, the euglenine quotient between 0 and 1 and the compound quotient between 0 and 8.75 (apart from the value 25 in Hulsø).

In the oligotrophic lakes of the dystrophic phase, Løvenholm Langsø, Store Øxsø and Store Gribsø, all quotients are = 0—$\frac{1}{3}$ or an indefinite figure because either the numerators or the denominators or both are 0; the only exception is one of the diatom quotients in Store Øxsø. None of the numerators or denominators of the quotients are above 3.

Both BOISEN BENNIKE (1943, p. 23) and CLEMENS PETERSEN (in a letter to me) seem to be a little sceptical for calling Store Gribsø dystrophic. pH may rise as high as 6.5, and the consumption of $KMnO_4$ per litre sometimes sinks to 33 mg; besides the animal production of the profundal region may be rather considerable (CLEMENS PETERSEN 1943, p. 57). On the other hand it cannot be denied that its colour apparently always lies between 15 and 40 "Ohle units," which shows us that Store Gribsø belongs to W. OHLE's (1934) Farbengruppe III ("eigentliche Braunwasserseen"); moreover repeated measurings gave a pH of 4.3 in this up to 13 m deep and only

slightly polluted lake, which is highly sheltered from winds. Both the quotients of Table I and the paucity in species and individuals and the composition of the phytoplankton are indicative of a close relationship to the lakes of the dystrophic phase.

In the oligotrophic Madum Sø of the acidotrophic phase the myxophycean quotient is always 0, the chlorophycean quotient 0—0.1, the diatom quotient and euglenine quotient 0 (or indefinite) while the compound quotient ranges as low as 0—0.1.

In the approximately oligotrophic lakes Hampen Sø, Vedsted Sø and Kalgaard Sø the myxophycean quotient lies at 0—0.4, the chlorophycean quotient at 0—0.7, the diatom quotient at 0 (or indefinite), the euglenine quotient at 0—0.2 while the compound quotient ranges between 0.25 and 1.

In the small heath lake Præstesø the diatom quotient is still 0, the myxophycean quotient 0.5, the chlorophycean quotient 0.65, the euglenine quotient 0.1 and the compound quotient reaches 1.2. *Lobelia Dortmanna*, *Littorella uniflora* and *Potamogeton crispus* were found in the lake.

According to information received from Dr. Johs. Iversen Slaaen Sø has strong submerse springs, which cause a comparatively rapid renewal of the lake water. If, in this case, we used only Thunmark's chlorophycean quotient and the myxophycean quotient, the conclusion would be: oligotrophic. Here the diatom quotient helps us because its value of 0.75 indicates eutrophy; the same does the euglenine quotient, which reaches the uncommonly high lake value of 1! As a matter of fact the September analysis of 1929 tells of rather considerable amounts of N and P in both surface and bottom water, quantities that cannot apparently be utilized without difficulty on account of the rapid renewal of the water (see Nygaard 1938, p. 555). The compound quotient of Slaaen Sø lies at 1.1.

In the eutrophic lakes the myxophycean quotient ranges between 0.8 and 3.0, 5 samples from the slightly eutrophic Nors Sø showing the values 0.8—1 and 4 samples from the more eutrophic lakes Mossø, Tissø and Salten Langsø the values 1.2—3.0. The chlorophycean quotient ranges between 0.7 and 3.5, in the slightly eutrophic lake between 0.7 and 1.1, in the 3 more eutrophic lakes between 2.1 and 3.5. The diatom quotient ranges between 0.2 and 3, the slightly eutrophic lake showing values between 0.2 and 1.5, the 3 more eutrophic lakes values between 1.25 and 3. The euglenine quotient is 0 in all lakes except in Nors Sø where, strange to say, it reaches the values 0—0.2 (mostly 0). The compound quotient varies between 2.0 and 8.75, the 5 samples from the slightly eutrophic Nors Sø showing values between 2.0 and 2.25, the 4 samples from the 3 more eutrophic lakes, however, values between 4.3 and 8.75. In the moderately eutrophic lake Furesø the compound quotient ranges between 3.5 and 4.4.

In the two eutrophic lakes of the mixotrophic phase, Hostrup Sø and Hulsø, the latter of which might just as well be classed as a pond, the myxophycean quotient is found to be 0.9—2.7 (3), the chlorophycean quotient 2.2—2.5 (9), the

diatom quotient 0.2—0.5 (1.75), the euglenine quotient always 0 in Hostrup Sø and always 0.3 in Hulsø, and the compound quotient 3.3—5.3 (7—25 in Hulsø).

The low values of the diatom quotients in Hostrup Sø (4 samples from 4 different years give the variation 0.2—0.5) must possibly be ascribed to the comparatively lime-deficient water of the lake. The lime-richer lake Hulsø shows the values 1.5 and 1.75. Also the paucity in pelagic diatoms of the oligotrophic lakes (no more than 4 species were ever found in one sample) is most probably connected with their calcium deficiency.

Survey of the phytoplankton quotients of 15 Danish lakes.

Types	Myxophycean quotient	Chlorophycean quotient	Diatom quotient	Euglenine quotient	Compound quotient
3 oligotrophic lakes of the dystrophic phase	0 (or indefinite)	0—0.3 (or indefinite)	0 (0.3?)	0 (or indefinite)	0—0.3 (or indefinite)
1 oligotrophic lake of the acidotrophic phase	0	0—0.1	0 (or indefinite)	0 (or indefinite)	0—0.1
3 approximately oligotrophic lakes	0—0.4	0—0.7	0 (or indefinite)	0—0.2	0.25—1
2 intermediate (mesotrophic) lakes	0.1—0.5	0.2—0.6	0 —0.75	0.1—1	1.1—1.2
1 slightly eutrophic lake	0.8—1	0.7—1.1	0.2 —1.5	0—0.2	2.0—2.25
1 moderately eutrophic lake	1.4—2	1.25—1.4	0.6 —1.7	0	3.5—4.4
3 more eutrophic lakes	1.2—3	2.1—3.5	1.25—3	0	4.3—8.75
1 eutrophic lake of the mixotrophic phase	0.9—2.7	2.2—2.5	0.2 —0.5	0	3.3—5.3

d. Ponds.

The ponds of this paper are much better known than the lakes dealt with above. Basing on Part I of the present investigations (Nygaard 1938, pp. 646—684) Table III gives the annual variations in chosen ponds for pH, calcium, consumption of potassium permanganate, phosphate phosphorus, ammonia-nitrogen, nitrate-nitrogen and the weight of the plankton together with its annual means. There are further some comments on the pollution of the ponds. Although this is but a small part of the total number of factors that influence the plankton organisms, and though the weight of the plankton includes the weight of detritus, Rotifers and the pelagic Crustacea, it is possible to distinguish between oligotrophy and eutrophy in their different phases.

In Table III the qualitative composition of the samples of both net plankton and nannoplankton are given with a view to comparison because the two samples in many cases originate from the same day.

The total number of species in the oligotrophic ponds of the dystrophic phase is 14—15 (nannoplankton 8—19) species, thus being larger than in the corresponding lakes. In the other oligotrophic ponds (of the acidotrophic phase) the number of species amounts to 9—42 per sample. Like the eutrophic lakes the eutrophic ponds may be very rich in species (35—67 per sample). Eutrophic ponds of the mixotrophic phase may be equally rich in species (17—71 species) whereas the pond of the saprotrophic phase is unusually poor in species (5—10 per sample).

Table III shows that in Danish ponds the myxophycean quotient ranges between 0 and 5, the chlorophycean quotient between 0.1 and 31, the diatom quotient between 0 and 6, the euglenine quotient between 0 and 8 and the compound quotient between 0.1 and 43. As might be expected the fluctuations of the ponds are much greater than those of the lakes.

In the 4 oligotrophic ponds of the dystrophic phase, Bøndernes Mose I and II, turf pit at Store Jenshøj and turf pit NE. of Skaansø the myxophycean quotient varies between 0 and 0.25, the chlorophycean quotient between 0.1 and 0.3; the diatom quotient is always 0 (or indefinite) while the euglenine quotient may be surprisingly high, up to 1! The compound quotient ranges between 0.1 and 0.6.

The 5 oligotrophic ponds of the acidotrophic phase are Holmsø, Skaansø, Mørksø, Klitsø at Højsande, and Lille Gribsø. The last-mentioned all the year round showed a "Vegetationstrübung" or "Vegetationsfärbung" caused by minute green algae: on December 16th, 1929 no less than 236000 *Stichococcus bacillaris* and 17500 *Cosmarium asphaerosporum* var. *strigosum* were counted per ml, to mention only the dominant and the sub-dominant. Lille Gribsø, which is pictured in "Dansk Plante-Plankton" (Nygaard 1945, p. 8), is surrounded by a broad zone of quaking bog composed of several *Sphagnum* species. The rest of the ponds were uncommonly poor in plankton when they were visited. The myxophycean quotient ranges between 0.1 and 0.3 (0.5), the chlorophycean quotient between 0.25 and 0.45 (1.25); the diatom quotient is always 0 (or indefinite), the euglenine quotient lies between 0 and 0.1 (0) and the compound quotient between 0.4 and 0.8 (1.75). The figures in brackets are taken from a sample of nannoplankton from Lille Gribsø, June 28th, 1929.

In the slightly eutrophic turf pit Blankeborg I of the mixotrophic phase the myxophycean quotient ranges between 0.1 and 0.7, the chlorophycean quotient between 0.6 and 1.9, the diatom quotient between 0.1 and 0.7, the euglenine quotient between 0.1 and 0.4 and the compound quotient between 1.4 and 3.55, all figures originating from 8 different plankton samples from the years 1925—30. For the 4 samples of net plankton the compound quotients were 1.4—2.2—1.8—2.2, for the 4 samples of nannoplankton 2.2—2.55—2.8—3.55.

The other eutrophic ponds of the mixotrophic phase (Blankeborg II, Sortedam II, Gadevang Mose and Vandingsdam) are more or less polluted, especially Vandingsdam. For the 14 plankton samples from these ponds the myxophycean quotient ranges between 0.25 and 3 (or indefinite), the chlorophycean quotient between 1.6 and 25 (or indefinite), the diatom quotient between 0.4 and 2 (or in-

definite), the euglenine quotient between 0 and 0.5 and the compound quotient between 2.8 and 33.

The eutrophic ponds Badstue-Ødam, Frederiksborg Slotssø, Jægerbakke Dam and Flødegaardens Dam are also polluted, particularly the last-mentioned. It must be emphasized, however, that the water of Flødegaardens Dam was amazingly poor in plankton on August 3rd, 1939, at which time the Limnophytes had occupied most of the pond, especially *Batrachium circinnatum*, but also *Potamogeton natans*; *Lemna trisulca* and *L. minor* were common. In the 15 plankton samples from these 4 ponds the myxophycean quotient is generally high, between 0.5 and 5 (or indefinite), the chlorophycean quotient varies between 2 and 31 (or indefinite), the diatom quotient between 0.4 and 6 (or indefinite in the calcium-deficient Jægerbakke Dam where no pelagic diatoms were found), the euglenine quotient between 0 and 0.4 and the compound quotient between 4.3 and 43 (or indefinite).

The 2 eutrophic ponds of the saprotrophic phase are Lynge Vandingsdam and Bistrup Dam; the former represents the transition stage between eutrophy and saprotrophy. In these ponds the myxophycean quotient is 0 (or indefinite), the chlorophycean quotient 12 (or indefinite), the diatom quotient 0.5 (in the lime-rich, but extremely polluted Bistrup Dam indefinite, no pelagic diatoms occurring here). The euglenine quotient, however, shows the high values of 1.5—8 (or indefinite). The compound quotient is 31 (or indefinite).

Survey of the phytoplankton quotients of 20 Danish ponds.

Types	Myxophycean quotient	Chlorophycean quotient	Diatom quotient	Euglenine quotient	Compound quotient
4 oligotrophic ponds of the dystrophic phase	0—0.3	0.1—0.3	0 (or indefinite)	0—1	0.1—0.6
4 oligotrophic ponds of the acidotrophic phase	0.1—0.3	0.25—0.45	0 (or indefinite)	0—0.1	0.4—0.8
1 approximately acidotrophic pond	0.1—0.5	0.3—1.25	0	0	0.55—1.75
1 slightly eutrophic pond of the mixotrophic phase	0.1—0.7	0.6—1.9	0.1—0.7	0.1—0.4	1.4—3.55
4 eutrophic ponds of the mixotrophic phase	0.5—3	1.6—25	0.4—2	0—0.5	2.8—33
4 eutrophic ponds	0.5—5	2—31	0.4—6	0—0.4	4.3—43
1 approximately saprotrophic pond	0 (or indefinite)	12 (or indefinite)	0.5	1.5—3	31 (or indefinite)
1 eutrophic pond of the saprotrophic phase	indefinite	indefinite	indefinite	3—8	indefinite

e. The quotient hypothesis.

It must be emphasized that it is no easy matter to base statistics on so small figures as those contained in certain quotients of Tables I and III. The highest figures are included in the compound quotient, which I therefore consider most suitable for a characterisation of the trophic degree. This makes me advance the following *hypothesis* on temperate lakes and ponds:

If the compound quotient is below 1, the water is probably oligotrophic; the lower the quotient, the poorer the assimilable nutrition. The lowest values (0—0.3) mostly suggest that the lake or pond belongs to the dystrophic phase though also waters of the acidotrophic phase may show equally low values.

If the compound quotient is above 1, the water is probably eutrophic; the higher the quotient, the richer the assimilable nutrition. Values of 1—2.5 indicate a slightly eutrophic ("mesotrophic") water; values of 3—5 indicate moderate eutrophy, and values between 5 and about 20 show that the lake or pond is distinctly or much eutrophicated and somewhat contaminated. Values between about 20 and 43 finally indicate a highly eutrophic water soiled by cattle.

The genuine saprotrophy seems to be revealed only by the euglenine quotient, the rest of the quotients in such extremely contaminated waters being indefinite. The border value between extreme eutrophy and saprotrophy is possibly about 2—3 for the euglenine quotient, but my material is much too small for an exact determination of this critical value.

If this hypothesis proves tenable, it is possible merely by means of a plankton sample to get a rather good notion of the trophic degree of some body of water. This will undoubtedly be of interest to fishery biologists and those who determine the pollution of stagnant water. The phytoplankton is a very sensitive indicator of pollution of the water. A determination of the compound quotient and the other quotients supposes either a detailed knowledge of the species of phytoplankton or a conversance with genera and an acute faculty of observation combined with a pronounced sense of delimitation of species, so that it can be determined how many species of *Staurastrum*, *Trachelomonas*, *Pediastrum*, *Cyclotella*, etc., are contained in the sample. For the calculation of the quotients it is unnecessary to be able to identify to species.

The reasons why certain ponds may exhibit very variable values for the compound quotient in comparison to the lakes is due to the fact that the conditions of life, for instance the weather or the contamination, may vary highly from year to year or even within a much shorter period. According to Tables III and IV Lynge Vandingsdam was highly eutrophic approximating saprotrophy in the summer of 1947. In the following summer, however, the pond was quite filled up with *Chara vulgaris*, which like all Charophyta does not endure pollution, *Batrachium aquatile* and *Batrachium trichophyllum*. On the other hand the water itself was exceedingly

poor in plankton species and individuals (very little *Volvox aureus*). Accordingly the pond has not been utilized as watering place for cattle in the spring and summer of 1948.

The compound quotient should never be given merely as a decimal fraction, since it is not indifferent whether the ratio is for instance $\frac{1}{1}$ or $\frac{12}{12}$. At any rate the numerator and the denominator should be given beside the decimal fraction.

The quotients should only be regarded as a help which together with the vertical distribution of carbon dioxide, calcium bicarbonate and oxygen, the qualitative and quantitative composition of the higher vegetation and the bottom fauna, the number of plankton generations per unity of time, the waterbloom phenomenon, the morphometry of the water piece, its bottom sediments and geological substratum, the occurrence of inlets and outlets, the climate, the exposition to winds, the quantity of humic substances, the hydrogen ion concentration, the annual cycle of nitrogen, iron, phosphate, etc., should make it possible to place the water in question in the trophic scale.

It is, however, possible only with difficulty to apply the hypothesis to the extreme parts of this scale, the dystrophic and saprotrophic phase, especially the former, being extremely poor in plankton species; as to the latter the compound quotient should be replaced by the euglenine quotient as mentioned above.

3. Some Remarks on the Ecology of Danish Phytoplankton Organisms.

In "Dansk Plante-Plankton" (Nygaard 1945) I discuss rather extensively the periodicity of the species, but besides this I have tried, on the basis of my Danish plankton material, to set up "indicatory species", which of course to some extent must be a corroboration of the results previously achieved by other investigators. It is well-known that within the Diatoms (loc. cit., pp. 18, 20) all the euplanktic *Melosira* species, *Cyclotella Meneghiniana*, *C. stelligera*, *Stephanodiscus Astraea*, *St. dubius* and particularly *St. Hantzschii*, together with *Rhizosolenia longiseta* and *Attheya Zachariasi* are characteristic of eutrophic lakes, likewise *Synedra acus* var. *angustissima* and especially *Nitzschia acicularis*.

Within the Flagellates (Nygaard 1945, p. 24) the following 3 species seem to be indicators of dystrophic localities: *Dinobryon pediforme*, *Goniostomum semen* and *Synura sphagnicola*[1]. *Uroglena americana* (*Uroglenopsis americana*) is rather characteristic of Danish oligotrophic lakes with clear acid or neutral water on sandy bottom. Species like *Euglena pisciformis*, *Eugl. tripteris*, *Lepocinclis Steinii*, *Phacus caudata* together with *Mallomonas Teilingii*, *Mall. tonsurata*, *Lepocinclis ovum*, *Trache-*

[1] given as *Synura uvella* f. *punctata*.

lomonas armata, *Phacus acuminata*, *Ph. pyrum*, *Ph. suecica* and *Ph. aenigmatica* are all characteristic of eutrophic waters, the 8 last-mentioned also of the mixotrophic phase. Species like *Lepocinclis texta*, *Lep. fusiformis*, *Phacus platyaulax*, and *Euglena sanguinea* are characteristic of highly eutrophic or even saprotrophic water.

Among the Dinoflagellates (NYGAARD 1945, p. 29) *Peridinium palustre*, *Glenodinium pusillum* and *Gymnodinium fuscum* are indicatory forms of oligotrophic water in the dystrophic or acidotrophic phase. Species like *Amphidinium lacustre*, *Diplopsalis acuta*, *Glenodinium aciculiferum*, *Gl. dinobryonis*, *Gl. gymnodinium*, *Gymnodinium excavatum*, *Gymn. hiemale*, *Gymn. inversum*, *Gymn. paradoxum*, *Gymn. tenuissimum*, and *Gymn. aeruginosum* are indicative of neutral-alkaline, lime-rich, more or less eutrophicated water. On the other hand *Peridinium bipes*, *Per. cinctum*, and *Per. Willei* are eurytrophic and otherwise very adaptive; but in this paper it must be added that among the *Peridinium* species *P. cinctum* is the form that is most commonly met with in eutrophic, whereas *P. Willei* mostly occurs in oligotrophic (acidotrophic and dystrophic) lakes.

Among the large numbers of green algae especially *Staurastrum brachiatum* but also *Bambusina Borreri* (*Gymnozyga moniliformis*) and *Cosmarium tetraophtalmum* seem to be characteristic of the dystrophic phase. *Oocystis solitaria*, however, is not exclusively confined to the dystrophic sub-type: during a re-examination of my plankton samples from the slightly eutrophic Nors Sø I found one individual of this species. In Danish oligotrophic waters *Arthrodesmus triangularis* and *Staurastrum anatinum* seem to be characteristic species, and also the 2 last-mentioned species of the dystophich phase are frequent here. None of these *Chlorophyceae* were found in Danish eutrophic (or mixotrophic) waters. In this country the species *Closterium Kützingii* was mainly observed in eutrophic ponds and lakes of the mixotrophic phase.

A great number of green algae, mainly *Chlorococcales*, may be found in eutrophic lakes and ponds; they are mentioned in "Dansk Plante-Plankton" at the bottom of p. 35 and the top of p. 36. Moreover *Cosmarium depressum* var. *planctonicum*, *Closterium aciculare* and a few *Staurastrum* species like *Staurastrum tetracerum* and its var. *validum* are typical Desmids of our eutrophic lakes.

Among the particularly adaptive green algae may be mentioned *Botryococcus Braunii*, *Chlamydomonas acidophila*, *Quadrigula closterioides*, *Sphaerocystis Schroeteri* and *Staurastrum gracile*, all of which may occur in both oligotrophic (dystrophic, acidotrophic) and eutrophic (mixotrophic) waters. Other species are conspicuous by a far-going indifference to extreme pH and calcium values; the names of these species are given in "Dansk Plante-Plankton" in the middle of p. 35.

4. Systematic Part.

Chlorophyceae.

Volvocales.

Chlamydomonadaceae.

Carteria agloëformis n. sp.

Fig. nostra 1.

Diagnosis. Cellulae parvae, subsphaericae vel late ellipsoideae. Membrana tenuis, adpressa, sine papilla antica. Flagellis 4, longitudine cellulae $1^1/_2$—2 plo longioribus. Chromatophorus tenuiter sacculiformis, supraaequatorialiter valde incrassatus, pyrenoide solitaria, sphaerica et axillari in parte transversali instructus. Nucleus in posteriore parte cellulae situs. Stigma ovale, supraaequatoriale vel raro aequatoriale. Vacuola contractilia bina. Longitudo cellularum 16—18 μ, latitudo 14—16 μ.

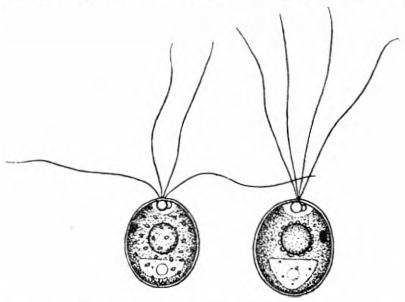


Fig. 1. *Carteria agloëformis* n. sp. from pond in western Stavnsholt, July 22nd, 1929. 800×.

Hab. In stagno parvo prope Stavnsholt, Selandia, Dania, libere natans.

This new species is closely related to *Carteria micronucleata* Korsch. (Pascher 1927, p. 156, Fig. 107), which, however, has a papilla, is more elongate and has an anteriorly situated stigma and shorter flagella than *Carteria agloëformis* mihi. Besides, the pyrenoid of the latter is situated more apically than that of the former.

Carteria agloëformis was observed once (July 22nd, 1929) in the said locality when it occurred in enormous quantities. This small polluted field pond was eutrophic (the dry weight of the plankton on the date mentioned was 160 mg/l); its water was of a pale yellow colour caused by large quantities of *Microcystis flos aquae*; the temperature was 26.5° C. and pH 9.8. The myxophycean quotient was $\frac{4}{5}$, chlorophycean quotient $\frac{13}{5}$, diatom quotient $\frac{0}{0}$, euglenine quotient $\frac{0}{17}$, and compound quotient $\frac{17}{5} = 3.4$.

Carteria fornicata n. sp.

Fig. nostra 2.

Diagnosis. Cellulae mediocres, late vel anguste ellipsoideae, raro subcylindricae apicibus late rotundatis, a vertice visae non compressae, ex 11 mensionibus 1.3—2.3 (saepe 1.5) plo longiores quam latiores. Membrana tenuis, adnata, basaliter

interdum a protoplasto discedens, apicaliter in papillam magnam vel ingentem, late rotundatam, 2—5 μ altam et 6—16 μ latam incrassata. Flagella 4 longitudinis cellulae circiter aequilonga. Chromatophorus urnaeformis, fere apicem attingens, cum pyrenoide ampla, ellipsoidea vel sphaerica, raro subangulata, medio vel paulo inferiore. Stigma parvum vel submagnum, late ovale vel rotundum, raro subangu-

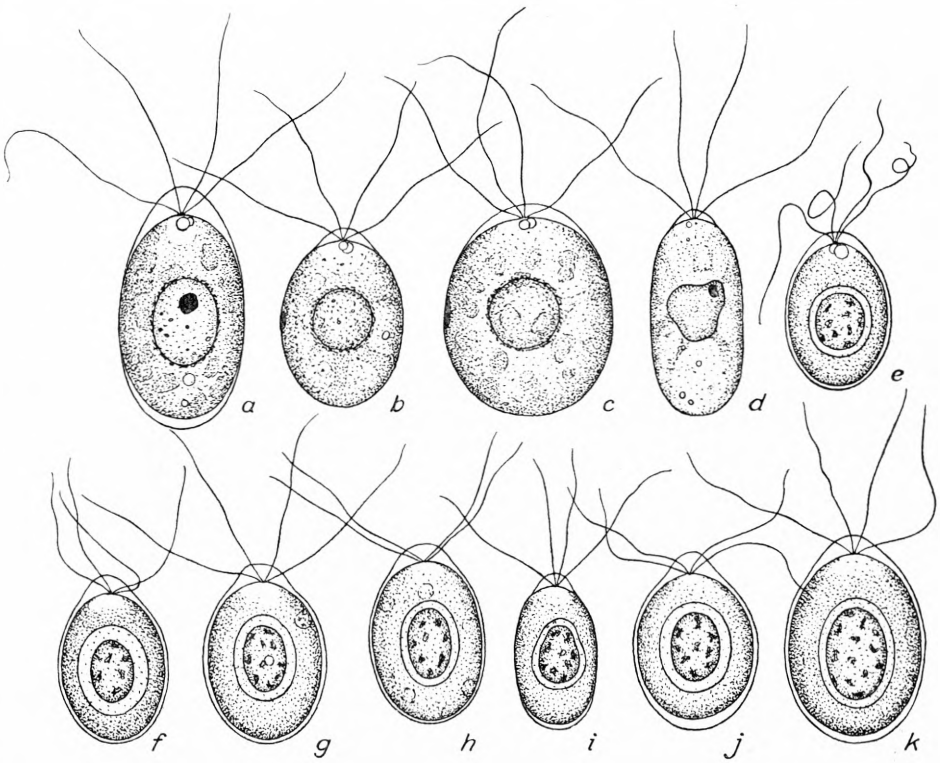


Fig. 2. *Carteria fornicata* n. sp. *a*—*e* from Sandberg Sø, September 4th-10th, 1937; *f*—*k* from Lynge Vandingsdam, June 30th, 1947. *a*—*d* are drawn after living material, *e*—*k* after material fixed in formalin. 800×.

latum, aequatoriale vel medio cellulae paulo superius. Cellulae 26—40 μ longae, 14—28 μ latae.

Hab. In Sandbjerg Sø prope Alssund et Lynge Vandingsdam prope Sorø, Dania, libere natans.

Systematics. In three cells I observed 2 contractile apical vacuoles, but I do not know whether this is a general feature, and so it has been omitted in the diagnosis. The fine granules in the chromatophore in certain individuals showed a very indistinct, asteroid arrangement, but in others they were indistinctly arranged in irregular, roundish groups. This arrangement of granules is perhaps due to the ± infavourable conditions of living under the coverslip: an individual cannot be drawn

until it is quiet or nearly quiet. In fixed material the chromatophore was without any indication of radial structure.

Carteria fornicata is presumably comparatively closely related to *Carteria Olivieri* West (PASCHER 1927, p. 152, fig. 100); the latter species, however, shows a quite different build of the papilla, which is as broad as the cell, it is true, but in the middle has a firm, conical verruca. Moreover it has cylindrical or narrowly ellipsoidical cells, whereas *Carteria fornicata* normally has rather broadly ellipsoidical cells.

Periodicity and Sociology. The species was observed only between September 4th and 10th, 1937 in Sandbjerg Sø and on June 30th, 1947 in Lynge Vandingsdam. It seems to be a warm water form.

In Sandbjerg Sø it was very rare in an *Os li*-association with *Mia pu* as subdominant, and in Lynge Vandingsdam it was rare in a *Tra vo*-association with *Chla ci* and bacteria as subdominants.

Ecology. Both Sandbjerg Sø and the small Lynge Vandingsdam are highly eutrophic, permanently alkaline, contaminated ponds, the latter to such a degree, that it approaches saprotrophy. The compound quotients of Sandbjerg Sø are found on p. 204, those of Lynge Vandingsdam in Table III; on the two dates mentioned above the compound quotient was $\frac{31}{0}$ and $\frac{31}{1}$, respectively. In other words the ecology of *Carteria fornicata* is characterized by a very strong eutrophy.

Carteria polysticta n. sp.

Fig. nostra 3.

Diagnosis. Cellulae late ellipsoideae. Membrana tenuis, adpressa, sine papilla antica. Flagella 4, longitudine cellulae paulo longiores. Chromatophorus grandis, cellulam totam fere explens, sine incrassitudine basali, incrassitudinibus lateralibus cum pyrenoidibus 7—8. Stigma elongatum, aequatoriale. Vacuola contractilia bina. Longitudo cellularum 27—28 μ, Latitudo 20 μ.

Hab. In Madum Sø, Jutlandia, Dania, libere natans.

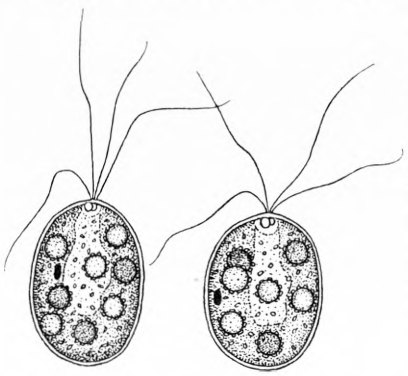


Fig. 3. *Carteria polysticta* n. sp. from Madum Sø, February 5th, 1930. 750×.

Systematics. On account of the many pyrenoids the species will easily be classed within the sub-genus *Carteriopsis*. Within the latter PASCHER (1927, p. 161) gives only one species, *Carteria coccifera* Pascher, which, however, differs from the present species by having egg-shaped cells, a papilla, and the stigma in the front third of the cell.

Periodicity. This new species is perhaps oligothermic, but the material on which this opinion

bases is very sparse. Only a few individuals were seen on February 5th, 1930 at a temperature of 0° or a little more (the lake being completely covered with ice). The species was never observed in the summer samples from this lake.

Sociology. The amount of plankton in Madum Sø was extremely small on February 5th, 1930. The association was mostly characterised by *Dinobryon pediforme*, to a less degree by *Staurastrum gracile* and *Peridinium bipes*.

Ecology. Madum Sø is oligotrophic of the acidotrophic phase and otherwise conspicuous by its extremely small content of organic matter dissolved in the water. Some ecological data of the species are: pH 5.1, consumption of $KMnO_4$ 6.6 mg/l, contents of CaO 4 mg/l, NO_3-N 0.04 mg/l, NH_3-N 0 mg/l, PO_4-P 0 mg/l; an analysis from March 1931 showed 0.01 mg/l of Fe.

Carteria stellifera n. sp.

Fig. nostra 4.

Diagnosis. Cellulae sphaericae vel subsphaericae. Membrana tenuis, adpressa, in polo antico papilla hemisphaerica praedita. Flagella 4, cellulae ad 2—3 plo longiores. Chromatophorus magnus, plusminusve urnaeformis cum processibus ab pyrenoide magna, axiali, late ovali, subbasali raro centrali radiantibus. Inter processus cavernae vacuoliformes, omnes cum corpusculo vel corpusculis moventibus paucis. Nucleus et vacuola bina contractilia in parte anteriore cellulae situs. Stigma parvius, ovale, aequatoriale vel paulum supra partem mediam dispositum. Longitudo cellularum 16—24 μ, latitudo $15^1/_2$—$23^1/_2$ μ.

Hab. In Vandingsdam et in stagno parvo prope Stavnsholt, Selandia, Dania, libere natans.

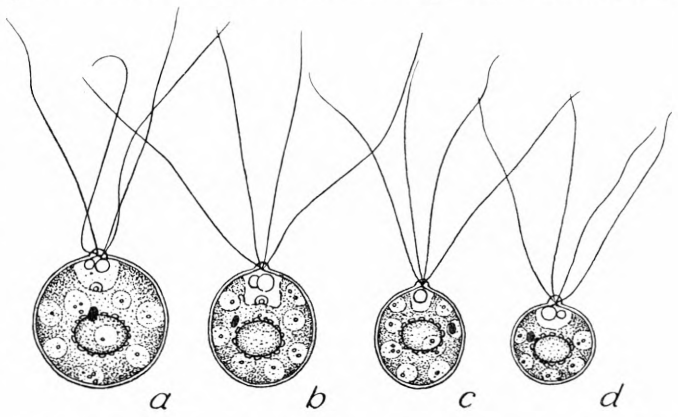


Fig. 4. *Carteria stellifera* n. sp. from Vandingsdam, July 6th, 1929; *a*, *b*, *c*, 750×, *d* 570×.

Systematics. The species shows some relationship to *Carteria radiosa* Korsch. (Pascher 1927, p. 155, fig. 105), which, however, has much shorter flagella, a flat and broad papilla and more numerous chloroplast lobes than *Carteria stellifera* mihi; besides it has no moving granules in the cavities between these lobes. During the swimming the motions of *Carteria stellifera* are trembling.

Periodicity. This Volvocale is meso- to polythermic: it was only found in the plankton during the period June-September, at temperatures between 12 and

26.5° C. In Vandingsdam it was comparatively rare on June 16th, 1930 (temp. 23° C.), but large quantities occurred on July 6th, 1929 (temp. 16° C.). In June, August and September 1929 it was extremely sparse; it disappeared before the beginning of October and did not reappear until June 16th, 1930. In the enclosed pond of the western part of Stavnsholt it was observed only on July 22nd, 1929 when it was very rare.

Sociology. In Vandingsdam the species was found in the following associations:

June 28th, 1929: *Dic pu*-association (*Carteria* very rare).
July 6th, — : *Dic pu*-association (*Carteria* common).
— 16th, — : *Sce arv—Ank fa mi du*-association[1] (*Carteria* very rare).
— 26th, — : *Sce fa*-association (*Carteria* very rare).
Aug. 10th, and
— 17th, 1929: *Sce fa*-association with *Mio pu ra* as subdominant (*Carteria* very rare).
— 24th, — : *Teë mi*-association with *Mio pu ra* and *Sce fa* as sub-dominants (*Carteria* very rare).
Sep. 3rd, — : *Teë mi*-association with *Miu pu ra* as sub-dominants (*Carteria* very rare).
— 9th, — : *Teë mi-Tra hi*-association (*Carteria* very rare).
— 13th, — : *Teë mi*-association with *Mio ho* and *Tra hi* as sub-dominants (*Carteria* very rare).
— 21st, — : *Sce arm*-association with *Mio ho*, *Mer te*, *Tra hi*, and *Teë mi* as subdominants (*Carteria* very rare).
— 23rd, — : *Teë mi-Tra hi*-association (*Carteria* very rare).
June 16th, 1930: *Teë mi*-associations with *Ank co mi* as subdominant (*Carteria* rare).

In the enclosed pond of western Stavnsholt the species was very rare in the following association:

Jul. 22nd, 1929: *Mio fl*-association with *Ca ag* as subdominant, see p. 20.

In other words *Carteria stellifera* mainly occurred in associations that were characterised by green algae (*Dictyosphaerium*, *Ankistrodesmus*, *Tetraëdron*, *Scenedesmus*), flagellates (*Trachelomonas*) and blue-green algae (*Microcystis*).

The most constant associates were *Pediastrum duplex*, *Ped. Tetras*, *Scenedesmus armatus*, *Sce. arvernensis*, *Sce. falcatus* and *Tetraëdron minimum*, which occurred in 100 % of the number of samples (14) that contained *Carteria stellifera*. *Closterium gracile*, *Cyclotella Meneghiniana*, *Dictyosphaerium pulchellum*, *Microcystis holsatica* and *Trachelomonas volvocina* occurred in 93 %, *Ankistrodesmus convolutus* var. *minutus*, *Chlamydomonas Reinhardii*, *Microcystis pulverea* var. *racemiformis* in 86 %, and *Ankistrodesmus falcatus* var. *mirabilis* f. *dulcis* and var. *spirilliformis*,

[1]) and indeterminable green algae.

Chlorogonium acus, *Lampropedia hyalina* and *Merismopedia tenuissima* only in 79 % of the samples.

Ecology. Both Vandingsdam and the enclosed pond in western Stavnsholt are highly productive small ponds without inlets or outlets and contaminated by cattle (maximum production 92.4 and 160 mg/l of dried plankton, respectively). Some ecological data of the species are: pH 7—9.8, consumption of $KMnO_4$ 81—92 mg/l, contents of CaO 19.5—27 mg/l, NO_3-N 0—0.01 mg/l, NH_3-N 0.08—0.2 mg/l, PO_4-P 0—0.03 mg/l, and Fe 0.35 mg/l (analysis of iron from June).

Platymonas incisa n. sp.

Fig. nostra 5.

Diagnosis. Cellulae late ellipsoideae, 1.3—1.5 plo longiores quam latiores, compressae, non contortae. Pars antica excavata et interdum protracta, pars posterior saepe leviter sed perspicue excavata, rarissime sine sinu basali. Flagella 4 cellula aequilonga. Chromatophorus poculiformis, sine pyrenoide, incisionibus verticalibus in quattuor lacinias divisus, quae basaliter continuae sunt. Incisiones partis frontalis alteriores et lateriores quam incisiones partis lateralis. Incisiones partis frontalis saepe cum granulis in serie una. Nucleus in media cellula situs. Stigma rotundum, parvius, semper in parte frontali, aequatoriale vel paulum supra partem mediam dispositum. Longitudo cellularum $13^1/_2$—$17^1/_2\,\mu$, latitudo $10^1/_2$—$13^1/_2\,\mu$, crassitudo 7—9 μ.

Hab. In Spejldam et Hesteskodam prope Hillerød, Dania, libere natans.

Systematics. On account of the appearance of the cells this characteristic species cannot be mistaken for any other *Platymonas* species described, and it may as well be called *Platymonas scherffelioides* mihi or perhaps even *Scherffelia incisa* mihi because the individuals in certain respects are much like *Scherffelia*. But they are not nearly so much flattened as the species of the *Scherffelia* genus (according to A. Pascher, 1927, p. 170, 4—6 times broader than thick), and I have therefore considered it correct to class the species within the genus *Platymonas*. But *Platymonas incisa* is a transition form between *Platymonas* and *Scherffelia*.

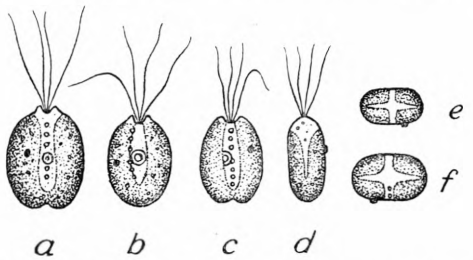


Fig. 5. *Platymonas incisa* n. sp. from Spejldam, November 22nd, 1929 and March 15th, 1930; *a*, *b*, *c* front views, *d* lateral view, *e* and *f* vertical views. 750×.

In fixed material, which shows a marked receding of the protoplast from the cell wall, it looks as if the apical incision in fact goes longitudinally round the whole cell, growing less deep at the basal end of the cell.

Periodicity. In Spejldam a few individuals of the species appeared on November 22nd, 1929 when the temperature had fallen to 4° C. During the following

winter months it was very rare in the plankton. At the beginning of March 1930 it grew more common, and in particular many individuals were observed on March 15th—when the ice was about to break—though it could not be said to prevail in the plankton. Already at the beginning of April it had disappeared from the plankton of Spejldam in spite of the fact that a few individuals were seen on April 4th, 1930 (temp. 5° C. and pH 7.4) in Hesteskodam, the outlet of which falls into Spejldam. During the warm half of the year the species was never observed. Thus *Platymonas incisa* is a stenothermic cold water form, being found only at temperatures between 0.5 and 5° C.

Sociology. In Spejldam the species occurred in the following associations:

Nov. 22nd, 1929: *Ma ak-Tra vo*-association (*Platymonas* very rare).
Jan. 15th, 1930: *Tra vo*-association (*Platymonas* very rare).
Feb. 17th, — : *Crym ov-Chla ac*-association (*Platymonas* very rare).
Mar. 1st, — : *Chla ac*-association with *Ma* sp_1 as subdominant (*Platymonas* not infrequent).
— 15th, — : *Ma se*-association with *Ank fa se br* as subdominant (*Platymonas* rather common).

In Hesteskodam the species was very rare in the following association:

Apr. 4th, 1930: *Ank fa se br*-association.

Platymonas incisa thus occurred in flagellate associations of *Mallomonas*, *Trachelomonas* and *Cryptomonas* and in green algae associations of *Chlamydomonas* and *Ankistrodesmus*.

The most constant associates are *Trachelomonas volvocina*, which occurred in 100 % of the number of samples (6) that contained *Platymonas incisa*. *Chlamydomonas acidophila*, *Mallomonas akrokomos* and *M. semiglabra* were found in 83 % of the samples.

Ecology. Both Spejldam and Hesteskodam are eutrophic, the latter approaching sapotrophy; the former is highly overshadowed and therefore cold in summer. Its water is of a light brown colour and mostly poor in plankton. The pond stands between the eutrophic and the mixotrophic types but it should perhaps rather be called eutrophic on account of its characteristic water-bloom of *Aphanizomenon flos aquae* in late summer. Some data of the ecology of the species are: pH 7.3—8.0, consumption of $KMnO_4$ 37 mg/l, contents of CaO 36.4—40.5 mg/l, Fe 0.17 mg/l, NH_3-N 0.08—0.2 mg/l, NO_3-N 0.06—0.175 mg/l, and PO_4-P 0.018—0.03 mg/l.

Chlamydomonas.

In Dansk Plante-Plankton I have described a *Chlamydomonas fusiformis* n. sp. (Nygaard 1945, p. 52, Fig. 24). According to Gerloff (1940, p. 485) a *Chlamydo-*

monas fusiformis Boye Petersen (1932) and an incompletely described species, *Chlamydomonas fusiformis* Schiller (1913) are previously known.

Chlamydomonas fusiformis Boye Petersen has been called *Chlamydomonas subfusiformis* (Boye Petersen) Gerloff, and to *Chlamydomonas fusiformis* Nyg. I hereby give the new name of *Chlamydomonas retroversa* Nygaard.

Originally I believed that the *Chlamydomonas retroversa* individuals were identical with *Chlamydomonas microscopica* G. S. West (1915, p. 77, Fig. 2F—I, sub nomine *Chlamydomonas gracilis* West). In his diagnosis West states that the stigma is lacking; Pascher (1927, p. 274) suggests that West may have overlooked it. On the chromatophore West only says, 'chromatophora singula cum pyrenoide singulo parvo submediano'; Pascher (*loc. cit.*) supposes that the chromatophore is girdle-shaped and parietal. If this supposition is correct, at any rate some of West's drawings are wrong for in all of them the pyrenoid is shown to be situated in the longitudinal axis of the cell. If West's drawing of the flagella is correct, his *Chlamydomonas microscopica* in this respect differs from *Chlamydomonas subfusiformis* and *Chlam. retroversa*, both of which in a resting state bend their flagella backwards along the cell. In his excellent 1940 paper Gerloff strangely enough does not mention *Chlamydomonas microscopica* under *species inquirendae* where it properly belongs.

Boye Petersen found *Chlamydomonas subfusiformis* in an earth sample from the drift-sand area of West Jutland; pH was 4.83 (1932, p. 396, Figs. 1—3). It appears (in part) from Table IV that *Chlamydomonas retroversa* was found only in Jægerbakke Dam, Vandingsdam, Flødegaardens Dam, Hesteskodam, and Frederiksborg Slotssø, all of them alkaline (pH as high as 9.8), highly eutrophic, contaminated ponds; moreover in the two alkaline, eutrophic ponds of the mixotrophic phase, Blankeborg I and II.

Apart from this conclusive difference in an ecological respect the two species also differ morphologically. *Chlamydomonas subfusiformis* has quite a small papilla and its stigma in the posterior half or third of the cell while the lateral pyrenoid is situated above the middle of the cell; moreover the cells are sometimes slightly curved. *Chlamydomonas retroversa* has no papilla, and its stigma is always situated in the anterior half or third of the cell while the lateral pyrenoid is found below, very rarely in the middle of the cell; the build of the cell is symmetrical.

Gerloff refers *Chlamydomonas subfusiformis* to *Bivacuolatae*; Boye Petersen mentions only one vacuole. Also *Chlam. retroversa* has only one vacuole.

Chlamydomonas anulata n. sp.

Fig. nostra 5 *bis.*

Diagnosis. Cellulae parvae, concinne ellipsoideae vel subglobosae, 0.6—0.95—plo longiores quam latiores. Membrana tenuis, adpressa, papilla antica plane truncata et brevissima instructa. Chromatophorus parietalis, a fronte et postremus exiliter evolutus, in parte aequatoriali valde incrassatus; haec incrassitudo anularis pyre-

noidem unam, magnam et lateralem continet. Stigma ovale, aequatoriale, semper prope pyrenoidem. Nucleus in lumine posteriore situs est, saepe subexcentricus. Vacuola contractilia bina in parte anteriori. Flagella bina cellula breviora. Longitudo cellularum 10.5—17.5 μ, latitudo 7.5—16.5 μ.

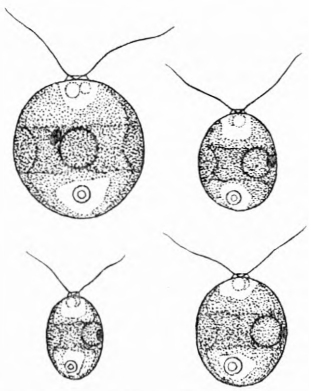


Fig. 5 bis. *Chlamydomonas anulata* n. sp. from a pond at Ragebøl, North Sleswick, April 2nd, 1938, 1070×.

Hab. In stagno prope Ragebøl, Sundeved, Jutlandia meridionali, Dania, libere natans.

Systematics. This species belongs to *Chlamydella*; within this subgenus it should rather be referred to the subsect. *Monopleura*. On account of the ring-formed and aequatorial thickening of the chromatophore and the aequatorial eye-spot which always lies close to the big, lateral pyrenoid, the species may hardly be mistaken for any other species described. This ring-formed thickening is locally so limited and well developed, that it gives the individuals the appearance of possessing two pyrenoids.

Chlamydomonas anulata was not infrequent in the pond at Ragebøl in North Sleswick on April 2nd, 1938. It occurred in a *Sce arm*-association with *Cym so* as subdominant. The pond is no doubt eutrophic as is evident from the plankton quotients of August 30th, 1937: the association was dominated by an undeterminable *Chrysophycea* with *Ste du* and *Tst st* as subdominants, the myxophycean quotient was $\frac{3}{3}$, the chlorophycean $\frac{27}{3}$, the diatom $\frac{2}{0}$, the euglenine $\frac{4}{30}$ and the compound quotient $\frac{36}{3} = 12$; number of species 43.

Chlamydomonas Bergii n. sp.

Fig. nostra 6.

Diagnosis. Cellulae oblonge oviformes, teretes, asymmetricae, 2—3 plo longiores quam latiores, parte apicali obtusa, parte posteriore in caudam hyalinam obliquam exeunte. Membrana tenuis, sine papilla, plerumque ad finem posteriorem a protoplasto discedit et hic caudam 5—6 μ longam, 1 μ crassam possidet. Chromatophorus parietalis, late taeniaeformis, marginibus non continuis; pars incrassata aequatorialis vel subbasalis pyrenoide grande sphaerica vel late ellipsoidea instructa. Nucleus in parte posteriore cellulae situs. Stigma ellipsoideum, aequatoriale vel paulum supra mediam cellulam. Vacuola contractilia bina, flagella bina $^1/_2$—$^2/_3$ longitudinis cellulae. Longitudo cellularum incl. cauda 17—30 μ, latitudo 7—12 μ.

Hab. In Rønhavegaard Dam, Alsia, et Lynge Kirkedam prope Sorø, Dania, libere natans.

Systematics. This quietly swimming species is closely related to *Chlamydomonas rigensis* Skuja (1927, p. 62, t. 1, fig. 11 a—d). However, the cells of the Latvian

species are subacute and provided with a papilla, but especially the caudal spine differs from that of the Danish species in being thick, more or less conical and with a smooth transition into the membrane of the cell. The species is called after Prof. Dr. KAJ BERG, who in so many ways has encouraged and prompted me in my studies on the limnic microflora of this country.

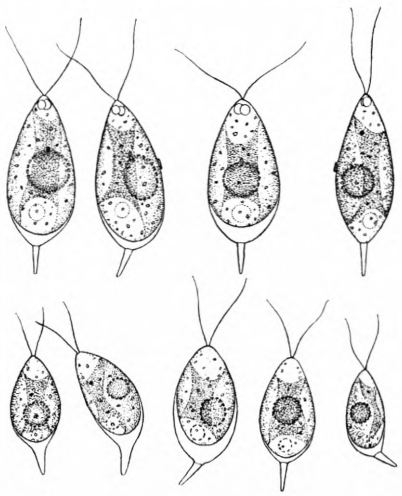


Fig. 6. *Chlamydomonas Bergii* n. sp. from Rønhavegaard Dam, March 12th, 1944. The upper row is drawn from living material, the lower from fixed material. 800×.

Periodicity. The species occurred in small quantities in Rønhavegaard Dam on March 12th and 19th, 1944 (temp. 4.5 and 6° C.) and in Lynge Kirkedam on November 15th, 1947 (temp. 2°) and is probably a cold water form like *Chlamydomonas rigensis*. In March 1945 it was not found again in Rønhavegaard Dam in spite of repeated samplings, so that a planned cultivation of clones for the purpose of elucidating its sexual conditions could not be carried out.

Sociology. On March 12th, 1944 the plankton of Rønhavegaard Dam consisted of a *Chrom No mi*-association with *Chla Re* and *Ste Ha* as subdominants, on March 19th of a *Chrom No mi*-association with *Ste Ha* as subdominant. For the rest *Chlamydomonas Berg'i*, here occurred together with several Chlamydomonads: *Chlamydomonas bicocca*, *Chl. multitaeniata*, *Chl. pseudoplatyrhyncha*, *Chl. sacculiformis*, *Chl. Reinhardii* and *Scourfieldia cordiformis*. On November 15th, 1947 the plankton of Lynge Kirkedam consisted of a *Chla Re-Phu py*-association with 6 other Chlamydomonas-species.

Ecology. Rønhavegaard Dam and Lynge Kirkedam are highly eutrophic ponds, polluted by ducks and swans. Already in March 1944 and also in March 1945 the quantity of plankton in Rønhavegaard Dam was enormous; an intense green coloration of the water was observed. pH measured 8.2 and 7.8 at the time when *Chlamydomonas Bergii* occurred. The former pond is undoubtedly rich in calcium because it is situated on a substratum of moraine clay.

Chlamydomonas capitis n. sp.

Fig. nostra 7.

Diagnosis. Cellulae parvae, tenuiter ellipsoideae vel longissime ovatae, 2.8—3 plo longiores quam latiores. Membrana tenuissima, adpressa, in polo antico papilla distincta, circiter 2 μ lata, cylindracea ordinata. Chromatophorus longe urnaeformis, basaliter valde incrassatus (incrassitudo partem dimidiam cellulae saepe explens), pyrenoide basali, axiali instructus. Nucleus centralis vel paulo supra medium situs. Stigma punctiforme, in media cellula vel in parte basali. Flagella bina, 22—35 μ

longa, 2—3 plo longitudinis cellulae. In polo antico vacuola bina contractilia sita sunt. Longitudo cellularum 10.5—17.5 μ sine papilla, latitudo 4—6.5 μ.

Hab. In Jægerbakke Dam prope Hillerød, Dania, libere natans.

Systematics. The species is closely related to *Chlamydomonas capitata* Scherffel et Pascher (PASCHER's Süsswasserflora, Heft 4, 1927, p. 246, Fig. 200). The cells of this species, however, are often obovate, and judging from the drawings they are 2.2—2.5 times longer than broad (6—8 μ broad), the flagella only 1.5 times the length of the cell, and the stigma is situated in the front third of the cell. *Chlamydomonas capitis* is also related to *Chlamydomonas solida* Pascher (1930, p. 136, fig. 31), which, however, has fusiform cells without papilla and pyrenoid, and the flagella of which are likewise 1.5 times the length of the cell.

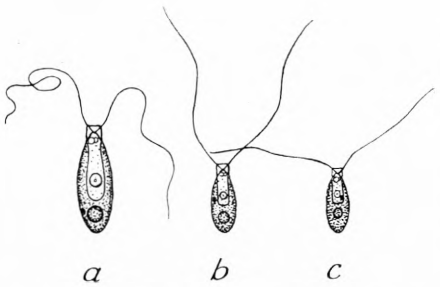


Fig. 7. *Chlamydomonas capitis* n. sp. from Jægerbakke Dam; *a* from December 16th, 1929, *b* and *c* from May 16th, 1930. 750×.

Periodicity. Only a few individuals of the species were observed and only on the dates of December 16th, 1929 and May 16th, 1930 at temperatures of 3° and 20.5° C., respectively. It thus seems to be eurythermic. It was not found in any of the other samples from Jægerbakke Dam although this pond was examined every 10th or 14th day throughout a whole year.

Sociology. The species occurred in the following associations:

Dec. 16th, 1929: *Ank fa se br-Ki mi*-association with *Ank fa spa* and *Mio ho* as subdominants (the species very rare).

May 16th, 1930: *Ank fa spa-Mio ho-Sce arm*-association, see Table IV (the species very rare).

It thus occurs in associations of green algae (*Ankistrodesmus*, *Kirchneriella* and *Scenedesmus*) and blue-green algae (*Microcystis*). On account of the paucity of the material no constant associates are given.

Ecology. Jægerbakke Dam is a highly eutrophic, lime-deficient pond, sheltered from winds and without inlets or outlets. The compound quotient was $\frac{35}{2} = 17.5$ on May 16th, 1930 (see also Table III). The following are data from the ecology of *Chlamydomonas capitis*, including the values of analysis from May 21st, 1930: pH 7.4, CaO 7.3—10.9 mg/l, consumption of $KMnO_4$ 32 mg/l, PO_4-P 0.005—0.008 mg/l, NH_3-N 0.05—0.75 mg/l, NO_3-N 0—0.01 mg/l.

Chlamydomonas clavata n. sp.

Fig. nostra 8.

Diagnosis. Cellulae parvae, clavatae, e 7 mensionibus 3.3—4.25 (saepe circiter 3.5) plo longiores quam latiores (a vertice visae circulares), leviter curvatae,

aut altero latere convexo, altero recto aut utroque latere curvato, polo antico obtuse acuto, sine papilla, polo posteriore rotundato. Membrana delicatissima, adnata. Flagellis binis, corpore aequilongis vel paulo longioribus, in statu quiescente secundum latera cellulae valde recurvatis. Chromatophorus unus, lateralis, alveiformis, saepe ad latus convexum cellulae, cum pyrenoide una in dimidio altitudine cellulae vel paulo inferiore; fines cellulae hyalini. Stigma minimum, ovale, in parte anteriore cellulae situm. Nucleus in parte posteriore cellulae. Vacuola contractilia bina. Cellulae 8.5—10.5 μ longae, 2—3 μ latae.

Hab. In Præstesø prope Oxbøl, Jutlandia occidentali, et Blankeborg II, Fionia, Dania, libere natans.

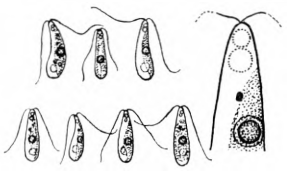


Fig. 8. *Chlamydomonas clavata* n. sp. from Præstesø, June 24th, 1930. 750×.

Systematics. This new species, which is easily distinguished by its clavate, small cells, shows the closest relationship to *Chlamydomonas minima* Korsch. (see PASCHER 1927, p. 280, fig. 241, or, as it is called by GERLOFF: *Chlamydomonas perpusilla*, because SCHILLER has formerly described a *Chlamydomonas minima*, which, however, according to GERLOFF is possibly no *Chlamydomonas* at all). KORSHIKOV's species differs by being thickest in the middle.

Periodicity and Sociology. *Chlamydomonas clavata* was found only on June 24th and 28th, 1930 (temp. 20—21° C.) in Præstesø and on June 10th, 1930 (temp. 21.5° C.) in Blankeborg II, in the following associations:

Præstesø: *Ana fl*-association (the species very rare; see Table II),

Blankeborg II: *Ste Ha*-association (the species extremely rare; see Table IV), i. e. in an *Anabaena* and in a *Stephanodiscus* association.

Ecology. Præstesø is a clear, "mesotrophic" heath lake, the compound quotient of which according to Table I was $\frac{21}{17} = 1.2$ on the dates mentioned, when pH was 7.0—7.1; see further p. 13. Blankeborg II is a eutrophic turf pit of the mixotrophic phase; in 1928—29 the consumption of $KMnO_4$ was 70—88 mg per litre, and January 6th, 1930 showed the following contents of CaO 153.5 mg/l, PO_4-P 0.6 mg/l, NH_3-N 0.9 mg/l, and NO_3-N 1.3 mg/l. On June 10th, 1930 the compound quotient was $\frac{20}{0}$.

Chlamydomonas excentrica n. sp.

Fig. nostra 8 bis.

Diagnosis. Cellulae concinne oviformes, 1.3—1.5-plo longiores quam latiores. Membrana adpressa, tenuis, sine papilla. Chromatophorus sine pyrenoide, forma ut chlamys aperta, obliqua, irregulariter lobata vel sinuata, fere ad polum anticum attingens, sed nunquam parte basali cellulae implens, et hic cum lumine incolorato et excentrico. Stigma mediocre vel grande, late ovale vel rotundum, rubrum vel saepe brunneorubrum, aequatoriale vel saepe subaequatoriale, raro basale. Nucleus semper basalis, subexcentricus, in lumine posteriore situs. Vacuola contractilia bina in polo antico sunt. Flagella bina, 1—$1^1/_2$-plo cellula longiora. Intus granula

saepe in seriebus decussatis ordinata sunt. Longitudo cellularum 8.5—13.5 μ, latitudo 5.5—9 μ.

Hab. In stagno turfaceo prope Søgaard Sø, Dania, libere natans.

Systematics. The species comes nearest to *Chlamydomonas anglica* Pascher (1927, p. 295, fig. 260) within the subgenus *Chloromonas*. The latter species differs from *Chlamydomonas excentrica* in the shape of the cells which are not typically ovate, the lack of eye-spot, the position of the nucleus, which is situated in the former half of the cell, and the flagella inserting relatively long from each other.

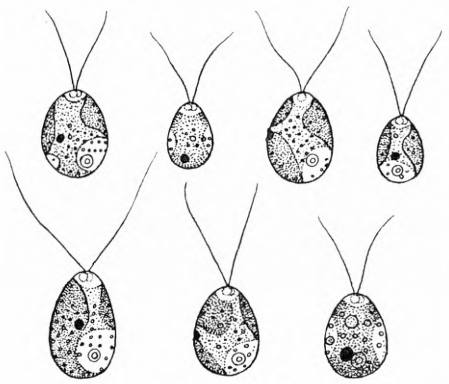


Fig. 8 *bis*. *Chlamydomonas excentrica* n. sp. from a Sphagnum bog south of Søgaard Sø in North Sleswick, July 16th, 1939. 1070×.

The species was found only on July 16th, 1939 (temp. 21.5° C.) in a *Sphagnum* bog ("Cirkelsø") south of Søgaard Sø, North Sleswick. This dystrophic locality has extensive quaking bogs at the margins, and its water is very acid and brownish. The compound quotient on July 23rd, 1926 (pH 4.0) was $\frac{2}{5} = 0.4$, on July 16th, 1939 (pH 4.3) it was $\frac{0}{3}$. *Chlamydomonas excentrica* was rather common on July 16th, 1939 in the plankton which was dominated of *Cryptomonas ovata*. This species and *Mallomonas caudata* were destroyed under the coverglass after a relatively short examination, whereas *Chlamydomonas excentrica* proved much more resistant under these conditions.

Chlamydomonas oleosa n. sp.

Fig. nostra 9.

Diagnosis. Cellulae mediocres, oviformes, interdum ellipsoideae. Membrana distincta, interdum mucosa, in polo antico papilla parva et hemisphaerica praedita. Protoplastus ad finem posteriorem rotundatus a membrana saepe leviter descedit. Chromatophorus parietalis, peripheriam excl. polo antico totam fere occupans, in partes numerosas, irregulares, inter se subaequales divisus. Pyrenoides abest. Protoplastus sphaera oleosa una vel sphaeris oleosis binis, rarissime numerosis instructus. Nucleus centralis vel paulo supra mediam cellulam situs est. Stigma breviter lineare, aequatoriale vel subaequatoriale est. Vacuola contractilia bina, Flagella bina, cellula aequilonga vel paulo longioria sunt.

Propagatio sexualis heterogama; gynogametae sphaericae, circiter 12 μ in diametro, majores quam androgametae oviformes, circiter 11 μ longae et circiter 8 μ latae.

Longitudo cellularum vegetativarum 17—23 μ, latitudo 13—18.5 μ; diameter zygotae immaturae 16.5—18.5 μ.

Hab. In Bistrup Dam, Selandia septentrionali, Dania, libere natans.

Systematics. The species differs from the closely related *Chlamydomonas polychloris* Pascher et Jahoda (1928, p. 277, fig. 29) by its minute and hemispherical papil the subaequatorial eye-spot and by having one or two oil drops, situated each in its cavity near the perifery of the protoplast. As far as I know big oil drops within the green, unicellular *Chlamydomonadaceae* are known only in *Carteria oleifera* Pascher (1927, p. 162, fig. 115).

After 18 years' stay in dilute formalin the material of *Chlamydomonas oleosa* was mounted in chlor-zinc-iodide; here the cell wall and a lot of small granules in

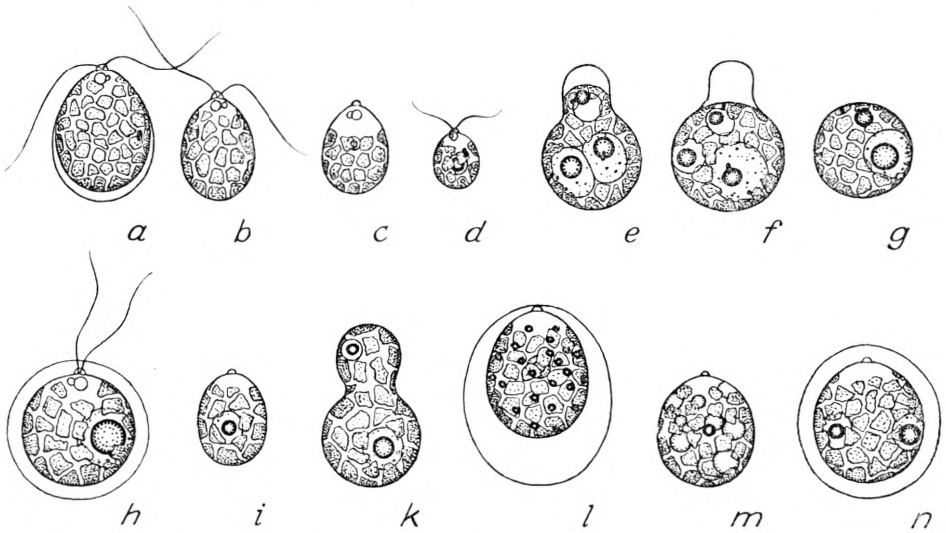


Fig. 9. *Chlamydomonas oleosa* n.sp. from Bistrup Dam, April 12th, 1930. The figures of the upper row are drawn after living material (750×), those of the lower row after material fixed in formalin (1070×). The nucleus is only delineated in *c* and *l*; *d* is a male gamet, *h* is presumably a female gamet; *e*, *f* and *k* are stages of copulation, *g* an immature zygote.

the chromatophore turned blue; the latter also turned blue in iodine potassium iodide, which shows that the product of photosynthesis is starch. The pale, brownish balls in the cells were not affected by this treatment, but in osmic acid they turned dark-brown, which seems to indicate that they consist of fat.

On April 12th, 1930 I repeatedly observed that small, ovate cells (presumably androgametes) united with slightly bigger, spherical cells (presumably gynogametes). The copulation started with a fusion of the front parts of the cells. The wall of the small, ovate cell then remained as an empty sheath on the zygote. Also the gametes contained 1—2 oil drops per cell and in their inner structure were quite like the vegetative cells.

Periodicity and Sociology. The species was found only on November 16th, 1929 (temp. 5° C.) when it was very rare, and on April 12th, 1930 (temp. 9° C.) when it was common and formed gametes.

Both associations were dominated by enormous quantities of bacteria. On the former of the dates mentioned (the composition of the associations appears from Table IV) *Euglena phacoides* was the most frequent, non-bacterial organism (60 cells per ml), but on April 12th *Chlamydomonas oleosa* itself was the dominant form among the non-bacterial organisms. In July, August, September, and October the species was never seen in the plankton of Bistrup Dam, which seems to indicate that *Chlamydomonas oleosa* is a cold water form.

Ecology. Bistrup Dam was distinctly eutrophic of the saprotrophic phase. Accordingly, the species must be characterized as α-mesosaprobic (or polysaprobic). On April 12th, 1930 Bistrup Dam contained 4 mg PO_4-P and 20 mg NH_3-N per litre! (On August 12th, 1929 the content of CaO was 118.7 mg/l).

Phacotaceae.

Pteromonas spinosa n. sp.

Fig. nostra 10.

Diagnosis. Cellulae parvae, a fronte visae hexangulatae, angulis rotundatis; a latere visae cum quattuor sinibus in utroque latere, pars anterior cellulae subconiformis, pars posterior subacuta, cum una spina robusta, decurva in utroque latere; a basi visae fusiformes cum sinu grandi in medio lateris utriusque. Margo cellulae ala hyalina, subhexangulata, satis lata circumdatus, anteriore profunde incisa. Membrana cellulae subcrassa. Chromatophorus cum pyrenoide grandi, basali et axiali. Stigma ovale, aequatoriale; flagellis binis, longitudine cellulae aequilongis. Longitudo cellularum sine ala 15—19.5 μ, latitudo sine ala 11—13 μ, crassitudo 9—11 μ, ala 2—4 μ lata, spinae 2—3 μ longae.

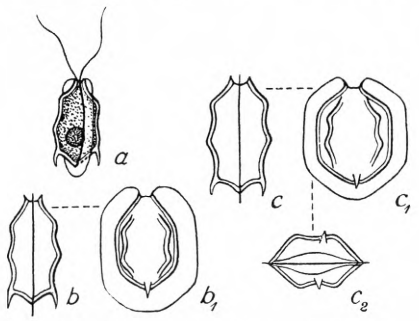


Fig. 10. *Pteromonas spinosa* n. sp. from Flødegaardens Dam. *a*: a living cell in obliquely lateral view from June 10th, 1930. The cell content is not depicted in the other figures (from August 3rd, 1939). *b* and *c* lateral views, b_1 and c_1 front views, c_2 basal view. 800×.

Hab. In Flødegaardens Dam, Fionia, et in stagno prope Hokkerup, Jutlandia meridionali, Dania, libere natans.

Systematics. By its 2 posteriorly directed, antapical spines the species is easily distinguished from *Pteromonas angulosa*, for which it may be mistaken on a superficial view.

The species is closely related to *Pteromonas varians* Frank Jane (1944, p. 38, Figs. 5—21). In his diagnosis the author says, "surface of cell beset with gently rounded, sometimes angular protuberances, of which two are posterior". Accordingly, *Ptero-*

monas varians does not seem to possess conspicuous and sometimes curved spines as in *Pteromonas spinosa*, neither according to diagnosis nor text-figs. The dimensions of *Pteromonas varians* are a little smaller than those of *Pteromonas spinosa*: longitudo cellae sine ala 14—15 μ, latitudo cellae sine ala 7—12 μ, altitudo 8 μ.

Periodicity. *Pteromonas spinosa* occurs very sporadically: out of 87 samples taken at regular intervals during the period 1926—30 (1939) only 3 samples from July 1st, 1926, June 10th, 1930 (temp. 20° C.) and August 3rd, 1939 contained this species which accordingly occurs in summer samples only. It was always very sparsely represented. Both *Pteromonas aculeata* and *Pteromonas angulosa* are more frequent in Flødegaardens Dam, occurring in 6 and 11 of the 87 samples, respectively.

Sociology. The species was found in the following associations:

Flødegaardens Dam.

July 1st, 1926: *Sce ec*-association with *Dic pu* as subdominant (the species very rare).

June 10th, 1930: association of indeterminable, minute green algae with *Chry mi* as subdominant (the species very rare).

Aug. 3rd, 1939: *Dic pu*-association with *Ste Ha* as subdominant (the species very rare),

Pond situated near the beginning of the Hokkerup road from the Graasten-Søgaard road.

Sep. 14th, 1944: *Ank co mi-Euglena*-association (the species very rare).

The qualitative composition of the plankton on the 3 dates first mentioned appears from Table IV. *Pteromonas spinosa* thus occurs in associations dominated by green algae, *Chlorococcales* (*i. a. Ankistrodesmus*, *Dictyosphaerium* and *Scenedesmus*) and *Euglena*. Constant associates cannot of course be given in this case.

Ecology. Flødegaardens Dam and the Hokkerup pond are highly eutrophic ponds, situated in open land, contaminated by cattle or geese and ducks. On the 3 dates mentioned above for Flødegaardens Dam the compound quotient reached the values $\frac{34}{1} = 34$, $\frac{46}{2} = 23$ and $\frac{35}{4} = 8.75$ (cp. also Table III). On July 1st, 1926 pH was 8.2. A couple of calcium analyses from 1927 and 1930 showed 90 and 82 mg CaO per litre.

The myxophycean quotient of the Hokkerup pond was $\frac{1}{0}$, the chlorophycean $\frac{15}{0}$, the diatom $\frac{2}{1}$, the euglenine $\frac{17}{15}$, and the compound quotient $\frac{35}{0}$. On the said date pH was 8.5.

Chlorococcales.

Chlorellaceae.

Micractinium pusillum Fresenius.

E. LEMMERMANN 1900, p. 90, t. 3, figs. 1—10 (*sub nomine Richteriella botryoides* Lemm.). *Fig. nostra* 11.

In Blankeborg II the species was very common on May 4th, 1930 (temp. 17° C.). The vegetative cells which were spherical or broadly ellipsoidical and 7—10.5 μ in

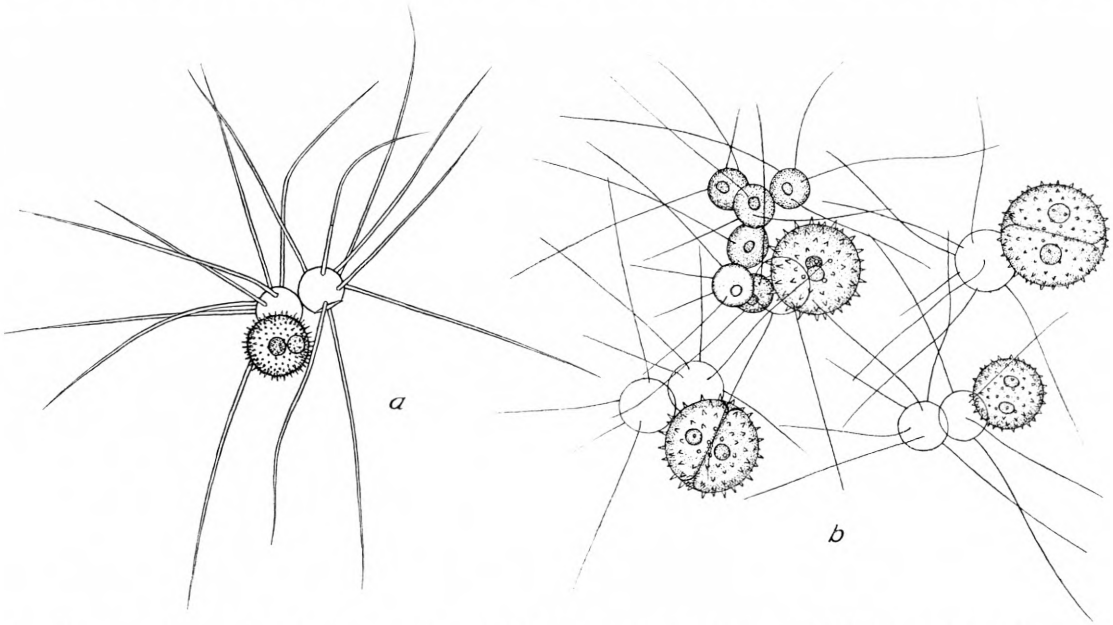


Fig. 11. *Micractinium pusillum* Fres.; *a* from Flødegaardens Dam, April 6th, 1928, *b* from Blankeborg II, May 4th, 1929. 800×.

size, each had up to 7 long, thin and flexible bristles. Some of the colonies frequently contained some spherical, prickled "spores" with a diameter of 12—17 μ. These resting stages were also found individually, but in such cases 1 or 2 empty *Micractinium* cells nearly always adhered to them. Among 20 spores examined only one had no adhering emtpy cells, and in this case it or they may of course have fallen off. The interior of the resting stage was distinctly composed of 2 equally great plasma parts, each with its pyrenoid. It is an obvious conclusion that the contents of the two adhering, empty cells have come out, have copulated and then surrounded themselves with a firm, prickly wall.

If this has really happened, we here have an instance of a sexual propagation within the family *Oocystaceae*, on which H. PRINTZ in his treatment of the *Chlo-*

rophyceae in ENGLER und PRANTL's "Natürlichen Pflanzenfamilien" (2. Aufl., vol. 3, 1927, p. 116) says, "Geschlechtliche Fortpflanzung ist bisher ganz unbekannt!"

Quite the same phenomenon was observed in Flødegaardens Dam. *Micractinium pusillum* here reached an enormous maximum on April 6th, 1928, during which many zygotes of the same kind as those of Blankeborg II were observed. In the same pond a few zygotes were seen on April 17th, 1927. These facts from the well examined ponds of East Funen seem to indicate that the copulation normally takes place in April-May at temperatures between 8 and 17° C.

After the description given above had been worked out, the study of F. MOEWUS' excellent treatise in Ergebn. d. Biol., vol. 18, 1941, called my attention to the fact that KORSCHIKOFF in 1937 has observed copulation of gametes in *Micractinium pusillum* (*loc. cit.* p. 302—03, fig. 3d). KORSCHIKOFF maintains that it is a question of oogamy, which also appears distinctly from the drawing. The present Danish findings, however, indicate an isogamous copulation unless the two equally great plasma parts in the zygote are the result of the first division stage of the content of the zygote. Whether the zygote is formed within a *Micractinium* cell, the wall of which is then burst and cast off, or the zygote completes its development outside the Micractinium cell, remains an open question.

Oocystaceae.

Oocystis crassa Wittrock var. **minor** nov. var.

Fig. nostra 12.

Diagnosis. A typo cellulis minoribus differt. Cellulae ellipsoideae, 1.4—1.6 plo longiores quam latiores, cum chromatophoris 2—8, vulgo 4, in singulis cellulis parietalibus, singulis pyrenoidibus instructis. Membrana apicalis interdum leviter incrassata. Cellulis solitariis raro in coloniis 2- vel 4-cellularibus consociatis intra membranam matricalem semper adpressam. Coloniae cum 8 cellulis rarissime observatae. Longitudo cellularum 12—16 μ, latitudo 7—11.5 μ.

Hab. In Store Dam, Selandia, Dania, libere natans.

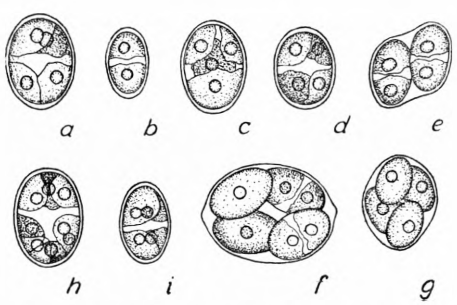


Fig. 12. *Oocystis crassa* Wittr. var. *minor* n. var. from Store Dam, *a*—*g* from November 2nd, 1929, *h*—*i* from September 21st, 1929. 800×.

Systematics. During the examination of WITTROCK's original material of *Oocystis crassa* (*Algae exsiccatae* no. 355) it was observed that the cells are 1.2—1.6, mostly 1.3—1.5 times longer than broad. The length of the cells was 16.5—22.5 μ, and the breadth 11—16 μ. On the basis of several measurings

PRINTZ (1913, p. 175) gives the lengths 14—26 μ and the breadths 10—20 μ and on t. 4, fig. 14 brings a good original illustration of *Oocystis crassa*.

The shape of the cells in the original material is typically ellipsoidical; about this the diagnosis also says that the cells are 'breviter ovatis'. However, other investigators like G. S. WEST refer colonies with subfusiform cells to *Oocystis crassa* (Treatise 1904, p. 227, fig. 97 C—D), and PRINTZ's *Oocystis crassa* f. *major* (1913, p. 176, t. 4, fig. 15) even has distinctly fusiform cells. Whether this is legitimate for the present remains an open question.

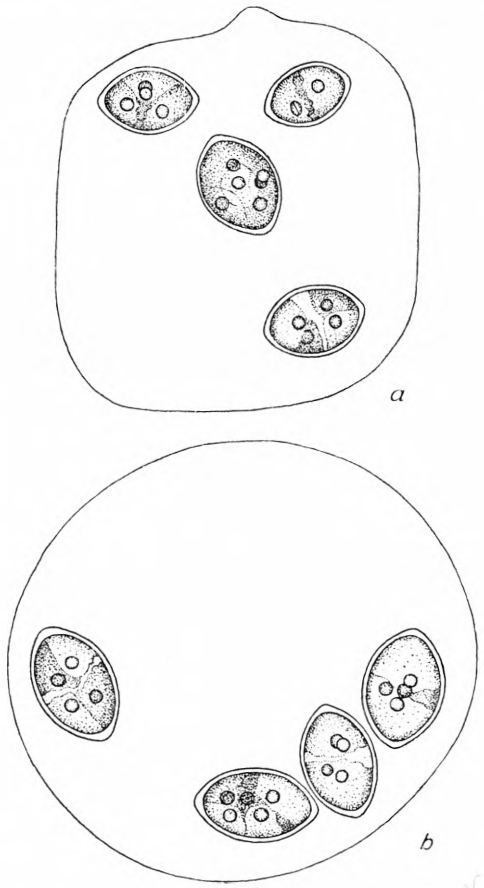


Fig. 13. *Oocystis natans* Lemm.; *a* from Mossø, August 18th, 1929, 560×; *b* from Salten Langsø, August 19th, 1929, 800×.

To begin with I identified the specimens illustrated in *Fig. nostra* 13 as *Oocystis crassa*; the cells are fusiform, 1.3—1.6 times longer than broad, 19—25 μ long and 12—18 μ broad, the colonies 76—102 μ long and 71—83 μ broad. As the number of chromatophores, however, normally is only 4, it will no doubt be more correct to call them *Oocystis natans* though the chromatophores do not seem to be stellately lobed.

The shape of cell in another species, *Oocystis Borgei* (see PRINTZ 1913, p. 173, t. 4, figs. 1—2), is quite like that of *Oocystis crassa*, i. e. ellipsoidical. According to measurings of the original figures of SNOW (reproduced in PRINTZ's paper quoted above) the ratio between length and breadth of the cells is 1.3—1.35—1.4—1.45—1.5 and in BORGE's original figure (1900, t. 1, fig. 3) 1.35—1.4—1.45, in other words ratios corresponding exactly to those of the original material of *Oocystis crassa*. Even if the colonies pictured in *Fig. nostra* 14 have cells with a normal of 2 or 4 chromatophores, each with one pyrenoid, and a length of 17—20 μ and a breadth of 12—15 μ, it will presumably be more correct to include them under *Oocystis Borgei*.

Periodicity. *Oocystis crassa* var. *minor* is a eurythermic plankton form with a temperature amplitude of 0.5—23.5° C. It plays a prominent part in the plankton of Store Dam.

At the beginning of July 1929 it was rare, but already in August it became very common (about 3000 cells and colonies per ml on August 17th at a temperature

of 17° C.). Throughout September and October (temp. 18—8.5° C.) it also predominated in the plankton of Store Dam. During this comparatively long period the water of the pond was green from the numerous *Oocystis* cells. The great maximum of 10.700 cells (and colonies) per ml occurred on November 2nd at a temperature of 6° C. From this date it decreased rapidly and was rare already on November 28th. During the winter months it was very rare, and it was not until May and June that it attained a slightly higher frequency though it did not in any way reach a dominating position within the plankton.

Sociology. *Oocystis crassa* var. *minor* was found in the following associations:

July 6th, 1929: *Gy ex*-association (variety rare).
Aug. 17th, — : *Oo cr mi*-association (about 3000 cells and colonies per ml) with *Gy ex* as subdominant (about 2800 cells per ml); variety very common.
Sep. 9th, — : *Oo cr mi*-association (variety very common).
— 21st, — : *Oo cr mi*-association (variety very common).
Oct. 11th, — : *Oo cr mi*-association (variety very common).
— 30th, — : *Oo cr mi*-association (variety very common).
Nov. 2nd, — : *Oo cr mi*-association (10.700 cells and colonies per ml); variety abundant.
— 28th, — : *Tra vo*-association (variety rare).
Dec. 16th, — : *Tra vo*-association (variety rare).
Jan. 15th, 1930: *Gle ac*-association (variety very rare).
Mar. 1st, — : *Gle ac*-association (variety very rare).
May 28th, — : *Gy ex- Sye ac an*-association (variety rare).
June 16th, — : *Tra vo*-association with *Gy ex* as subdominant (variety rare).

Besides being itself the dominant form of associations *Oocystis crassa* var. *minor* occurs in dinophycean associations of *Gymnodinium* and *Glenodinium*, euglenine associations of *Trachelomonas* and diatomaceous associations of *Synedra*.

The most constant associates were *Trachelomonas volvocina*, which occurred in 100 % of the number (13) of samples that contained *Oocystis crassa* var. *minor*, *Peridinium palatinum* and a *Chlamydomonas* species, presumably identical with *Chl. cingulata* var. *globulifera*, both of which occurred in 85 % of the samples, and *Trachelomonas intermedia*, which occurred in 77 % of the samples.

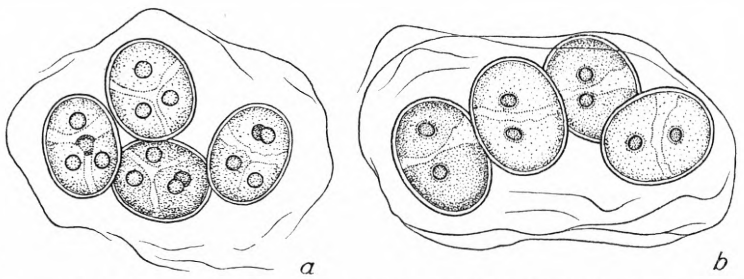


Fig. 14. *Oocystis Borgei* Snow; *a* from Hostrup Sø, July 24th, 1926; *b* from Tissø, July 13th, 1929. 800×.

Ecology. Store Dam is a forest-bordered, eutrophic pond approaching mixotrophy, with ample vegetations of *Helodea canadensis*. Values of the compound quotient are found on p. 112. The following data briefly illustrate certain features of the ecology of *Oocystis crassa* var. *minor*: pH 7.4—8.5, content of CaO 92—97.9 mg/l, consumption of $KMnO_4$ 48-65 mg/l, contents of PO_4-P 0.005—0.015 mg/l, NH_3-N 0.08—0.2 mg/l, NO_3-N 0—1 mg/l, Fe 0.03—0.3 mg/l.

Oocystis Marssonii Lemm.

Lemmermann 1899, p. 24, t. 1, figs. 15—19; Printz 1913, p. 176, t. 4, figs. 16—17. *Fig. nostra* 15.

Diagnosis. Cells ellipsoidical, subfusiform or subcylindrical with rounded or subacute apices, sometimes a little asymmetrical, 1.5—2 times longer than broad. As regards the point last-mentioned it is worth noticing that even "ellipsoidical" cells may sometimes be asymmetrical relatively to the longitudinal axis of the cell. Apices not or only very slightly thickened. 1—3 chromatophores in every cell, with or without pyrenoid. Sometimes oil droplets occur in the cells. Cells very rarely single, as a rule united into 4-celled, sometimes 8-celled, very rarely 2-celled colonies. Membrane of mother cell sometimes without, sometimes with apical, rounded thickenings. Cells 6.5—14 μ long, 3.5—9 μ broad; 4-celled colonies according to 10 measurings 15—60 μ long and 10—50 μ broad; 8-celled colonies according to 3 measurings 27—87 μ long and 21—83 μ broad.

Distribution. Widely distributed (see Tables II and IV), no doubt a cosmopolite.

Systematics. In his diagnosis Lemmermann says: cellulis ovatis vel interdum fusiformibus; Printz's figures cited above only show fusiform cells. On the other hand there is a discrepancy between Lemmermann's diagnosis (Cellulis circ. 1.5 plo longioribus quam latioribus) and his figures which demonstrate an axial ration of 1.75—2. In the Danish material the measurements of the cells were 6.5—13 $\mu \times 3.5$—9 μ with an axial ration of 1.5—2.

As will appear from *Fig. nostra* 15c one colony may contain both cells of a long ellipsoidical shape and subfusiform cells. In other colonies subcylindrical cells may have subacute apices (Fig. 15h), and in one locality as for instance Frederiksborg Slotssø or Badstue-Ødam the membrane of the colonies and the shape of the cells may vary extensively within the scope of the extended description of species (see Fig. 15f—i, a—b).

Printz (loc. cit.) is of opinion that *Oocystis Marssonii* may be regarded as a variety of *Oocystis crassa*. In my opinion the species is nearer related to *Oocystis lacustris*, the chromatophores of which are also present in a number of 1—3 per cell, as a rule 2, and often situated terminally. Chodat's fig. 22 of *O. lacustris* (in Printz's paper) incidentally shows the same as *Fig. nostra* 15c, viz. that one and the same

colony may contain both ellipsoidical and fusiform cells. In his monographical treatment of the *Oocystis* species PRINTZ makes a point of the presence or absence of pyrenoid; from personal experience I am of opinion that this character is by no means constant in a green alga.

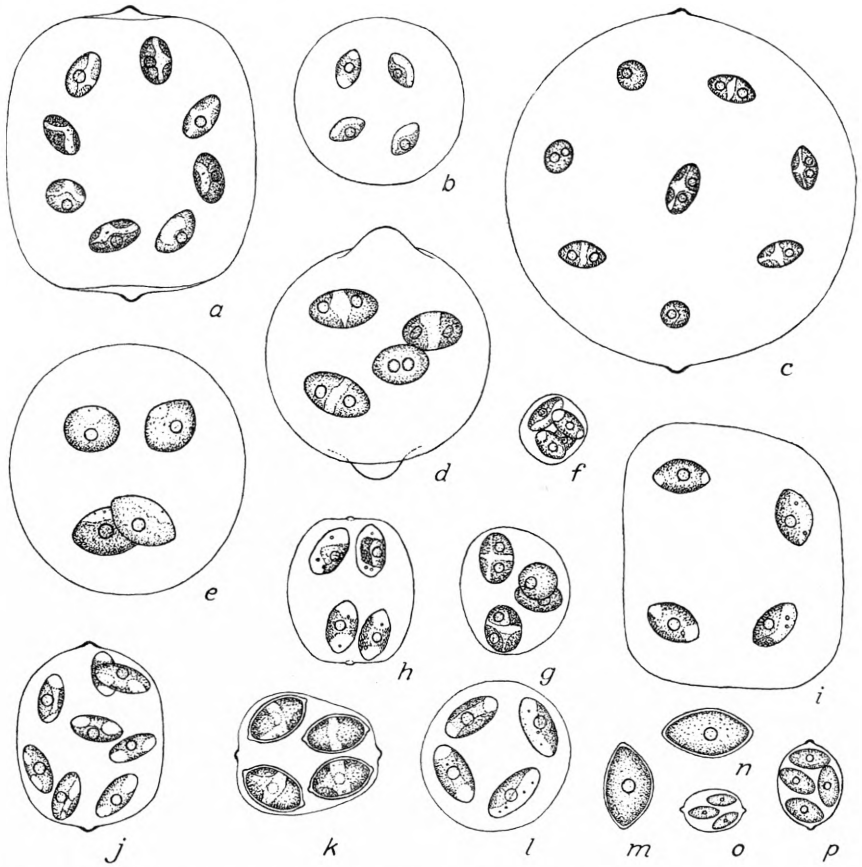


Fig. 15. *Oocystis Marssonii* Lemm.; *a*—*b* from Badstue-Ødam, October 5th and September 5th, 1929; *c* from Teglgaard Sø, September 6th, 1929; *d* from a pond in Ragebøl at Alssund, August 30th, 1937; *e* from Flødegaardens Dam, September 15th, 1928; *f*—*i* from Frederiksborg Slotssø, August 21st and September 6th, 1929, April 3rd and May 13th, 1930; *j* from Gadevang Mose, July 6th, 1929; *k* from Skaansø in Salling, July 5th, 1938; *l* from Vandingsdam, July 6th, 1929; *m*—*p* from Blankeborg I, June 28th, 1925 and August 18th, 1928. *a*, *b*, *c*, *f*, *g*, *h*, *i*, *j*, *l*, *o* an *p* 560×, *d*, *e*, *k*, *m* and *n* 800×.

Oocystis parva West (1893) is very closely allied to *Oocystis Marssonii* (1898); if identical the alga should be named *Oocystis parva*.

It would be of interest through experiments with pure cultures (clones) of *Oocystis* species to clear up which variations are only modifications (see p. 180). During such experiments it should be examined whether a cell is ellipsoidical when seen from one side and fusiform when seen from the other or whether 2 types of cells may in fact be present in the same colony.

Hydrodictyaceae.

Pediastrum alternans n. sp.

Fig. nostra 16.

Diagnosis. Coenobia 64- vel 32-cellularia, ex foraminibus parvis, subsemicircularibus vel subtriangulis perforata. Cellulae marginales in medio sinu profundo et late rotundato et cum cornibus binis, longis, cavis, proximaliter plusminusve in-

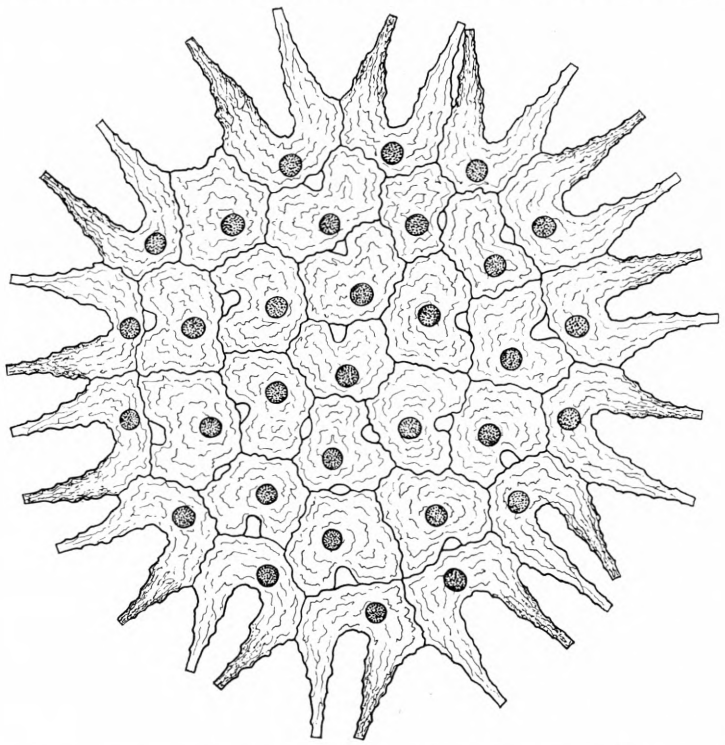


Fig. 16. *Pediastrum alternans* n. sp. from Mossø, August 18th, 1929. 800×.

flatis, apicaliter truncatis, circiter 2-2$^1/_2$ plo longioribus quam est spatium inter fundum sinus et membranam intimam, alternis deflexis ad latera diversa. Cellulae mediae coenobii quinquangulae vel sexangulae. Membranae inter cellulas plusminusve undulatae; membrana ceterum rugulis delicatissimis et irregularibus instructa.

Hab. In Mossø, Jutlandia septentrionali, Dania, libere natans.

Systematics. This new species comes nearest to *Pediastrum angulosum* Menegh. (Bigeard 1934—36, p. 344), the coenobia of which may exhibit small perforations (Bigeard loc. cit., p. 37, fig. 49). The cells of *Pediastrum angulosum* also have a very deep emargination between the two processes (both being, however, situated in the plane of the coenobium) deeper than the sinus between the adjacent processes of two

neighbouring cells; its membrane is likewise provided with ridges. *Pediastrum alternans* thus differs in having extremely delicate ridges (those of *Pediastrum angulosum* are much coarser and more regularly disposed), by its long processes more or less inflated at the base, every second process being directed obliquely downwards, every second obliquely upwards; further the adjacent cell walls are more or less undulate and the perforations as a rule smaller then the pyrenoids. Of 10 coenobia 3 were 32-celled and 7 were 64-celled.

Pediastrum Boryanum Menegh. forma.

Fig. nostra 17.

Diagnosis. Coenobia 32-cellularia, a foraminibus satis magnis, ellipticis vel triangulis cum marginibus convexis perforata. Cellulae marginales cum cornibus binis, longis, cavis, proximaliter non inflatis, circiter duplo longioribus quam est

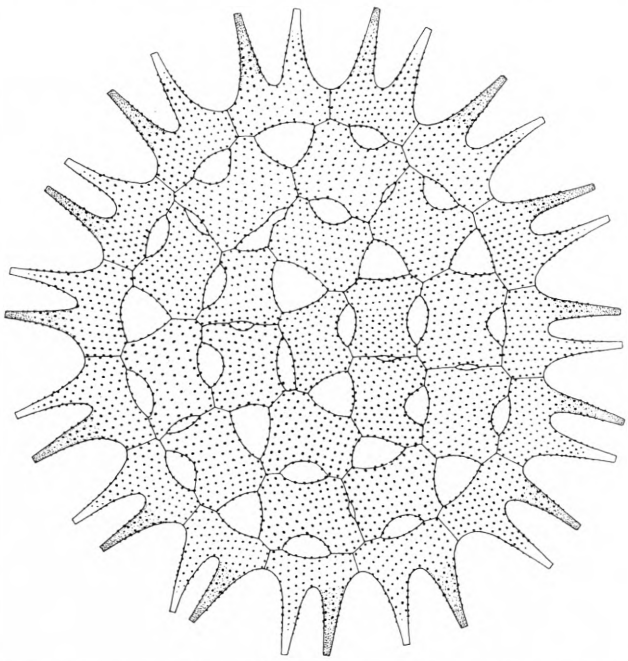


Fig. 17. *Pediastrum Boryanum* Menegh. forma from Mossø, August 18th, 1929. 800×.

spatium inter fundum sinus et membranam intimam, alternis deflexis ad latera diversa. Membrana cellulae granulis satis densis instructa.

Hab. In Mossø, Jutlandia septentrionali, Dania, libere natans.

Systematics. As the occurrence of perforations is a relative criterion, the surface structure of the membrane a reliable one, the coenobia in question are called

Pediastrum Boryanum. The granules are disposed in oblique decussating series, 8—10 series pro 10 μ. The form seems to be closely allied to *Pediastrum Boryanum* var. *longicorne* f. *granulata* (BRUNNTHALER 1915, p. 101, fig. 61 d). Apart from the rather large perforations the marginal cells of the present coenobia are somewhat different as to the granulation and the shape of the processes.

KRIEGER has described and figured a very similar form from the raised bog at Diebelsee in Germany (1929, p. 285, t. 3, fig. 9). It was called *Pediastrum duplex* var. *longicorne* nov. var. *punctatum*, a name which also I originally intended to use!

Both *Pediastrum* forms were found in an *Api fl-Mio aer ma*-association with *Mio vi* and *Ste as* as subdominants. Its qualitative composition appears from Table II, its plankton quotients are found in Table I.

Mossø is distinctly eutrophic; its compound quotient was $\frac{35}{6} = 5.8$ on August 18th, 1929. pH was 8.0, and the surface water contained PO_4-P 0.005 mg/l, NH_3-N 0.2 mg/l, NO_3-N 0 mg/l (the quantities of the bottom water are given in Table I). According to BRØNSTED & WESENBERG-LUND (1912, p. 478) Mossø contained 60 mg CaO per litre in July 1909.

Coelastraceae.

Coelastrum microporum Näg. f. **astroidea** (de-Not.) mihi.

Syn.: *Coelastrum astroideum* de-Notaris 1867, p. 80, t. 9, fig. 93 pro parte. *Coelastrum sphaericum* in CHODAT 1902, p. 231, fig. 156. – *Fig. nostra* 18.

Diagnosis. A typo coloniis 4- vel 8-cellularibus differt. Cellulis in stratis duobus ordinatis; in coloniis 4-cellularibus duo strata cellularum binarum gradus arci 90 inter se contorta; in coloniis 8-cellularibus duo strata cellularum quaternarum gradus arci 45 inter se contorta. Coloniae a vertice visae cum foramine oblonge quadrangulo, minore quam sunt cellulae finitimae. Cellulae subovatae, interdum sphaericae, raro subconiformes apicibus late rotundatis; margo extremus saepe leviter incrassatus. Longitudo cellularum 5.5—12.5 μ, latitudo 4—12.5 μ; diametro coloniarum 13—29.5 μ.

Hab. In Flødegaardens Dam, Blankeborg I et II et stagno prope Stjerneskansen, Fionia orientali; Birkerød Sø, Hulsø, Frederiksborg Slotssø, Vandingsdam, Gadevang Mose, Store Dam, Badstue-Ødam, Sortedam II, Jægerbakke Dam et Lynge Vandingsdam, Selandia; stagno prope Hokkerup, Jutlandia meridionali, Dania, libere natans.

Systematics. De-NOTARIS in t. 9, fig. 93 depicts a 4-celled colony (= f. *astroidea* mihi, but the cells are erroneously drawn as if they were situated in one plane) and two 16-celled colonies (= *Coelastrum microporum*), all three with rather pointed cells. As far as I understand his diagnosis, which is written in Italian, he has seen 8-celled colonies in the characteristic position where they appear like 5-rayed stars with one cell above the centre of the colony (see *Fig. nostra* 18 *a*, *c* and *h*).

Between the cells of the Danish colonies I never observed a square opening of a size as that shown in DE-NOTARIS' figure.

Incidentally each of the 4 layers of cells in 16-celled colonies is twisted 45° as compared to the layer situated above.

It is a fact that in certain ponds the colonies are always 4- or 8-celled; 16- or 32-celled colonies were never observed. This is true of Flødegaardens Dam, Blanke-

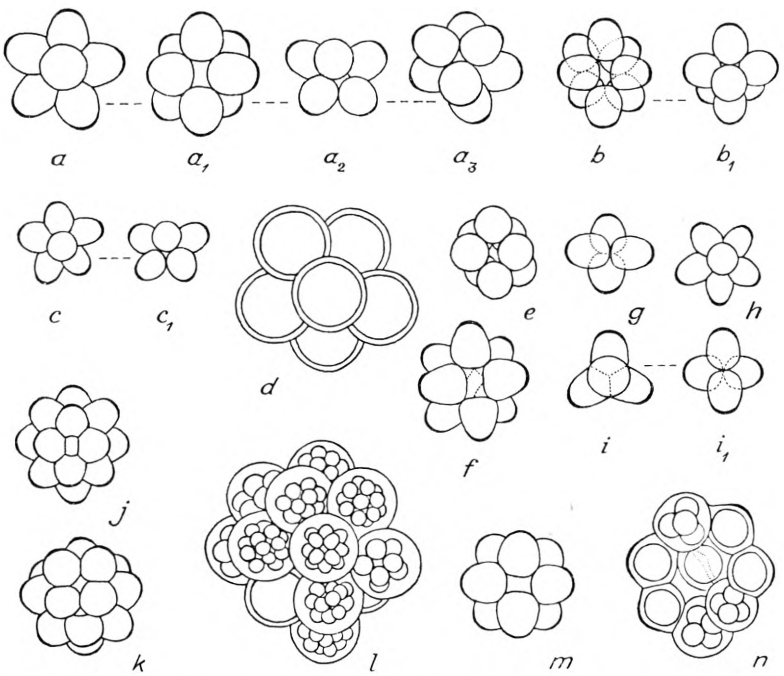


Fig. 18. *Coelastrum microporum* Näg. f. *astroidea* (de Not.) mihi. *a*, a_1, a_2, a_3, *b*, b_1, *c* and c_1 from the Hokkerup pond, September 14th, 1944; *d* and *e* from Blankeborg II, July 25th, 1928; *f* from Birkerød Sø, August 12th, 1929; *g*, *h*, *i* and i_1 from Flødegaardens Dam, June 19th, 1928; *j*—*n* from Sortedam II, *j*, *k* and *n* from July 1st, 1929, *l* and *m* from May 17th, 1930. a_1, *b*, *e*, *f*, *g*, i_1, *j*, and *m* vertical views, a_2 and c_1 lateral views. 800×.

borg II, Store Dam, Vandingsdam, Jægerbakke Dam, pond at Stjerneskansen E. of Nyborg, Birkerød Sø, Lynge Vandingsdam and pond at the beginning of the road to Hokkerup from the Søgaard Road.

In other ponds are found both 4-, 8- and 16-celled colonies (Badstue-Ødam, Sortedam II and Blankeborg I), but never 32-celled colonies.

In lakelets like Frederiksborg Slotssø both 8-, 16-, and 32-celled colonies are found.

In the larger Danish lakes I never observed 4- or 8-celled colonies; here the colonies were always 16- or 32-celled.

All these facts show that a very close relationship exists between *Coelastrum microporum* and '*Coelastrum astroideum*', so close indeed that it must be supposed

that '*Coelastrum astroideum*' is only a modification of *Coelastrum microporum*, indigenous to small bodies of water and ample nutrition. In this paper it has therefore been termed *Coelastrum microporum* f. *astroidea* (de-Notaris). The proof of the correctness of this hypothesis, however, can only be found from culture experiments.

It is interesting to notice that the colonies show a pronounced tendency to double (or quadruplicate) their cell-number during the maximum as will appear from the following survey.

Coelastrum microporum and f. *astroidea* in Frederiksborg Slotssø.

Dates	Frequency	32- : 16- : 8-celled colonies
May 1st, 1930	rrr	0 : 0 : 1
— 10th, —	r	0 : 6 : 6
— 21st, —	r+	0 : 10 : 4
— 31st, —	c	65 : 51 : 0
June 16th, —	+	1 : 25 : 5

Coelastrum microporum and f. *astroidea* in Badstue-Ødam.

Dates	Frequency	16- : 8- : 4-celled colonies
June 6th, 1929	rrr	0 : 2 : 0
— 20th, —	c	73 : 16 : 0
July 1st, —	c	73 : 16 : 0
— 5th, —	+	41 : 25 : 0
— 12th, —	r+	15 : 12 : 2
— 17th, —	r	6 : 10 : 5
— 26th, —	rr	3 : 7 : 2
Aug. 10th, —	rrr	1 : 5 : 0
— 23rd, —	rrr	0 : 1 : 0

However, it is not in all ponds that *Coelastrum microporum* turns 16- or 32-celled during the maximum; even under its favourable conditions of living they remain 8- and 4-celled:

Coelastrum microporum f. *astroidea* in Flødegaardens Dam.

Dates	Frequency	8- : 4-celled colonies
July 4th, 1927	c	50 : 2
June 5th, 1928	c	44 : 16
— 19th, —	c	50 : 28

Periodicity. In Flødegaardens Dam f. *astroidea* in 1927 appeared on May 1st (temp. 8° C.) and reached a considerable maximum on July 4th (temp. 19° C.); for the rest of the year it was very rare and was seen for the last time on December 1st (temp. 6.5° C.). In 1928 it reappeared on May 6th (temp. 17.5° C.); the considerable maximum in this year occurred on June 5th and 19th (temp. 12.5—15° C.), and the form was also rather common on July 13th (temp. 26.5° C.); during the rest of the year it was very rare and was seen for the last time on December 28th (temp. 1.5° C.). In 1929 it appeared already on April 11th (temp. 4.5° C.); the comparatively inconspicuous maximum occurred on June 2nd (temp. 16° C.), after which the species was found only in small quantities for the rest of the year, the last time on December 27th (temp. 0.5° C.). In 1930 the form was still found on January 6th (temp. 4° C.), but then it disappeared and did not turn up again until April 19th (temp. 8° C.) when it was rare as in May and June, at which time the examination was terminated.

In the likewise regularly examined Blankeborg II f. *astroidea* was found only in July, August and October without ever forming a maximum during the period 1928—30.

In the well-examined Jægerbakke Dam the form was always remarkably rare and was found only between October and January and in May.

In Vandingsdam the form also occurred in small quantities within the period June—December 1929 and May—June 1930.

In Badstue-Ødam, however, f. *astroidea* throve well, reaching a considerable maximum on June 20th and July 1st (temp. 22.5 and 16.5° C.). During July its frequency decreased uniformly, and for the rest of the year it was very rare. The last colonies were seen as late as January 15th, 1930 (temp. 3° C.). As was the case in the ponds mentioned above it disappeared completely during the ice period and did not turn up again until April 25th, 1930 (temp. 12.5° C.); from this date till the termination of the examination on June 16th it was very rare.

As will appear from the survey mentioned above (p. 46) f. *astroidea* occurred together with *Coelastrum microporum* in Frederiksborg Slotssø. The form was not infrequent on June 11th, 1929 (temp. 15° C.), but during the rest of the year it showed a highly sporadic occurrence and was observed for the last time on December 16th (temp. 4.5° C.). In 1930 it did not appear until May 1st (temp. 15° C.) and after this date was comparatively rare in May and June in contrast to the main species, which, as shown on p. 46, reached a considerable maximum at the end of May.

In Sortedam II, where the species and form also occurred together, though only in the samples from June (1929 and 1930), f. *astroidea* in 1929 was found only on June 8th (temp. 16.5° C.) and December 16th (temp. 3° C.), both times being very rare. In 1930 it did not appear until April 26th (temp. 12° C.) and was very rare on this date as well as in May and June.

In the well-examined Gadevang Mose f. *astroidea* was observed only on July 6th, 1929 (temp. 16° C., very rare).

In Blankeborg I, which was examined fortnightly for 4 years, the form was only observed with certainty on June 10th, 1930 (temp. 19° C., very rare).

In the pond E. of Stjerneskansen at Nyborg f. *astroidea* was very rare on June 16th, 1938 (temp. 19.5° C.).

In the regularly examined pond Store Dam the appearance of the form was very sporadic: it occurred only on July 6th, November 2nd and 28th, December 16th, 1929 and June 16th, 1930, and was always very rare.

In the pond situated at the beginning of the road to Hokkerup from the Søgaard road f. *astroidea* was not infrequent on September 14th, 1944.

In Birkerød Sø f. *astroidea* was observed in very small quantities on July 22nd (temp. 23° C.) and August 12th, 1929 (temp. 20.5° C.).

In Hulsø the form occurred together with the main species on August 8th and December 23rd, 1946; the form was rare in both samples.

Sociology. *Coelastrum microporum* f. *astroidea*

Myxophyceae associations	Euglenineae associations	Bacillariophyceae associations	Chrysophyceae associations	Cryptophyceae associations	Bacteria associations
1 *Ana af in te* -assoc.	1 *Eug ob* -assoc.	4 *Cyc st su* -assoc.	2 *Chry ma* -assoc.	4 *Crym ov* -assoc.	2 *La hy* -assoc.
1 *Ana fl* -assoc.	8 *Tra vo* -assoc.	1 *Frg cr* -assoc.	1 *Chry mi* -assoc.		
1 *Ana in* -assoc.		1 *Mel gr an* -assoc.	1 *Din di* -assoc.		
1 *Mio fl ma* -assoc.		7 *Rhi lo* -assoc.	1 *Syu sp* -assoc.		
7 *Mio ho* -assoc.		11 *Ste Ha* -assoc.	1 *Ura vo* -assoc.		
1 *Os Ag* -assoc.			1 assoc. of an indeterminable *Chrysophycea*		

In Lynge Vandingsdam very small quantities of f. *astroidea* occurred on June 30th and August 6th, 1947.

If we confine ourselves to the ponds and lakelets that were examined fortnightly for at least one year, the following general conclusions may be made with regard to this widely distributed green alga. The vegetation period of *Coelastrum microporum* f. *astroidea* ranges from April (May) to December (very rarely January) at temperatures between 0.5 and 26.5° C., the form thus being eurythermic. In February and March, however, when the ponds at any rate periodically are covered with ice, f. *astroidea* was never observed. A maximum was by no means reached by the form in all the ponds, not even during a period of 4 years. In the few ponds where a considerable maximum occurred, it was reached in June—the beginning of July (rarely in May) at temperatures between 12.5 and 22.5° C.

was found in the following 119 associations:

Chlorococcales associations	Volvocales associations	Desmidiaceae associations	Ulothricales associations	Dinophyceae associations	Mixed associations	
1 *Ank fa spa* -assoc.	3 *Chla Re mi* -assoc.	1 *Cl ac va* -assoc.	2 *Ul pe* -assoc.	1 *Ce hi* -assoc.	*Mio fl*, *Os Ag* 1	*Ank co mi*, *Eug pr* 1
3 *Dic pu* -assoc.	1 *Chla Re* -assoc.			1 *Gy ex* -assoc.	*Mio ho*, *Ank co mi* 1	*Sye ac an*, *Din so* 1
1 *Ki mi* -assoc.					*Mio ho*, indeterm. green alg. 1	*Ste Ha*, *Sye ac an* 1
1 *Na be* -assoc.					*Mio ho*, *Ki mi*, *Ni ac* 2	*Crym ov*, *Chla Re mi* 1
1 *Oo er mi* -assoc.					*Mio ho*, *Ki mi*, *Ste Ha* 1	*Se ca*, *Chla Re mi*, *Ste Ha*, *Tst st* 1
5 *Sce arm* -assoc.					*La hy*, *Teë mi* 1	*Crym ov*, *Ank fa spi*, *Sce arm* 1
1 *Sce ec* -assoc.					*Mio ho*, *Ank fa*, *Ank fa spi* 1	*Ste Ha*, *Tst st*, *Pa mo* 1
1 *Sce fa* -assoc.					*Mio ho*, *Ank fa spa*, *Sce arm* 1	*Ste Ha*, *Sce fa*, *Sce arm* 1
2 *Se ca* -assoc.					*Ki mi*, *Ank fa se br* 1	*Teë mi*, *Sce arm* 1
3 *Teë mi* -assoc.					*Cyc Me*, *Ste Ha* 1	*Sce fa*, *Ped du*, *Tra vo* 1
4 *Tst st* -assoc.					*Ank co mi*, *Ank fa spi* 1	*Coa mi as*, *Cru qu* 1
1 *Trochiscia* -assoc.						
4 indeterm. -assoc.						

Briefly stated the associations were dominated first and foremost by the following *Chloroccoccales*: *Ankistrodesmus*, *Crucigenia*, *Dictyosphaerium*, *Kirchneriella*, *Nannokloster*, *Oocystis*, *Pediastrum*, *Scenedesmus*, *Selenastrum*, *Tetraëdron*, *Tetrastrum* and *Trochiscia* and by the following Diatoms: *Cyclotella*, *Fragilaria*, *Melosira*, *Nitzschia*, *Rhizosolenia*, *Stephanodiscus* and *Synedra* and by the following blue-green algae: *Anabaena*, *Microcystis* and *Oscillatoria*.

In addition *Chrysophyceae* play no small part in the picture of the sociology of *Coelastrum microporum* f. *astroidea* with genera like *Chrysococcus*, *Dinobryon*, *Synura* and *Uroglena*.

The form is not so frequently found in euglenine associations (*Trachelomonas* and *Euglena*), cryptophycean associations of *Cryptomonas*, *Volvocales* associations (*Chlamydomonas* and *Pandorina*), *Ulothricales* associations of *Ulothrix*, Bacteria associations of *Lampropedia*, dinophycean associations of *Ceratium* and Desmid associations of *Closterium*.

Coelastrum microporum f. *astroidea* reveals its unmistakably "eutrophic" character through the many *Chloroccoccales*, centric Diatoms and blue-green algae that dominate in its associations.

The most constant associates were *Scenedesmus armatus*, which occurred in 90.75 % of the number (119) of samples that contained *Coelastrum microporum* f. *astroidea*, and *Microcystis holsatica*, which occurred in 75.6 % of the samples.

Ecology. The phytoplankton quotients for Flødegaardens Dam, Blankeborg I and II, Jægerbakke Dam, Vandingsdam, Badstue-Ødam, Frederiksborg Slotssø, Sortedam II, Gadevang Mose, and Lynge Vandingsdam are found in Table III. The quotients of Hulsø are found in Table I, those of the Hokkerup pond on p. 156 and those of Store Dam on p. 112. From Birkerød Sø they are given on p. 149 for July 22nd, 1929; on August 12th, 1929 the plankton consisted of a *Mio fl-Os Ag*-association with a total of 31 species; the myxophycian quotient was $\frac{8}{3}$, the chlorophycean quotient $\frac{17}{3}$, the diatom quotient $\frac{0}{0}$, the euglenine quotient $\frac{2}{25}$, and the compound quotient $\frac{27}{3} = 9$. In the pond E. of Stjerneskansen, which incidentally was filled up between 1939 and 1942, the plankton consisted of a *Trochiscia* association with *Act Ha* as subdominant, a total of 20 species; the quotients (mentioned in the same order as above) were: $\frac{0}{0}$, $\frac{12}{0}$, $\frac{0}{0}$, $\frac{6}{12}$, $\frac{18}{0}$.

All the said localities that contain *Coelastrum microporum* f. *astroidea* are eutrophic. The great majority of them are contaminated and highly eutrophic, a few of them even to such a degree that they approach the saprotrophic phase (Hokkerup pond, Lynge Vandingsdam); only one of them is slightly eutrophic ("mesotrophic", Blankeborg I). In other words f. *astroidea* may be characterized as a plankton organism that is confined to ponds and lakelets and is found only in eutrophic localities. Its optimal development takes place under highly—extremely eutrophic conditions. It was never found in the oligotrophic types of ponds, nor in the genuine saprotrophic; in slightly eutrophic localities it shows a poor development.

The following data are expressive of its ecological demands: pH 6.3—9.4, CaO 7.3—97.9 mg/l, consumption of $KMnO_4$ 32—97 mg/l, contents of PO_4-P 0—1.25 mg/l, NH_3-N 0.05—1.5 mg/l, NO_3-N 0—3 mg/l, Fe 0.01—0.45 mg/l (Blankeborg II contained 153.5 mg of CaO per litre on January 6th, 1930).

Ulotrichales.

Ulotrichaceae.

Ulothrix pelagica n. sp.

Fig. nostra 19.

Diagnosis. Trichomata uniseriata, simplicia, cylindracea, recta vel irregulariter flexuosa. Cellulae elongatae, 5—23 plo longiores quam latiores, membrana tenuissima. Chromatophorus unus, parietalis, partem interiorem majorem membranae cellulae obtegens, granulis amylaceis parvissimis numerosis instructus; pyrenoides abest. Cellula terminalis saepe acuminata. Longitudo cellularum 7—34 μ, latitudo 1—1.5 μ.

Hab. In Flødegaardens Dam, Fionia; Badstue-Ødam, Gadevang Mose, Frederiksborg Slotssø, Selandia; Sønderborg Mølledam, Jutlandia meridionali, Dania, libere natans.

Systematics. Of thin *Ulothrix* species *Ulothrix limnetica* var. *minor* Teiling is known (1912, p. 276). It is likewise without pyrenoid and is stated to have 6—11 μ long and 2 μ broad cells and a 1 μ thick sheath. I am indebted to Dr. Einar Teiling for his sending a copy of his drawing of *Ulothrix limnetica* var. *minor* from the only 4 m deep Råstasjön near Stockholm. For comparison's sake I have reproduced this copy in *Fig. nostra* 20, and it shows that *Ulothrix pelagica* is more closely related to Teiling's variety than to the following species. Further G. S. West (1915, p. 81, fig. 5) has described a spirally twisted species (also without pyrenoid), *Ulothrix spiroides*, the cells of which are only 1 μ broad and 4.5—8.5 μ long. *Ulothrix pelagica* differs from both of these forms by its pointed endcell and its uncommonly long cells, 5—23 times longer than broad.

In staining material of *Ulothrix pelagica* with chlor-zinc-iodide it was observed that the very delicate cell-wall turned slightly violet and the many granules of the chromatophore deep violet like in the cells of *Actinastrum Hantzschii* of the same sample. Both cell-wall and chromatophore consequently contain carbohydrates. Pyrenoids were always absent.

By low magnification *Ulothrix pelagica* is easily mistaken for *Tribonema taeniatum* Pascher (see *Fig. nostra* 21). This *Xanthophycea*, specimens of which were found in the plankton from Hostrup Sø and Esrom Sø but never in the plankton of Danish ponds, is known by the H-shaped pieces of the cell-wall, its somewhat

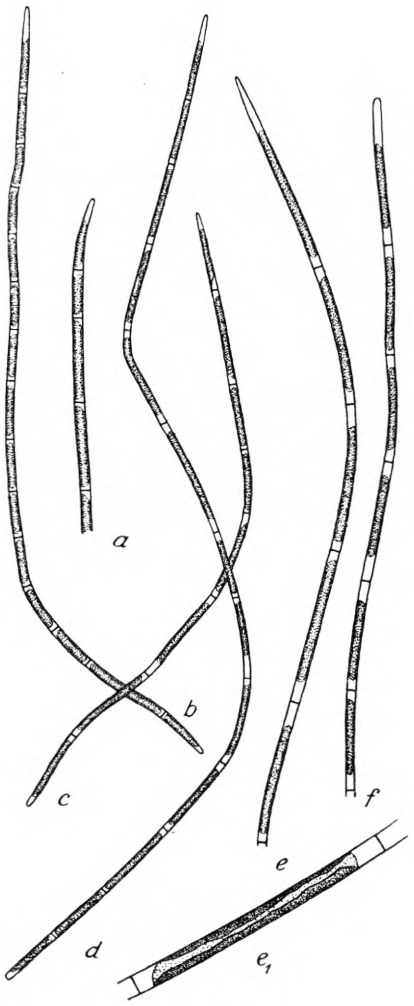


Fig. 19.

Fig. 20.

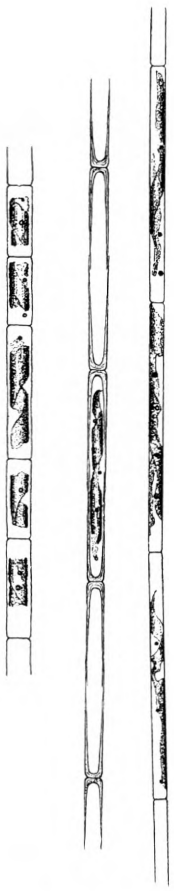


Fig. 21.

Fig. 19. *Ulothrix pelagica* n. sp.; *a*—*d* from Flødegaardens Dam, *a*—*b* from July 5th, 1928, *c*—*d* from June 2nd, 1929; *e*, e_1 and *f* from Badstue-Ødam, December 16th, 1929. e_1 1600×, the other figures 800×.

Fig. 20. *Ulothrix limnetica* Lemm. var. *minor* Teiling from Råstasjön, Sweden. After the original drawing made by Dr. EINAR TEILING.

Fig. 21. *Tribonema taeniatum* Pascher from Hostrup Sø, July 24th, 1926. 800×.

greater thickness (2.5—4 μ) and by the fact that neither cell-wall nor chromatophores turn bluish violet in chlor-zinc-iodide; the length of the cells were 11—47 μ.

Periodicity. In Flødegaardens Dam the species was not seen in 1926 or 1927 but appeared in 1928 on June 19th (temp. 15° C.) and reached a great maximum on July 5th (temp. 15.75° C.). It then disappeared, but during the period September—December (temp. 19.5—1.5° C.) it was present in the plankton in small but com-

paratively constant quantities. In 1929 it was very rare when the ice broke at the beginning of April (temp. 6.5° C.), grew common during May and reached a great maximum on June 2nd (temp. 16° C.), only to disappear before July; the species reappeared in small amounts on December 16th (temp. 2.5° C.). In 1930 only a few specimens were observed on January 6th (temp. 4° C.).

In Badstue-Ødam the species only appeared during the cold season, from October 23rd, 1929 till February 17th, 1930 (temp. 9.5—0.5° C.) with a small maximum on December 16th (temp. 4° C.).

In Frederiksborg Slotssø *Ulothrix pelagica* was found only in April 1930 in very small quantities (temp. 5.5—12° C.).

In Gadevang Mose it was seen only on June 28th and July 6th, 1929 (temp. 20.75 and 16° C., respectively). The inconsiderable maximum in this pond occurred on July 6th.

Besides in these regularly examined ponds *Ulothrix pelagica* also occurred in Sønderborg Mølledam in September 1934.

It is no easy matter to determine the periodicity of this eurythermic species. In Flødegaardens Dam and Gadevang Mose the maxima occurred in June or July (temp. 15.75—16° C.) though not every year. In Frederiksborg Slotssø it appeared in April only. In Badstue-Ødam the species within the period July 1929—June 1930 surprisingly reached a small but distinct maximum in December (temp. 4° C.)! If, however, we look at the occurrence of the species in Flødegaardens Dam within the same period, we find the corresponding feature that here it appeared only in December—January (temp. 2.5—4° C.).

Sociology. The species occurred in the following associations:

Flødegaardens Dam.

June 19th, 1928: *Mio ho*—indeterm. green algae-association with *Ank fa* and *Ank fa spi* as subdominants (the species very rare).
July 5th, — : *Mio ho-Ul pe*-association with *Ank fa spi*, *Chry mi* and *Coa mi as* as subdominants (the species very common).
Sep. 7th, — : *Mio ho*-association (the species very rare).
— 15th, — : dito.
— 21st, : *Mio ho-Ni ac*-association (the species very rare).
Oct. 1st, — : *Ki mi-Mio ho-Ni ac*-association (the species very rare).
— 10th, — : dito.
— 22nd, — : *Ki mi-Mio ho-Ste Ha*-association (the species rare).
Nov. 18th, — : *Ste Ha*-association with *Mio ho* and *Ki mi* as subdominants (the species very rare).
Dec. 28th, — : *Ste Ha*-association (the species very rare).
Apr. 2nd, 1929: dito.
— 11th, — : *Ste Ha*-association with *Mia pu* as subdominant (the species very rare).

April 30th, 1929: *Ste Ha-Chry mi*-association (the species very rare).
May 10th, — : *Ste Ha*-association with *Tst st* and *Tra vo* as subdominants (the species not infrequent).
— 22nd, — : *Ul pe*-association with *Cru qu* as subdominant (the species common)
June 2nd, — : *Ul pe*-association (the species very common).
— 19th, — : *Tra vo*-association with *Sce arm* as subdominant (the species very rare).
Dec. 16th, — : *Tst st*-association with *Ank fa spi* and *Sce arm* as subdominants (the species very rare).
Jan. 6th, 1930: *Tst st*-association (the species very rare).

Badstue-Ødam.

Oct. 23rd, 1929: *Crym ov*-association with *Chry ma* as subdominant (the species very rare).
Nov. 30th, — : *Chry ma-Crym ov*-association (the species very rare).
Dec. 16th, — : *Chry ma-Crym ov-Ul pe*-association (the species rather common).
Jan. 15th, 1930: *Chry ma*-association (the species very rare).
— 31st, — : *Gle ac*-association (the species very rare).
Feb. 17th, — : *Ank fa mi lo*-association with *Chry mi* as subdominant (the species very rare).

Frederiksborg Slotssø.

Apr. 1st, 1930: *Trochiscia*-association (about 24.400 cells per ml) with *Ste Ha* as subdominant (about 10.400 cells per ml), (the species very rare).
Apr. 3rd, — : *Ste Ha*-association (the species very rare).
— 25th, — : *Ste Ha*-association with *Sce arm* as subdominant (the species very rare).

Gadevang Mose.

June 28th, 1929: *Din di*-association with *Syu sp* and *Ce hi* as subdominants (the species very rare).
July 6th, — : *Din di*-association (the species not infrequent).

Sønderborg Mølledam.

Sep. 7th, 1934: *Mel gr an*-association with *Sce fa* as subdominant (the species rare).

Ulothrix pelagica itself may be the dominant form of plankton associations; moreover it is found first and foremost in myxophycean associations of *Microcystis* and diatomaceous associations of *Stephanodiscus*, *Melosira* and *Nitzschia*; further in chlorophycean ass.s of *Kirchneriella*, *Tetrastrum*, *Ankistrodesmus* and *Trochiscia* and chrysophycean ass.s of *Dinobryon* and *Chrysococcus*; rarely in euglenine associations

of *Trachelomonas*, cryptophycean ass.s of *Cryptomonas* and dinophycean ass.s of *Glenodinium*.

The most constant associates were *Scenedesmus armatus*, which occurred in 87 % of the number (31) of samples that contained *Ulothrix pelagica*; *Stephanodiscus Hantzschii* (84 %), *Ankistrodesmus falcatus* and *Trachelomonas volvocina*, both of which were found in 77.5 % of the samples.

Ecology. *Ulothrix pelagica* is a typical pond form. It was found only in highly eutrophic ponds, some of them of the mixotrophic phase. The phytoplankton quotients for Flødegaardens Dam, Badstue-Ødam, Frederiksborg Slotssø and Gadevang Mose are found in Table III; the only values to be mentioned here are those of the compound quotient: Flødegaardens Dam 8.75—43, Badstue-Ødam 10—12.7, Frederiksborg Slotssø 8—10 and Gadevang Mose 11—22.

In Sønderborg Mølledam the compound quotient on September 7th, 1934 was $\frac{24}{0}$, in other cases $\frac{16}{1}$ and $\frac{18}{1}$ (see p. 179).

Some data illustrating the ecology of *Ulothrix pelagica* are: pH 6.3—9.4, content of CaO 14.6—82 mg/l, consumption of $KMnO_4$ 43—52 mg/l, contents of PO_4-P 0.015—0.095 mg/l, NH_3-N 0—1.5 mg/l, NO_3-N 0—3 mg/l, Fe 0.3 mg/l.

Conjugales.

Desmidiaceae.

Closterium Baillyanum Breb. var. **parvulum** Grönblad.

Grönblad 1919, p. 13, t. 1, figs. 14—16.

Systematics. Measurements of the Danish specimens from Præstesø, June 28th, 1930:

450 $\mu \times 31$ μ, ratio 14.5.
468 $\mu \times 30$ μ, ratio 15.6, 8 + 11 pyrenoids.

Lille Gribsø, September 19th, 1926:

365 $\mu \times 27$ μ, ratio 13.5, apices 13—15 μ.
385 $\mu \times 28$ μ, — 13.8.
427 $\mu \times 30$ μ, — 14.2.
473 $\mu \times 33$ μ, — 14.3.

From the two localities mentioned the measurements accordingly were 365—473 $\mu \times 27$—33 μ, and the cells were 13.5—15.6 times longer than broad. In his diagnosis Grönblad gives the dimensions 281—391 $\mu \times 24$—30 μ, apices 13—15 μ broad; his 4 measurings show that the cells were only 11—13 times longer than broad. Grönblad further mentions (1919, p. 8) that Heimerl in 1891 found specimens with the measurements 300—470 $\mu \times 27$—32 μ.

Carl Huzel (1936, p. 78, t. 9, figs. 28—29; t. 15, figs. 1—4) gives similar dimensions for the variety as Grönblad; his fig. 28 shows a ratio of 12. In Huzel's cultures of var. *parvulum* most individuals were considerably longer than in nature, up to 580 μ, and had girdle-bands beside the connecting bands. These culture individuals, which Huzel and Grönblad consider abnormal forms, according to t. 15, figs. 1—3 are 15.2—15.8—15.9 times longer than broad: in this respect they are not very different from one of the measured individuals from Præstesø.

Dr. Rolf Grönblad, to whom I am indebted for opinions on the Danish specimens and several other desmids, approved of the determination and remarked that the shape of the cell is like that of *Closterium Baillyanum*, the membrane like that of *Closterium didymotocum*. W. and G. S. West gave *Closterium Baillyanum* as a synonym for *Closterium didymotocum* (Monograph I, p. 116).

While the specimens mentioned above do not deviate much from Grönblad's individuals, the following 2 specimens are so slender, that they may be regarded as a new form.

Store Gribsø, September 19th, 1926:

385 $\mu \times 18$ μ, ratio 21; apices 11—12 μ, not striate, 10 + 11 pyrenoids.

Lille Gribsø, September 19th, 1926:

502 $\mu \times 28$ μ, ratio 18, apices 13.5—15 μ, 7 striae pro 10 μ.

f. **tenuis** n. f.

Fig. nostra 22.

A varietate cellulis gracilioribus differt. Longitudo 385—502 μ, latitudo 18—28 μ, ratio axium 18—21. Membrana cellulae ochracea, levis vel cum 7 striis pro 10 μ.
Hab. In Lille Gribsø et Store Gribsø prope Hillerød, Dania, libere natans.

Periodicity and Sociology. The variety and the form were found in Præstesø on June 24th—28th, 1930 (temp. 20—21° C.), in Lille Gribsø on September 19th, 1926, June 28th, 1929 (temp. 19.25° C.) and August 28th, 1929 (temp. 21° C.) and in Store Gribsø on September 19th, 1926. In all these summer samples it was very rare except in the sample from August 28th, in which it was rare.

In Præstesø it occurred on June 24th—28th, 1930 in an *Ana fl*-association (variety very rare).

In Lille Gribsø:

Sep. 19th, 1926: association of a minute *Tetrasporale*(?) with *Sti ba* as subdominant (variety and form very rare).

June 28th, 1929: net plankton, *Ura am*-association; nannoplankton, *Se ca*-association (variety very rare; see Table IV).

Aug. 28th, 1929: *Cos as st*-association with *Sti ba* as subdominant (variety rare; see Table IV).

In Store Gribsø the form was found on September 19th, 1926 in a *Per Wi*-association (form extremely rare; see Table II).

In other words the variety and the form have been found in a myxophycean association of *Anabaena*, a chrysophycean association of *Uroglena*, a dinophycean association of *Peridinium* and in chlorophycean associations of *Selenastrum*, *Cosmarium* and an indeterminable *Tetrasporale*(?).

The constant associates of the variety were *Ankistrodesmus falcatus* (with variety), which occurred in 100 % of the number (4) of samples that contained *Closterium Baillyanum* var. *parvulum*; *Glenodinium pusillum*, *Peridinium Willei*, *Stichococcus bacillaris*, *Selenastrum Westii*, *Cosmarium asphaerosporum* var. *strigosum*, *Cosmarium subarctoum* f. *minor* and *Arthrodesmus triangularis* were found in 75 % of the samples.

Ecology. The two lakelets Præstesø and Lille Gribsø are clear lakes standing between oligotrophy and eutrophy. The compound quotient in Præstesø on June 28th, 1930 was $\frac{21}{17} = 1.2$, in Lille Gribsø on September 19th, 1926 (net- + nannoplankton) $\frac{3}{6} = 0.5$, on June 28th, 1929 $\frac{4}{7} = 0.6$ for net plankton and $\frac{7}{4} = 1.75$ for nannoplankton, on August 28th, 1929 (net- + nannoplankton) $\frac{5}{9} = 0.55$.

Store Gribsø is a somewhat larger, 13 m deep, oligotrophic lake of the dystrophic phase. The compound quotient was $\frac{0}{1} = 0$ on September 19th, 1926; see further Table I.

The variety was found at pH 4.9—7.1. On August 12th and September 12th the content of CaO in Lille Gribsø was 2.2 and 2.5 mg/l, respectively, and in August 1929 the following data were observed in the same lake: PO_4-P 0 mg/l, NO_3-N 0.02 mg/l, NH_3-N 0.1 mg/l, consumption of $KMnO_4$ 38 mg/l.

Carl Huzel found the variety at pH values between 5.3 and 6.8.

The form was found at the pH value 5.4 in Store Gribsø, which is also lime-deficient (see Table I).

Closterium gracile Breb. var. **elongatum** West f. **longissima** n. f.

Fig. nostra 23.

Diagnosis. Cellulae gracillimae, e sex mensionibus 96—119 plo longiores quam latiores, lineares, ad apices subtruncatae et leviter inflexae, longe attenuatae. Membrana glabra, pallide ochracea, sine suturis transversis. Pyrenoidibus in utraque semicellula 10—16 in serie unica dispositis. Locellis apicalibus brevissimis, circiter 10 μ longis. Longitudo cellularum 379—475 μ, latitudo $3^1/_2$—4 μ, latitudo apicum 2.3—2.5 μ.

Hab. In Grovsø prope Oxbøl, Jutlandia, Dania, libere natans.

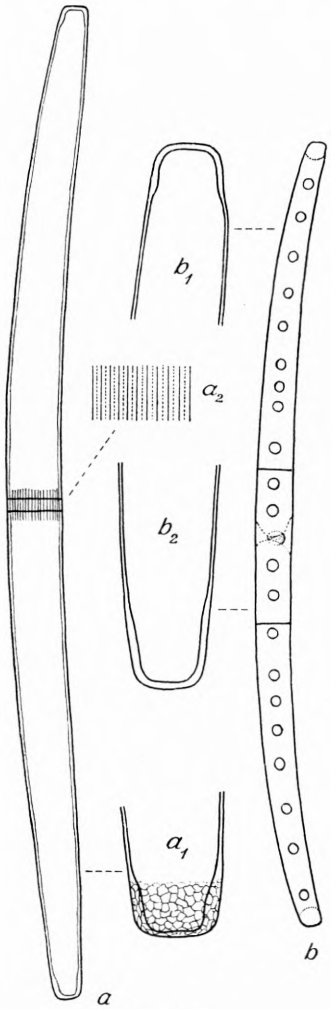


Fig. 22.

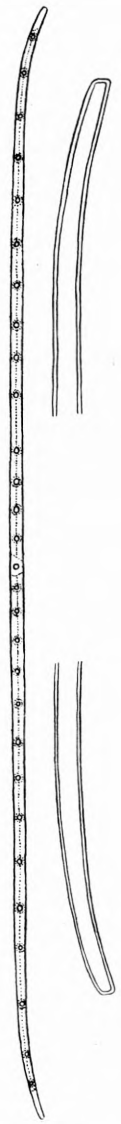


Fig. 23.

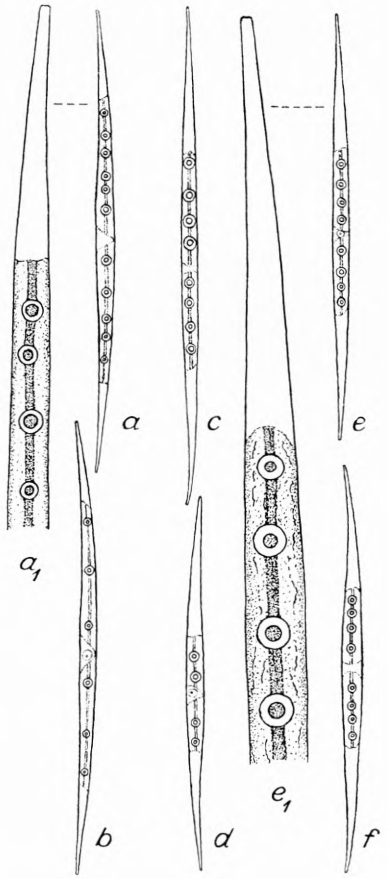


Fig. 24.

Fig. 22. *Closterium Baillyanum* Breb. var. *parvulum* Grönblad f. *tenuis* n. f. *a*, a_1 and a_2 from Lille Gribsø, September 19th, 1926; *b*, b_1 and b_2 from Store Gribsø, September 19th, 1926. *a* and *b* 260×, a_1, b_1 and b_2 apices, 800×, a_2 the striation on the middle of the cell, 800×.

Fig. 23. *Closterium gracile* Breb. var. *elongatum* West f. *longissima* n. f. from Grovsø, June 27th, 1930. 350× and 1070× (apices).

Fig. 24. *Closterium idiosporum* West; *a*, a_1 and *b* from turf pit at Store Jenshøj, June 25th, 1930; *c*, *d*, *e*, e_1 and *f* from Sortemose at Farum Sø, April 28th, 1929. a_1 and e_1 800×, the other figures 260×.

According to W. & G. S. WEST (Monograph I, 1904, p. 168, t. 21, figs. 14—16) the variety is 85—95 times as long as broad and reaches a length of 276—360 μ; its apices are not subtruncate, and the wall is not brownish (according to information by letter from Dr. ROLF GRÖNBLAD, to whom drawing and measures have been shown, var. *elongatum* may have a brownish wall). The number of the pyrenoids and the lengths of the terminal vacuoles do not appear from WEST's description and figures. In spite of these differences it is perhaps hardly legitimate to term the present individuals *Closterium gracile* Breb. var. *fuscatum* nov. var., which I originally intended.

A short description of Grovsø and its plankton on June 27th, 1930 (temp. 18° C., PH 5.4) when *Closterium gracile* var. *elongatum* f. *longissima* was comparatively rare, is found sub *Closterium juncidum* Ralfs var. *elongatum* Roy et Biss. f. *truncata* n. f. (see p. 60).

Closterium idiosporum West.

W. and G. S. WEST: Monograph I, 1904, p. 180, t. 23, figs. 20—21.—*Fig. nostra* 24.

This rare species was found in the turf pit S. of Store Jenshøj at Oxbøl, Jutland, and in Sortemose at Farum Sø, N. Seeland. The individuals were straight, slightly curved or slightly sigmoid and had truncate, 1.8—2 μ broad apices; the inner margin was sometimes slightly tumid, especially in the individuals from Sortemose.

According to 4 measurings of specimens from Sortemose the length was 188—252 μ, the breadth 8.5—10 μ, ratio 21—28, 2—4 pyrenoids per semicell, terminal vacuoles 62—73 μ.

10 measurings of specimens from the turf pit at Store Jenshøj gave the lengths 195—235 μ, the breadths 8—10 μ, ratio $20\frac{1}{2}$—29, 3—8 pyrenoids per semicell, terminal vacuoles 40—46 μ.

As will be seen the Danish individuals are a little slenderer ($20\frac{1}{2}$—29 times longer than their diameter) than the British ones (20—23 times), show a somewhat greater variation in length (188—252 μ against 221—238 μ) and a breadth of 8—10 μ against the 10—10.5 μ of the British specimens.

The species was very rare on April 28th, 1929 in Sortemose and on June 25th, 1930 in turf pit at Store Jenshøj (temp. 18° C.).

In Sortemose *Closterium idiosporum* occurred in a *Cos de*-association with *Ce co* as subdominant. In the turf pit at Store Jenshøj it was also very rare in an *Aso su-Oe It*-association (see Table IV). In other words it was found only in green algae associations.

Both localities mentioned are acid, oligotrophic turf pits of the dystrophic type. The phytoplankton quotients of the turf pit at Store Jenshøj (PH 4.0) appear from Table III. The plankton of Sortemose was composed of 31 species with the following quotients: myxophycean quotient $\frac{1}{19}$, chlorophycean $\frac{2}{19}$, diatom $\frac{0}{0}$, euglenine $\frac{2}{3}$ and the compound quotient $\frac{5}{19} = 0.25$.

Closterium juncidum Ralfs var. **elongatum** Roy et Biss. f. **truncata** n. f.

Fig. nostra 25.

Diagnosis. Cellulae graciles et elongatae, 38—52 plo longiores quam latiores, subrectae, ad apices truncatae et leviter incurvatae, aequaliter attenuatae. Membrana ochracea, subtiliter striata, striis 5 pro 5 μ in media cellula, spatium inter strias non semper aequidistantes, 1—1.2 μ. Suturae transversales non observatae. Pyrenoidibus in utraque semicellula 19—26 in serie unica dispositis. Locellis apicalibus brevissimis, 5—7$\frac{1}{2}$ μ longis, corpuscula gypsi singula includentibus. Longitudo cellularum 378—512 μ, latitudo 10 μ, latitudo apicum 5—6 μ.

Hab. In Grovsø prope Oxbøl, Jutlandia, Dania, libere natans.

It is stated about this variety that it is 35—45 times longer than broad, 295—473 μ long and 8.5—13 μ broad. If it is like the main species in other respects, the present individuals differ in having truncate apices and only one moving gypseous granule in each of the terminal vacuoles. According to West's Monograph I, t. 14, figs. 10—14 the terminal vacuoles are also considerably longer in the main species than in the present individuals.

The form was rare in Grovsø on June 27th, 1930 (temp. 18° C., pH 5.4). The plankton was at this time a typical desmid-flagellate plankton with *Arthrodesmus incus* var. *extensus*, *Arthr. octocornis*, *Closterium setaceum* var. *elongatum*, *Clost. intermedium*, *Clost. Dianae* var. *arcuatum*, *Clost. gracile* var. *elongatum* f. *longissima* n. f., *Cosmarium subtumidum* f. *parva* n. f., *Staurastrum brachiatum*, *Staur. hirsutum* and the flagellates *Uroglena americana* and *Dinobryon sertularia* var. *protuberans* as particularly characteristic organisms though they were not frequent in the plankton.

The dominant organism was *Arthrodesmus incus* var. *extensus*, the total number of species was 29, and the phytoplankton quotients were instructive: myxophycean quotient $\frac{2}{18}$, chlorophycean quotient $\frac{6}{18}$, diatom quotient $\frac{0}{1}$, euglenine quotient $\frac{1}{5}$, compound quotient $\frac{9}{18} = 0.5$.

Grovsø is oligotrophic. The very shallow pond is surrounded by heath and is overgrown with vast thickets of reed swamps. Boisen Bennike (1943, p. 34) examined it on July 19th, 1940 and found that pH was 6.7, the colour corresponded to 0.12 mg/l methylorange, the consumption of $KMnO_4$ was 36 mg/l and the content of CaO was very small.

Closterium polystictum Nyg. var. **breviusculum** n. var.

Fig. nostra 26.

Diagnosis. Cellulae longae, graciles, subrectae vel ad apices leviter incurvae, e decem mensionibus 32—45 plo longiores quam latiores. Medium cellulae rectum, cylindricum, ad apices chromatophororum paulum attenuatum; ex hoc loco cellula ad apicem abrupte acutata. Membrana glabra, achroo, sine suturis transversis. Py-

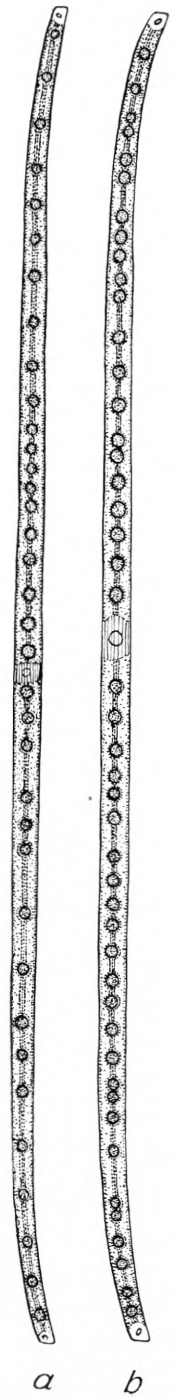
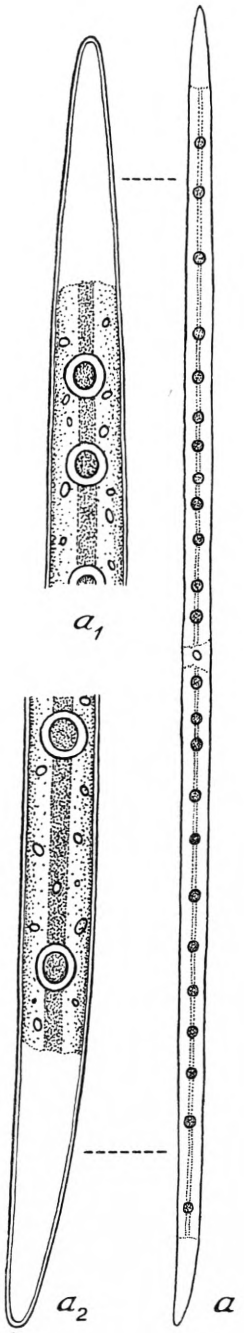


Fig. 25.



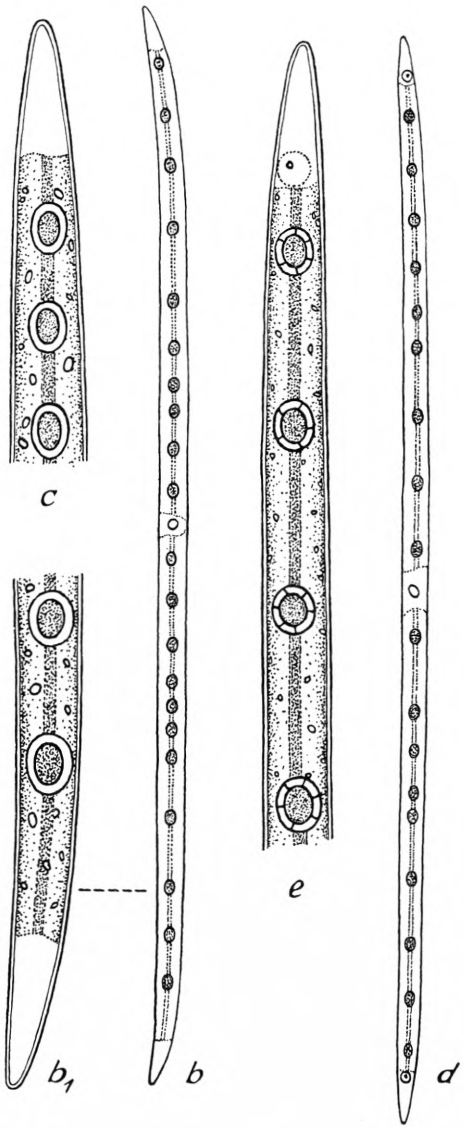


Fig. 26.

Fig. 25. *Closterium juncidum* Ralfs var. *elongatum* Roy et Biss. f. *truncata* n. f. from Grovsø, June 27th, 1930. *a* 350× and *b* 465×.

Fig. 26. *Closterium polystictum* Nyg.; *a*, a_1 and a_2 are delineated from the type material of Vaal River, Transvaal. *b*—*e* var. *breviusculum* n. var.; *b*, b_1 and *c* from Flyndersø, July 6th, 1938, *d*—*e* from Nordborg Sø, July 11th, 1938. *a*, *b* and *d* 350×, a_1, a_2, b_1, *c* and *e* 1070×.

renoidibus in utraque semicellula 8—13 (vulgo 10) in serie unica dispositis. Locellis apicalibus brevibus, 17—20 μ longis, corpuscula gypsi singula includentibus. Longitudo cellularum 323—418 μ, latitudo 9—11 μ; cellulae ad fines chromatophororum 6—7 μ latae.

Hab. In Flyndersø, Jutlandia septentrionali, et Nordborg Sø, Alsia, Dania, libere natans.

Systematics. For the sake of comparison I have drawn a typical specimen of *Closterium polystictum* from the original material (Vaal River, Vereeniging, Transvaal, July 25th, 1928). The cell ends of the Danish specimens are seen to look like the South African ones, and they are of the same thickness. The main species measures 479—585 μ in length, 9—11 μ in breadth, is 48—60 times as long as broad, has 12—16 pyrenoids per semi-cell and terminal vacuoles of 25—43 μ length; at the ends of the chromatophores the breadth was 6.5—8 μ. The variety thus differs from the main species by its shorter cells, the smaller number of pyrenoids (as a rule only 10) and the shorter terminal vacuoles. In fact var. *breviusculum* stands between the main species and var. *Nordstedtii* Krieger (1937, p. 266, t. 13, fig. 4), the latter being 9 μ broad but only 207—245 μ long.

On the periodicity of the species can only be said that it was comparatively common on July 6th, 1938 (temp. 18° C.) in Flyndersø and occurred sparsely in Nordborg Sø on July 11th, 1938 (temp. 18° C.). On December 9th, 1940 it was not present in the plankton of Nordborg Sø.

Sociology. In Flyndersø the plankton of the said time may be characterised in this way: *Api fl*-association, 34 species, myxophycean quotient $\frac{7}{4}$, chlorophycean quotient $\frac{8}{4}$, diatom quotient $\frac{8}{4}$, euglenine quotient $\frac{0}{15}$, compound quotient $\frac{23}{4} = 5.75$. In Nordborg Sø a typical *Oo Ma* association occurred in July 1938 with *Cl ac va* as subdominant, 34 species, myxophycean quotient $\frac{6}{6}$, chlorophycean quotient $\frac{12}{6}$, diatom quotient $\frac{3}{2}$, euglenine quotient $\frac{2}{18}$, compound quotient $\frac{23}{6} = 3.8$.

Ecology. Both Nordborg Sø and Flyndersø are rich in plankton and typically eutrophic in spite of the fact that the latter lies in heathy land. In Nordborg Sø, which is no doubt rich in CaO, pH was 8.8, in Flyndersø 9.0 on the dates mentioned.

Closterium setaceum Ehrb. var. **elongatum** West.

W. and G. S. West: 1905, p. 499, t. 6, fig. 21.—*Fig. nostra* 27.

Cells very slender, almost straight, according to 10 measurements 38—65 times longer than broad. The central part of the cells of a slender spindle-shape, both sides equally convex; the wall of a pale brown colour and with a fine longitudinal striation, 7—8 striae per 5 μ in the middle of the cell, the distance between the striae 0.7—0.8 μ. The ends very long, slender, bristle-like, palish brown, at the apices rounded and slightly curved. Chromatophores short, with 3—7, mostly 4 pyrenoids

per semicell. Terminal vacuoles with only one moving granule situated at the end of the chromatophores. Cells 396—469 μ long, 7—11 μ broad, apices 2 μ broad.

Occurrence: Grovsø at Oxbøl, SW. Jutland, pelagic.

The variety, which was observed only in quite a few localities of the world, differs from the main species in so many points, that it might be legitimate to consider it a separate species. *Closterium setaceum* is only 25—40 times longer than broad; its chromatophores normally contain only 2 pyrenoids per semicell; its striation is a little coarser: 5—6 striae per 5 μ; its apices are but 0.7—1.5 μ broad, and each of the terminal vacuoles contains 3—4 moving granules.

The species was rather common in the Grovsø plankton on June 27th, 1930 (temp. 18° C., pH 5.4). A comment on the composition of the plankton and on the locality is found under the discussion of *Closterium juncidum* Ralfs var. *elongatum* Roy et Biss. f. *truncata* n. f. (see p. 60).

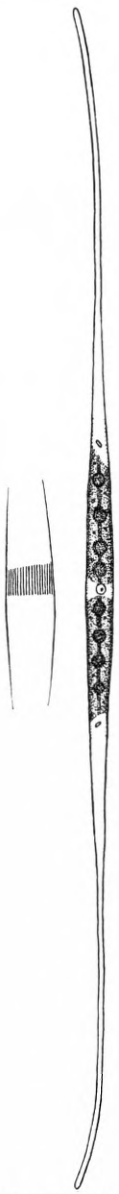


Fig. 27. *Closterium setaceum* Ehrenb. var. *elongatum* West from Grovsø, June 27th, 1930. 350× and 560×.

Closterium Venus Kg. f. **torta** (Griff.) mihi.

Syn. *Closterium tortum* Griffiths (1925, p. 90, t. 1, figs. 4—6); *"Closterium Venus* Kg?" J. Woloszynska 1914, p. 192, fig. 1 B.—*Fig. nostra* 28.

Diagnosis. Cellulae parvae, ad apices subacutos aequaliter attenuatae, $9\frac{1}{2}$—10 plo longiores quam latiores, valde curvatae, dorso convexo, gradus arci 151—164 metienti. Semicellulae inter se contortae, saepe tantum ut formae sigmoideae vulgares sint. Membrana levis, sine colore et suturis transversis. Pyrenoidibus in utraque semicellula 1—3, vulgo 2, in serie unica dispositis. Locellis apicalibus corpuscula gypsi singula includentibus. Longitudo cellularum 81—90 μ, latitudo 8—9 μ, locelli apicales 10—28 μ longi.

Hab. In Nordborg Sø, Alsia, et Furesø, Selandia, Dania, libere natans.

Griffiths gives the dimensions 90—100 $\mu \times$ 8—10 μ; his specimens contained 3 (or 4) pyrenoids per semicell.

In the eutrophic lake Nordborg Sø, which presumably is rich in CaO (see Johs. Iversen 1929, p. 322) pH was 8.8 and the temperature 18° C. on July 11th, 1938. The species was not infrequent in the plankton of the lake, but in spite of the fact that nearly a hundred individuals were seen not a single "normal" (not twisted) specimen was found! On the said date the plankton community mainly consisted of *Oocystis Marssonii* Lemm., *Closterium acutum* Breb. var. *variabile* Krieger, *Scenedesmus armatus* Chodat and *Microcystis aeruginosa* Kg. Among the rest of the 30 more or less common

species special attention must be drawn to the two characteristic desmids *Cosmarium biretum* Breb. var. *trigibberum* Nordst. and a new variety of *Closterium polystictum* Nygaard (see p. 62 where the phytoplankton quotients of the sample are given). It is a rare thing to find a plankton community in which the *Closterium* species prevail to such a degree, especially when the water is polluted and at the same time of a comparatively strong alkalinity.

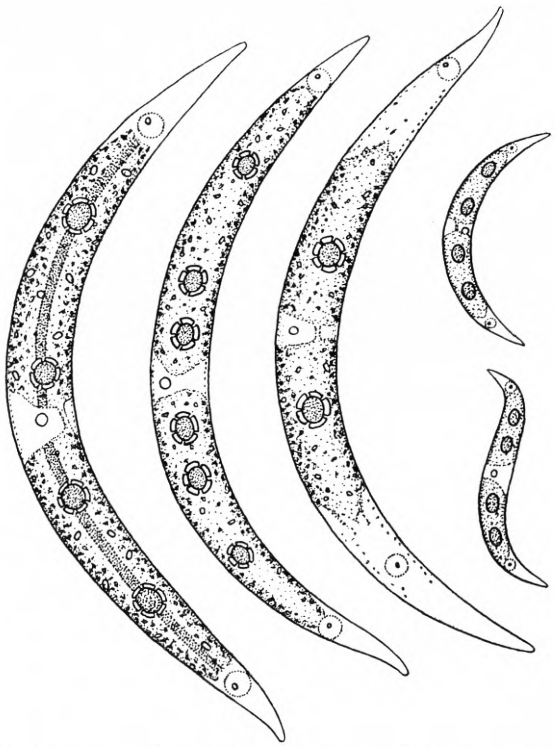


Fig. 28. *Closterium Venus* Kg. f. *sigmoidea* n. f. from Nordborg Sø, July 11th, 1938. 1070× and 350×.

In Furesø a few individuals of f. *torta* were observed on September 1st, 1946 at a temperature of 17.5° C. and pH 8.4. The plankton consisted of a typical *Ce hi* association (15 individuals per ml) with 54 species, myxophycean quotient $\frac{15}{8}$, chlorophycean quotient $\frac{10}{8}$, diatom quotient $\frac{3}{8}$, euglenine quotient $\frac{0}{25}$, compound quotient $\frac{28}{8} = 3.5$.

In a small article (1925, pp. 158—63) G. DEFLANDRE mentions sigmoid forms of 2 Closterium species, *Cl. Leibleinii* Kg. and *Cl. acerosum* Ehrb. In the former species the cells under culture were twisted, but the chromatophores unaltered; in the latter a spiral twisting of the chromatophores could be found both in the twisted and untwisted, cultivated individuals. Under the same conditions of cultivation the two species at the same time produced sigmoid forms, which generally speaking cannot therefore be regarded as accidental or morbid forms, but as forms that could be produced experimentally if we knew the physical-chemical conditions under which they arise. No doubt DEFLANDRE is right in supposing that sigmoid forms are modifications produced by special ecologic factors though it has not yet been tried whether they will "revert" under normal conditions of life.

Closterium Venus Kg. has a very wide geographical distribution. In their great monograph the experienced algologists W. & G. S. WEST say nothing about a spiral twisting of the cells. In the tropic Victoria Nyanza, however, J. WOLOSZYNSKA found sigmoid specimens "in allen Proben zerstreut", and now we also know the sigmoid form from the temperate lakes Marbury Mere, England, Nordborg Sø and Furesø, Denmark. In these three localities there is occasionally a realization of the special physical-chemical conditions that compel *Closterium Venus* Kg. to produce the sigmoid modification.

Cosmarium subarctoum Racib. var. **latum** n. var.

Fig. nostra 29.

Diagnosis. Cellulae parvae, tam longae quam latae, non profunde constrictae, sinu acutangulo mox ampliato. Semicellulae transverse ellipsoideae, a vertice visae ellipticae, ratio axium 1: circiter $1\frac{1}{2}$. Membrana punctata. Longitudo cellularum 20—22 μ, latitudo 19—22 μ, latitudo isthmi 11—12 μ, crassitudo 12 μ.

Hab. In Kalgaard Sø in medio Jutlandiae, Dania, libere natans.

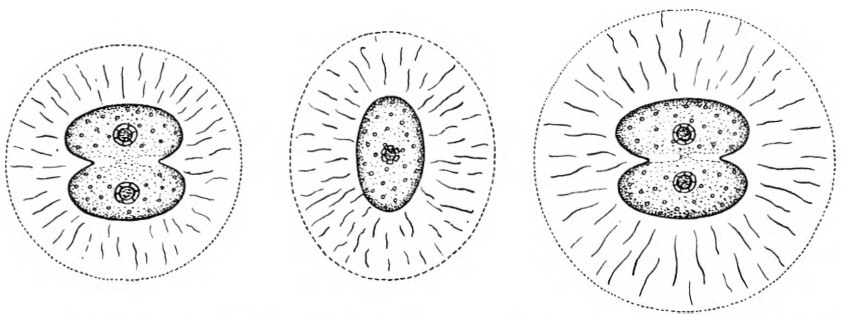


Fig. 29. *Cosmarium subarctoum* Racib. var. *latum* n. var. from Kalgaard Sø, May 17th, 1929. 750×.

This new variety differs from the type by its comparatively broad semicells. In the month of May it was surrounded by a nearly spherical gelatinous envelope with a radiate fibrillary structure. In June, however, the individuals like the rest of the desmids present were without gelatinous envelope.

Cosmarium subarctoum Racib. var. *latum* was found in Kalgaard Sø on May 17th, 1929 in several specimens, on June 23rd, 1929 in small quantities.

On May 17th the plankton was dominated by *Tabellaria fenestrata* Kg. var. *asterionelloides* Grun. and var. *intermedia* Grun. f. *asterionelloides* Bachm. (see Bachmann 1907, p. 68, Fig. VIII, 15—16; both are connected by transition forms). The phytoplankton quotients were very instructive: myxophycean quotient $\frac{1}{8}$, chlorophycean quotient $\frac{1}{8}$ and diatom quotient $\frac{0}{3}$, euglenine quotient $\frac{0}{2}$, compound quotient $\frac{2}{8} = 0.25$. On June 23rd, the phytoplankton was dominated by *Uroglena americana*; myxophycean quotient $\frac{2}{6}$, chlorophycean quotient $\frac{3}{6}$ and diatom quotient $\frac{0}{2}$, euglenine quotient $\frac{1}{5}$, compound quotient $\frac{6}{6} = 1$, (see Table II where the composition of the phytoplankton of Kalgaard Sø is given).

Kalgaard Sø is a clear and shallow, approximately oligotrophic lake; pH was 6.9 on June 23rd, 1929, and the same day it was impossible to make out the least traces of phosphate, ammonia and nitrate.

Cosmarium subtumidum Nordst.

WEST: Monograph, vol. II, 1905, p. 192, t. 63, figs. 18—20; incl. var. *Klebsii* West (*loc. cit.*, p. 193, t. 63, figs. 21—23).

In the place cited above W. and G. S. WEST say, "This variety (var. *Klebsii*) differs so little from the type that it is scarcely possible to distinguish between them". I fully accept this point of view. The authors state the ratio (in vertical view) of axes to be $\frac{1}{1.84}$. 4 measurings of Danish material gave the results $\frac{1}{1.76}$ $\frac{1}{1.8}$ $\frac{1}{1.82}$ $\frac{1}{2.05}$. The Danish specimens showed the following sizes: length 30.5—40 μ, breadth 29—40 μ, thickness 17—19 μ, breadth of isthmus 9—10 μ.

Distribution: Furesø, Nors Sø, Skaansø, Blankeborg I, dune lake at Højsande, shallow turf pit near Store Jenshøj at Oxbøl, pelagic.

Systematics. The species bears some resemblance to *Cosmarium depressum* Lund. var. *planctonicum* Reverdin (in "Dansk Planteplankton", 1945, given as *Cosmarium depressum* Lund. var. *limneticum* West), which is also pelagic and is characteristic of eutrophic lakes. *Cosmarium depressum* var. *planctonicum*, however, is much smaller and shorter than broad. The Danish specimens measured 19—24 μ in length, 22—27 μ in breadth, 9.5—12 μ in thickness, and the breadth of isthmus was 7.5—8.5 μ. The ratio of axes (in vertical view) also differs from that of *Cosmarium subtumidum*, being $\frac{1}{2.3 - 2.4}$ for the Danish material.

Periodicity. As will appear from the following section *Cosmarium subtumidum* was found only in the months of May—August, especially in August, at temperatures between 14 and 21° C.: in Blankeborg I, which was examined repeatedly for several years, it occurred only in the August samples (temp. 16.5—21° C.) and was never seen during the rest of the year. Accordingly, the species is periodic and meso- to polythermic, though chiefly polythermic. It was rare or very rare in all the samples and appears to thrive mainly in July-August.

Sociology. The species occurred in the following associations:

Blankeborg I (see Table IV).

Aug. 1st, 1926: *Din di*-association with *Per Vo* as subdominant (the species very rare).
— 15th, — : *Ce hi*-association (the species very rare).
Aug. 17th, 1927: *Ce hi*-association with *Din di* as subdominant (the species very rare).
Aug. 18th, 1928: *Din di*-association with *Ce hi* as subdominant (the species very rare).

Nors Sø (see Table II).

Jul. 18th, 1925: *Ana ci-Mio fl ma*-association with *Ce hi*, *Eut gl* and *Sta pi tr* as subdominants (the species rare).

June 13th, 1927: *Ana fl*-association with *Ank la* and *Eut gl* as subdominants (the species very rare).
May 13th, 1929: *Din di*-association with *Din so st* as subdominant (the species very rare).
Aug. 31st, — : *Cyc Kü ra*-association with *Cyc co* as subdominant (the species rare).
Aug. 18th, 1939: *Ana fl-Mio fl ma*-association (the species very rare).

Furesø (see Table II).

Aug. 7th, 1932: *Ana fl-Asi fo*-association (the species rare).

Store Jenshøj turf pit (see Table IV).

June 25th, 1930: *Aso su-Oe It*-association (the species rare).

Skaansø (see Table IV).

July 4th, 1938: *Din cy pa*-association (the species very rare).

Dune lake at Højsande, Læsø (see Table IV).

June 30th, 1925: *Tsp Ny*-association with *El ge* as subdominant (the species very rare).

This means that *Cosmarium subtumidum* was found in myxophycean (*Anabaena, Microcystis*), dinophycean (*Ceratium*), chrysophycean (*Dinobryon*), diatomaceous (*Cyclotella, Asterionella*) and chlorophycean associations (*Tetraspora, Asterococcus*).

The constant associates were *Ceratium hirundinella*, which occurred in 92 % of the number (13) of samples that contained *Cosmarium subtumidum*; *Botryococcus Braunii* and *Pediastrum Boryanum* (85 %).

Ecology. The species, which is found both in small waters and in our largest lakes, seems to be very adaptive, occurring in very different biotopes. Store Jenshøj turf pit is oligotrophic of the dystrophic phase, Skaansø and dune lake at Højsande are oligotrophic lakelets of the acidotrophic phase, whereas Blankeborg I is a slightly eutrophic turf pit of the mixotrophic phase; Nors Sø is also slightly eutrophic, and Furesø, our deepest lake, is moderately eutrophic. Tables I and III give the compound quotients for all these localities. In the highly eutrophic lakes and ponds, however, *Cosmarium subtumidum* is unknown; apparently it endures only a very slight contamination of the water.

The species was found at pH values between 4.0 and 8.3 and at a lime content of 43.1—91 mg CaO per litre though the lower limit is no doubt below 5 mg/l. In Blankeborg I the consumption of $KMnO_4$ was found to be 77—81 mg/l, but in the oligohumic Skaansø and dune lake at Højsande the consumption of $KMnO_4$ was no doubt below 10 mg/l and presumably much higher than 81 mg/l in Store Jenshøj turf pit with its very brown water.

f. **punctata** n. f.

Fig. nostra 30.

Diagnosis. A typo cellulis regularioribus et dispersioribus punctatis differt. Longitudo cellularum 35—42 μ, latitudo 34—39 μ, crassitudo 17 μ, latitudo isthmi 10.5—11.5 μ.

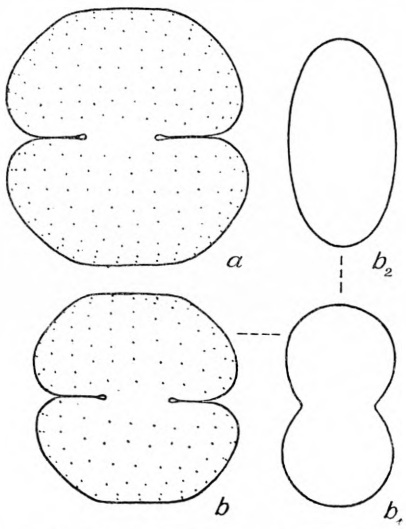


Fig. 30. *Cosmarium subtumidum* Nordst. f. *punctata* n. f. from Slaaen Sø, September 4th, 1929; *a*—*b* front views, b_1 lateral view, b_2 vertical view. 800×.

Hab. In Slaaen Sø, Jutlandia, Longet Sø prope Nyborg, Fionia, et Furesø, Selandia, Dania, libere natans.

Systematics. In their Monograph, vol. II, t. 63, fig. 23 the WESTS picture a specimen of *Cosmarium subtumidum* var. *Klebsii* with punctate cell-wall; these points are completely disorderly. The cell-wall of the f. *punctata* individuals is not nearly so densely punctate, and the points show a distinct tendency of an order of longitudinal and transversal series. One measuring of the axes (in the vertical view) gave the ratio $\frac{1}{2}$.

Periodicity. As will appear from the section on sociology the form was found only in July, August and September in the plankton of the 3 localities mentioned; it was always rare or very rare.

Sociology. The form was found in the following 4 associations:

Slaaen Sø.

Sep. 4th, 1929: *Ce hi*-association (the form very rare).

Furesø.

Aug. 21st, 1943: *Mel gr an*-association (the form very rare).
Sep. 1st, 1946: *Ce hi*-association (the form very rare).

Longet Sø at Nyborg.

July 28th, 1926: *Per Wi*-association containing *Merismopedia major*! (the form rare).

Accordingly, *Cosmarium subtumidum* f. *punctata* occurred in dinophycean associations of *Ceratium* and *Peridinium* and a diatom association of *Melosira*.

The constant associates were *Dinobryon divergens*, which occurred in 100 % of the number (4) of samples that contained the form; the following species occurred in 3 of the samples: *Sphaerocystis Schroeteri*, *Closterium aciculare*, *Cosmarium depressum* var. *planctonicum*, *Staurastrum avicula*, *Staurastrum gracile*, *Stephanodiscus*

Astraea, Asterionella formosa, Fragilaria crotonensis, Synedra ulna, Ceratium hirundinella and *Microcystis holsatica.*

Sociology. Slaaen Sø is a very clear lake, cold in summer and standing between eutrophy and oligotrophy (compound quotient 1.2); Furesø is also clear but moderately eutrophic (compound quotients 4.4—3.5—3.5) with a lime content of 54.5—65.4 mg CaO per litre (BRØNSTED and WESENBERG-LUND 1912, p. 453); see further Table I. Longet Sø at Nyborg is a large, slightly eutrophic pond of the mixotrophic phase, partly overgrown with reed swamps; on the date mentioned pH was 7.8 and the consumption of $KMnO_4$ 61 mg/l. A few other data of the ecology of *Cosmarium subtumidum* f. *punctata*: pH 7.8—8.4, contents of PO_4-P 0.07 mg/l, NH_3-N 0.05 mg/l, NO_3-N 0 mg/l.

f. **parva** n. f.

Fig. nostra 31.

Diagnosis. A typo cellulis multo minoribus differt. Longitudo cellularum 16—18.5 μ, latitudo 15—18 μ, crassitudo 8—10 μ, latitudo isthmi 5—7 μ, ratio axium (semicellulae a vertice visae) 1:1.8—1.9.

Hab. In Grovsø prope Oxbøl, et Madum Sø, Jutlandia, Dania, libere natans.

Systematics. This variety resembles the type in all respects with the exception of the size, which is about half as great. K. MÜNSTER STRØM describes a var. *minor* of *Cosmarium subtumidum* (1919, p. 7, t. 2, figs. 14, 14a, 14b). The apex of this variety, however, is semicircular, not flattened as in f. *parva*, and its cells are much longer than broad.

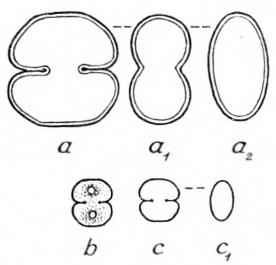


Fig. 31. *Cosmarium subtumidum* Nordst. f. *parva* n. f.; *a*, a_1 and a_2 (800×) from Madum Sø, June 24th, 1928; *b*, *c* and c_1 (350×) from Grovsø, June 27th, 1930. *a*, *b* and *c* front views, a_1 lateral view, a_2 and c_1 vertical views.

Periodicity. *Cosmarium subtumidum* f. *parva* was found only in the month of June. In Grovsø it was not infrequent on June 27th, 1930 (temp. 18° C.), but in Madum Sø it was very rare in both samples from June.

Sociology. The form occurred in the following 3 associations:

Grovsø.

June 27th, 1930: *Ar in ex mi*-association (the form not infrequent).

Madum Sø.

June 24th, 1928: *Din cy pa*-association (the form very rare).

June 24th, 1929: *Din cy pa*-association with *Per Wi* as subdominant (the form very rare).

Cosmarium subtumidum f. *parva* thus occurred in a desmid association of *Arthrodesmus* and in two chrysophycean associations of *Dinobryon.*

Ecology. Both lakes are oligotrophic, Grovsø mainly of the dystrophic phase. Madum Sø, however, belongs to the acidotrophic phase: its pH was 4.6—5.1, and its water was sometimes just as clear as in the alpine lakes of Central Europe (consumption of $KMnO_4$ 4—6.6 mg per litre): on June 24th, 1929 the transparency was more than 8 m! The lime content of this lake was only 2.4—4 mg CaO per litre. Further data of the ecology of *Cosmarium subtumidum* f. *parva* are: pH 4.8—5.4, contents of PO_4-P, NH_3-N and NO_3-N: 0 mg/l.

Euastrum occidentale West var. **danicum** nov. var.

Fig. nostra 32.

Diagnosis. A typo cellulis minoribus cum granulis 13—14 in utroque latere semicellulae differt. Longitudo cellularum 54—58 μ, latitudo 46—50 μ, crassitudo 21—27 μ, latitudo isthmi 11.5—14 μ, latitudo apicis 12—15 μ.

Hab. In Nors Sø, Jutlandia boreali, Dania, libere natans.

Systematics. The specimens pictured deviate so much from West's specimens in the size and number of the granules, that it seems legitimate to consider the Danish specimens a new variety. W. Krieger is of opinion that *Euastrum occidentale* West is a *Cosmarium* species (Rabenhorst Kryptogamenflora, Bd. 13, 1937, p. 657); however, the apical sinus and the concave side-walls justifies the use of the generic name of *Euastrum*. The variety should also be compared with *Cosmarium Turpinii* Breb. and varieties (West's Monograph of the British Desmidiaceae, vol. 3, 1908, p. 189, t. 82, figs. 16—17 and t. 83, figs. 1—3), which *i.a.* is different, however, in having 1—2 central tumours, set with big granules, on the frontal side of either semicell. From *Cosmarium Botrytis* Menegh. var. *emarginatum* Hansg. (West *loc. cit.* p. 6, t. 103, fig. 8), which also has 13—15 granules along each of the side-walls of either semicell, it differs by its distinctly concave side-walls.

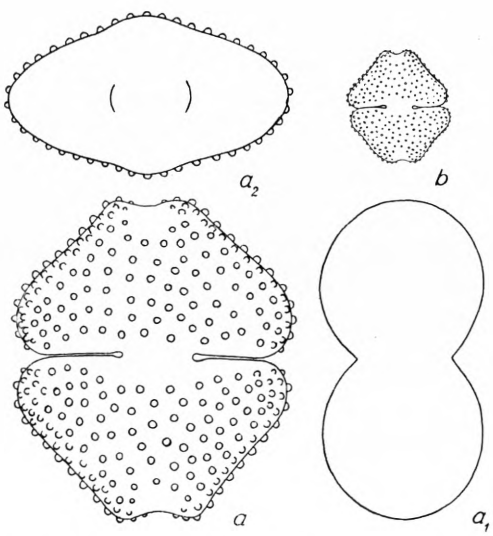


Fig. 32. *Euastrum occidentale* West var. *danicum* n. var. from Nors Sø, August 18th, 1939. *a*—*b* front views, a_1 lateral view, a_2 vertical view. *a*, a_1 and a_2 800×, *b* 260×.

Euastrum occidentale var. *danicum* was found only in a few specimens in Nors Sø on August 18th, 1939 (legit Sigurd Olsen). At this time the plankton of the lake consisted of a myxophycean association characterized by *Ana-*

baena flos aquae and *Microcystis flos aquae* var. *major*; the qualitative composition of the association appears from Table II.

Nors Sø is slightly eutrophic, the compound quotient reaching the following values during a series of years: $\frac{27}{12} = 2.25$, $\frac{22}{10} = 2.2$, $\frac{16}{8} = 2$, $\frac{11}{5} = 2.2$ and $\frac{24}{12} = 2.0$, the last-mentioned value applying to August 18th, 1939. Though the lake is situated on cretaceous bottom, its content of CaO is only 43.1—52 mg/l. The found pH values range between 7.3 and 8.3 (Nygaard 1938, p. 605, Boye Petersen 1943, p. 23).

Arthrodesmus incus Hass. var. **extensus** Andersson.

Andersson (Borge) 1890, p. 13, t. 1, fig. 7; Borge 1913, p. 25, t. 2, fig. 23. *Fig. nostra 33.*

Systematics. In the original description Borge states: Longitudo 17—20 μ, latitudo 13—14 μ. His fig. 23 (quoted above) shows the following measurements:

	Borge's fig. 23 (1 ind. measured)	Grovsø (8 ind.s measured)	Turf pit NE. of Skaansø; B. Mose II and L. Gribsø (13 individuals measured)	
Long. cum spin.	32 —33 μ	27 —36 μ	18.5—30 μ	19 —25 μ
Long. sine spin.	19 μ	18.5—21 μ	12 —16 μ	13.5—15.5 μ
Lat. cum spin.	31 —32 μ	34 —42 μ	18 —30 μ	23 —32 μ
Lat. sine spin.	14 —15.5 μ	13 —16.5 μ	11 —14.5 μ	11 —14 μ
Long. spin.	10.5—13 μ	13 —16 μ	4.5—11 μ	8 —10 μ
Lat. isthmi	5 μ	5 — 6.5 μ	5 — 6 μ	5 — 6 μ
Crassitudo	..	6 — 7 μ	..	..

It appears from this table, in which the 3rd vertical column is from the turf pit NE. of Skaansø while the last vertical column represents Bøndernes Mose II and Lille Gribsø, and from *Figurae nostrae* 31 and 32 that the specimens from turf pit NE. of Skaansø, Bøndernes Mose II and Lille Gribsø may be regarded as f. *minor* n. f. while the specimens from Grovsø are probably identical with var. *extensus* though their spines are longer and apex is flat. Incidentally, both form and variety are found in Grovsø though f. *minor* is very rare; no transition forms between f. *minor* and var. *extensus* were observed.

f. **minor** n. f.

Fig. nostra 34.

A varietate cellulis et spinis brevioribus differt; longitudo sine spinis 12—16 μ, cum spinis 18.5—30 μ, latitudo sine spinis 11—14.5 μ, cum spinis 18—32 μ, latitudo isthmi 5—6 μ, longitudo spinarum 4.5—11 μ.

Hab. In stagno turfaceo prope Skaansø, Jutlandia, et in Bøndernes Mose II et Lille Gribsø prope Hillerød, Dania, libere natans.

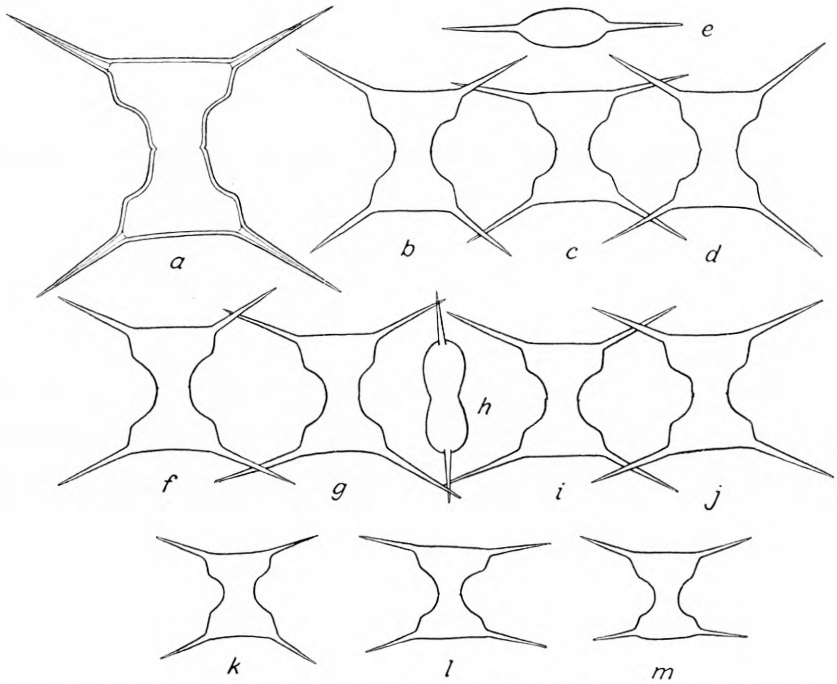


Fig. 33. *a*—*j*: *Arthrodesmus incus* Hass. var. *extensus* Andersss. from Grovsø, June 27th, 1930; *k*—*m*: f. *minor* n. f. from the same locality and date. *e* vertical view, *h* lateral view, the other figures front views. *a* 1200×, *b*—*m* 800×.

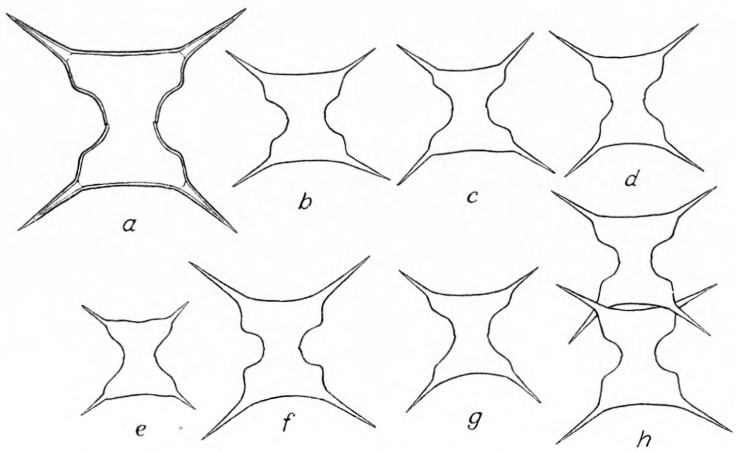


Fig. 34. *Arthrodesmus incus* Hass. var. *extensus* Andersss. f. *minor* n. f.; *a*—*d* from Bøndernes Mose II, June 18th, 1929; *e*—*h* from turf pit NE of Skaansø, July 4th, 1938. *a* 1200×, *b*—*h* 800×.

Periodicity. In Bøndernes Mose II var. *extensus* f. *minor* occurred from June till the beginning of October 1929 at temperatures between 9.5 and 24° C. It was always very rare except in the sample from August 12th, (temp. 21.5° C.) in which it was rare. During the remaining months of the year it was not found and therefore seems to be meso- to polythermic.

In Lille Gribsø, which was also examined regularly, it was extremely rare: only a few specimens were seen on July 5th, 1929 (temp. 18° C.). In the turf pit NE. of Skaansø, which was nearly overgrown with *Sphagnum cuspidatum*, the form was rare on July 4th, 1938 (temp. 18.5° C.).

In Grovsø var. *extensus* was the dominant form of the plankton on June 27th, 1930 (temp. 18° C.).

Sociology. Var. *extensus* f. *minor* was found in the following associations:

Bøndernes Mose II.

June 18th, 1929 — July 5th, — — — 17th, — Aug. 12th, — — — 22nd, — Sep. 7th, — — — 22nd, — } *Crym ov cu*-association (form very rare; Aug. 12th, rare).

Oct. 9th, — June 16th, 1930 } *Crym ov cu*-association with *Tra vo* as subdominant (form very rare).

Turf pit NE. of Skaansø.

July 4th, 1938: *Sta br*-association with *Sta de lo* as subdominant (form rare); see Table IV.

Lille Gribsø.

July 5th, 1929: *Se ca*-association with *Se We* as subdominant (form very rare).

Var. *extensus* was found in the following association:

Grovsø.

June 27th, 1929: *Ar in ex*-association (the variety common and the form very rare); see p. 60.

Arthrodesmus incus var. *extensus* f. *minor* thus occurred in cryptophycean associations of *Cryptomonas*, desmid associations of *Staurastrum* and *Arthrodesmus* and a chlorophycean association of *Selenastrum*. Var. *extensus* itself may be a dominant organism.

The most constant associates were *Cryptomonas ovata* var. *curvata*, *Goniostomum semen*, *Staurastrum dejectum* and *Trachelomonas volvocina*, which occurred

in 75 % of the number (12) of samples that contained *Arthrodesmus incus* var. *extensus* f. *minor*.

Ecology. Bøndernes Mose II and the turf pit NE. of Skaansø are small, very lime-deficient, oligotrophic turf pits of the dystrophic phase, and Lille Gribsø is a likewise very lime-deficient, but clear, 'mesotrophic' little forest lake; the phytoplankton quotients of these three localities are found in Table III. Grovsø is discussed on p. 60. A few data from the ecology of *Arthrodesmus incus* var. *extensus* f. *minor* are: pH 4.2—5.4, CaO (2.2—)2.9 mg/l, consumption of $KMnO_4$ 166—202 mg/l (in Lille Gribsø 38 mg/l on August 22nd, 1929), contents of PO_4-P 0 mg/l, NH_3-N 0.9—1.25 mg/l (in Lille Gribsø 0.1 mg/l on August 22nd, 1929), NO_3-N 0 mg/l and Fe 0.25 mg/l.

Arthrodesmus incus var. *extensus* was found at the pH value 5.4.

Staurastrum barbulae n. sp.

Fig. nostra 35.

Diagnosis. Cellulae mediocres; longitudo cum processibus paulo minor quam latitudo cum processibus; sinus extrorsum valde ampliatus, apice acuto. Corpus semicellulae cyathiforme vel subcylindricum, margine dorsali plano; anguli in processus longos, valde divergentes, rectos vel leviter curvatos, perspicue dentatos, terminaliter quadri- vel quinquecuspidatos extenuantes, quisque processus seriebus dentium 9—11 ordinatus. Anulus granulorum vel spinarum minimarum in utraque parte isthmali semicellulae. Cellulae a vertice visae triangulares, lateribus corporis concavis, raro rectis vel leviter convexis. Apex semicellulae cum 3 spinis intramarginalibus, robustis, ad 2.5 μ longis, vel 3 seriebus intramarginalibus spinarum quinarum minorum ordinatus; saepe spinae singulae vel binae reliquis robustiores, quae valde defectae esse possunt. Longitudo sine processibus 37—39 μ, cum processibus 59—69 μ, latitudo cum processibus 67.5—77 μ, latitudo isthmi 9—10 μ.

Hab. In Mørksø et Skaansø, Jutlandia boreali, Dania, libere natans.

Systematics. To begin with I considered the individuals to be triradiate forms of *Staurastrum leptocladum* Nordstedt (see G. M. Smith 1924, p. 102, t. 78, figs. 1—7; W. and G. S. West 1895, p. 79, t. 9, figs. 12—13). This species, quite apart from its being always biradiate, differs from the present specimens in having 11—19 denticulations on its very long arms, which always terminate in 2 spines, and in showing a pronounced inflation of the isthmal part of the body of the semicell and a distinct convexity of the dorsal part.

As will appear from *Fig. nostra* 35 there is a considerable variation in the apical ornamentation: there are all transition forms between the two extremes, the 3 strong, intramarginal spines situated in the 3 symmetry planes and the 3 intramarginal series with about 5 spines in each.

Staurastrum barbulae should also be compared with *Staurastrum Sebaldii* var. *ornatum* forma Grönblad (1942, p. 42, t. 5, fig. 10), which has an apical ornamentation of spines much like that of certain individuals within the form cycle of *Staurastrum barbulae*. Grönblad's form, however, is much more robust: length and breadth

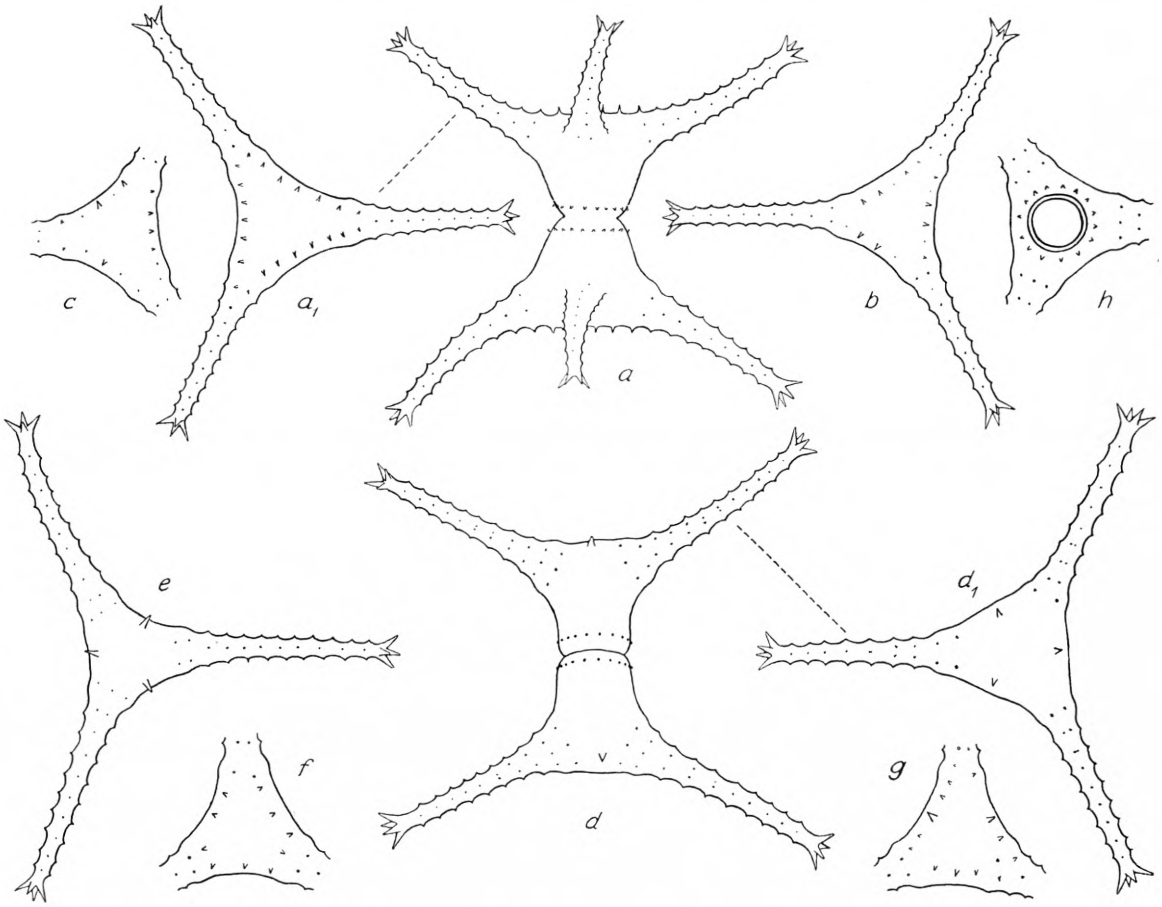


Fig. 35. *Staurastrum barbulae* n. sp.; *a*, a_1, *b* and *c* from Mørksø, July 6th, 1938; *d*, d_1, *e*, *f*, *g* and *h* from Skaansø, July 4th, 1938. *a* and *d* front views; the other figures vertical views with exception of *h*: basal view. 800×.

with processes 122 and 137 μ, respectively; breadth of isthmus 23 μ; besides this the isthmal granulation is quite different. The processes, which are dentate on the dorsal side only, are strongly tapering from the proximal to the distal part while the processes of *Staurastrum barbulae* with their dentation on all sides are slightly tapering from the base to the top.

Staurastrum cingulum G. M. Smith and its varieties have quite another apical ornamentation and the sides of the body (seen in vertical view) are undulate or dentate.

Periodicity. The species was found only in the beginning of July, 1938 (temp. 17.5—18° C.) in the two lakes mentioned. It was rare in both samples, and nothing can be said about the periodicity of the species on this basis.

Sociology. The species occurred in the following associations, the qualitative composition of which appears from Table IV:

Skaansø, July 4th, 1938: *Din cy pa*-association (the species very rare).
Mørksø, — 6th, — : *Per Wi*-association (the species very rare).

In other words *Staurastrum barbulae* was found in a *Dinobryon* association and a *Peridinium* association.

Ecology. Both Skaansø and Mørksø are oligotrophic lakes, the former on open heath, the latter surrounded by spruce forest; Table III gives their phytoplankton quotients. The compound quotient was $\frac{4}{10} = 0.4$ and $\frac{2}{4} = 0.5$, respectively. pH was 5.6 in Skaansø, 4.9 in Mørksø.

Staurastrum Bergii n. sp.

Fig. nostra 36.

Diagnosis. Cellulae mediocres, longitudine aequale ac est latitudo sine spinis, profunde constrictae, sinu acutangulo, extrorsum modice ampliato. Semicellulae a fronte visae concinne ellipticae vel subellipticae cum margine ventrali convexiore quam est margo dorsalis; anguli in processus brevissimos vix protracti vel prorsus sine processibus; quisque angulus 4 spinis divergentibus, rectis instructus; margo dorsalis semicellulae 6 vel 8 verrucis parvis, applanatis, emarginatis instructus; ab quaque verruca series una verticalis granulorum parvorum, acutorum exit, quae isthmum semicellulae fere attingit. Semicellulae a vertice visae triangulae cum lateribus rectis vel leviter concavis, 6- vel 8-denticulatis et undique serie una 6 vel 8 verrucarum intramarginalium, parvarum instructae; ab quaque verruca series una radialis granulorum parvorum et acutorum exit; medium semicellulae glabrum; anguli in processus brevissimos vix producti vel prorsus sine processibus, sed 4 spinis rectis, divergentibus ordinati. Semicellulae a basi visae cum 3 vel 4 seriebus concentricis granulorum parvorum et acutorum in quoque tri-

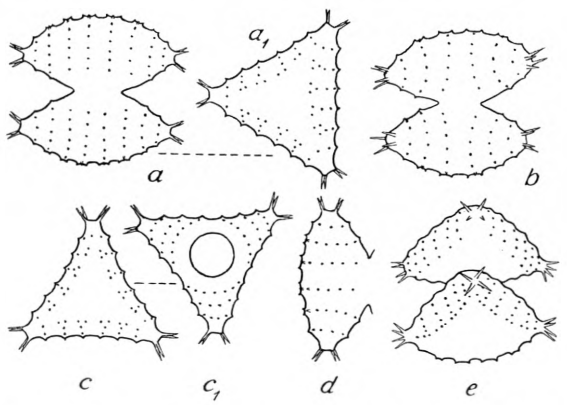


Fig. 36. *Staurastrum Bergii* n. sp. from Eriophorum moor, July 9th, 1947. *a*, *b* and *d* front views, a_1 and *c* vertical views, c_1 basal view. 800×.

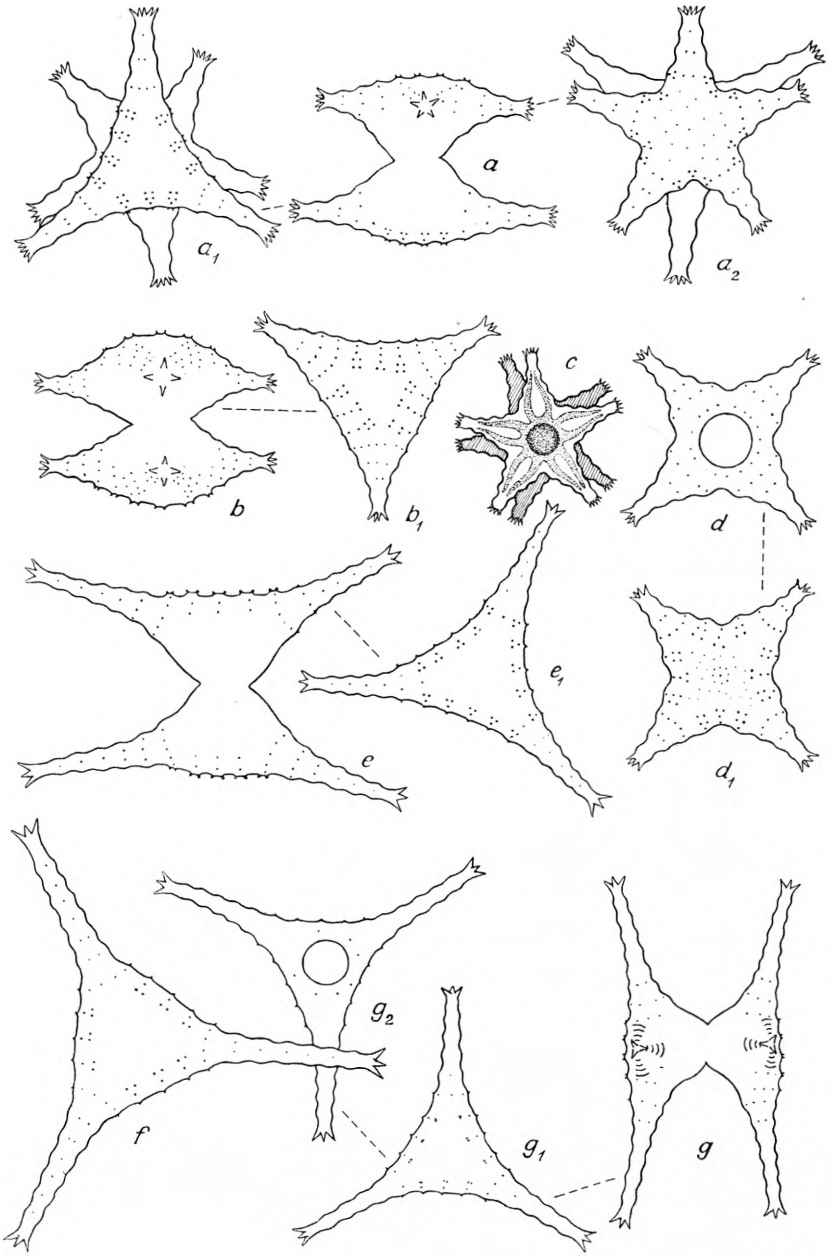


Fig. 37. *Staurastrum gracile* Ralfs; *a*, a_1, a_2, *b*, b_1, *c*, *d* and d_1 from Sortedam II, *a*, a_1 and a_2 demonstrate a 3-+5-radiate specimen, *b* and b_1 a 3-radiate, *c* a 5-radiate specimen, all from September 18th, 1929, *d* and d_1 demonstrate a 4-radiate specimen from June 8th, 1929; *e* and e_1 from Mossø, August 18th, 1929; *f* from Salten Langsø, August 19th, 1929; *g*, g_1 and g_2 from Slaaen Sø, September 4th, 1929; *a*, *b*, *e* and *g* front views, a_1, a_2, b_1, *c*, d_1, e_1, *f* and g_1 vertical views, *d* and g_2 basal views. All figures 800× except *c*, 560×.

ente semicellulae. Longitudo cellularum 22.5—25 μ = latitudo sine spinis, latitudo isthmi 7—8 μ, longitudo spinarum 2—3 μ.

Hab. In palude *Eriophori* prope Sorø, Selandia, Dania, libere natans.

Systematics. For our undergraduates' curriculum in 1947 Professor KAJ BERG on July 9th took a plankton sample, which was unique by its richness in both species and individuals of *Desmidiaceae*. Among other things it contained enormous quantities of a *Staurastrum* species, which I have named after Professor BERG. The species has an ornamentation that is much like that of *Staurastrum gracile* (see *Fig. nostra* 37). In Sortedam II, where *Staurastrum gracile* occurs in tri-, quadri- and quinqueradiate forms, even as tri- + quinqueradiate individuals (cp. GRÖNBLAD 1942, p. 41, t. 4, figs. 21—22), the triradiate specimen pictured (*Fig. nostra* 37 b—b_1) has the same ornamentation and shape of semicell as *Staurastrum Bergii*, but it has distinct arms.

Staurastrum hexacerum Wittr. (see W. and G. S. WEST's Monograph, vol. 5 by NELLIE CARTER, 1923, p. 138, t. 142, figs. 11—14), however, has very short arms and nearly the same dimensions as *Staurastrum Bergii*, but its cells are broader than long and have 5—6 concentric series of granules round each third of the semicell, no emarginate verrucae on the apex and only 3 tiny spines on the end of each of the very short arms.

Periodicity. As will appear from the section on sociology *Staurastrum Bergii* reached a great maximum on July 9th, 1947. During the following months it constantly decreased in frequency and was seen for the last time in the October sample. On March 20th, 1948 it had not yet reappeared; the species thus seems to be a typical summer form.

Sociology. The species occurred in the following associations:

July 9th, 1947: *Sta Be*-association with *Dic pu* as subdominant (the species very common).
Aug. 6th, — : *Tra ch*-association (the species rather common).
Sep. 6th, — : *Tra ch*-association (the species not infrequent).
Oct. 4th, — : *Tra*-association (the species very rare).

On October 4th the dominant species were *Trachelomonas Manginii*, *Tr. intermedia*, *Tr. volvocina* and its var. *compressa*, *Tr. hispida* var. *coronata*, *Tr. bernardinensis*, etc.

Ecology. The species, which was often surrounded by a roundish gelatinous envelope, is no doubt tychoplanktic. A comment on the characteristic locality, in which it occurred, is given under *Euglena phacoides* n. sp. on p. 166. The water of the margin is brownish and slightly acid (PH 6.5—6.8), but contaminated by cattle.

Staurastrum Bieneanum Rabh. var. **angulatum** nov. var.

Fig. nostra 37 *bis.*

Diagnosis. A typo semicellulis non-punctatis, angulatioribus, angulariter rotundatis differt; cellulis vix longioribus quam latioribus. Longitudo cellularum 42—45 μ, latitudo 39—43 μ, latitudo isthmi 10—12 μ.

Hab. In Jægerbakke Dam in Hillerød, Dania, libere natans.

Systematics. *Staurastrum Bieneanum* Rabh. (see the WESTS' monograph IV, p. 135, t. 120, figs. 4—6) has a distinctly punctate cell-wall and the angles of both front and vertical views are subacute, the dorsal margin is rather regularly convex (but truncate or slightly retuse in the middle). The new variety differs in all these respects as evident from Fig. 37 *bis*; especially the apical part of the semicell is more or less trapeziform. Some of the Danish specimens have angles a little more acutely rounded than shown in Fig. 37 *bis a*, but never so much as in the cited fig. 4 b in the WESTS' monograph.

E. MESSIKOMMER (1927, II, t. 1, fig. 13) has figured *Staurastrum Bieneanum* var. *ellipticum* Wille. This variety, however, has punctulations arranged in concentric series around the angles; further the semicells are subelliptic in front view. MESSIKOMMER's and my individuals are very similar in vertical view, but not in the shape of the dorsal margin in front view; besides the Swiss specimens are irregularly punctate.

The variety was found in small quantities (6 cells pro 5 ml) in Jægerbakke Dam on November 25th, and December 4th, 1944. The pond was icebound and the temperature of the water 2° C. I am indepted to professor C. WESENBERG-LUND and professor KAJ BERG for sending me plankton and water samples from the two dates mentioned.

It is peculiar to find this desmid in Jægerbakke Dam since it was never observed by the regular examination every fortnight during the period of June 1929 to June 1930. Further it is peculiar that a pelagic desmid occurs so late as in December when ponds are freezing up. The net plankton was quite dominated by *Eudorina elegans*,

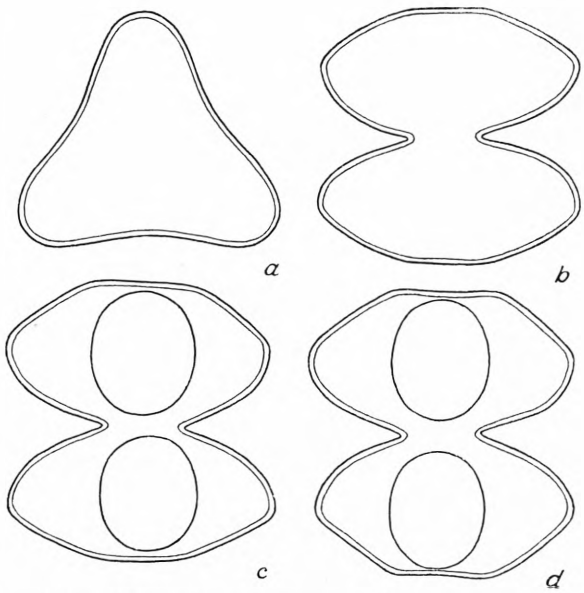


Fig. 37 *bis*. *Staurastrum Bieneanum* Rabh. var. *angulatum* nov. var. from Jægerbakke Dam, November 25th, 1944; *a* vertical view, *b*—*d* front views. 800×.

though *Gonium sociale* and *Volvox aureus* also played a rather prominent part; the latter, too, has never been observed previously in Jægerbakke Dam. The real dominant was, however, *Geminella minor* which occurred in enormous quantities in the water sample; it had apparently passed through the pores of the tow-net.

Staurastrum cingulum G. M. Smith var. **inflatum** nov. var.

Fig. nostra 38.

Diagnosis. Cellulae mediocres; longitudo cum processibus latitudine cum processibus aequilonga vel minor; cellulae profunde incisae, sinu aperto, sed intime acuto. Corpus semicellulae a fronte visum inflate poculiforme, lateribus convexis, apice perspicue vel valde convexo, 3—4 verrucis parvis ordinato; sub illis verrucis series obliquae vel verticales granulorum acutorum et minimorum; corpus saepe cum anulo isthmali granulorum minimorum; anguli superiores corporis in processus longos, tenues, 5—9-undulatos, valde divergentes, leviter incurvos, raro rectos abrupte producti sunt. Corpus semicellulae a vertice visum triangulum cum lateribus rectis vel vix convexis, tenuiter denticulatis, et cum 3 seriebus intramarginalibus verrucarum parvarum, rarissime spinarum vel granulorum bigeminorum, 3—4 pro serie; quisque angulus in processum longum, tenuem, 5—9-(rarissime 4-)undulatum, rectum productus, terminaliter 4 spinis parvis et divergentibus instructus. Longitudo sine processibus 20—28 μ, cum processibus 35.5—53 μ, latitudo sine processibus 13.5—20 μ, cum processibus 36—69 μ, latitudo isthmi 6—8 μ.

Hab. In Mossø, Salten Langsø et Hostrup Sø, Jutlandia, et Frederiksborg Slotssø, Selandia, Dania, libere natans.

Systematics. The fact that the sides of the body in vertical view are denticulate on account of the radial series of granules centering in the small verrucae on apex and the occurrence of a basal ring of acute granules shows that the individuals are closely related to *Staurastrum cingulum* (see G. M. Smith 1924, p. 84, t. 72, figs. 12—14). The 3 verrucae of each series in small individuals may be reduced into one central spine + 2 granula bigemina (see *Fig. nostra* 38). The present variety is characterized by its inflated, nearly round bodies of semicell and by the abrupt transition between the body and the thin, highly divergent processes, which are not denticulate but undulate both in front view and vertical view.

There is no small likeness between *Staurastrum cingulum* var. *inflatum* and *Staurastrum tetracerum* var. *validum* West (Monograph, vol. V, 1923, t. 149, fig. 5), which apparently has a *cingulum* granulation, cp. Nygaard 1945, t. 4, fig. 59. By medium magnification I once observed a var. *inflatum* individual, one semicell of which was bibrachiate while the other was triradiate. The sparse material, however, does not allow us to decide whether or not *Staurastrum tetracerum* var. *validum* is only a bibrachiate modification of *Staurastrum cingulum* var. *inflatum*.

Periodicity. In the three lakes Hostrup Sø, Salten Langsø and Mossø (all in Jutland) the variety occurred in very small quantities in June and August. In the regularly examined lakelet Frederiksborg Slotssø, where it was also very rare in all

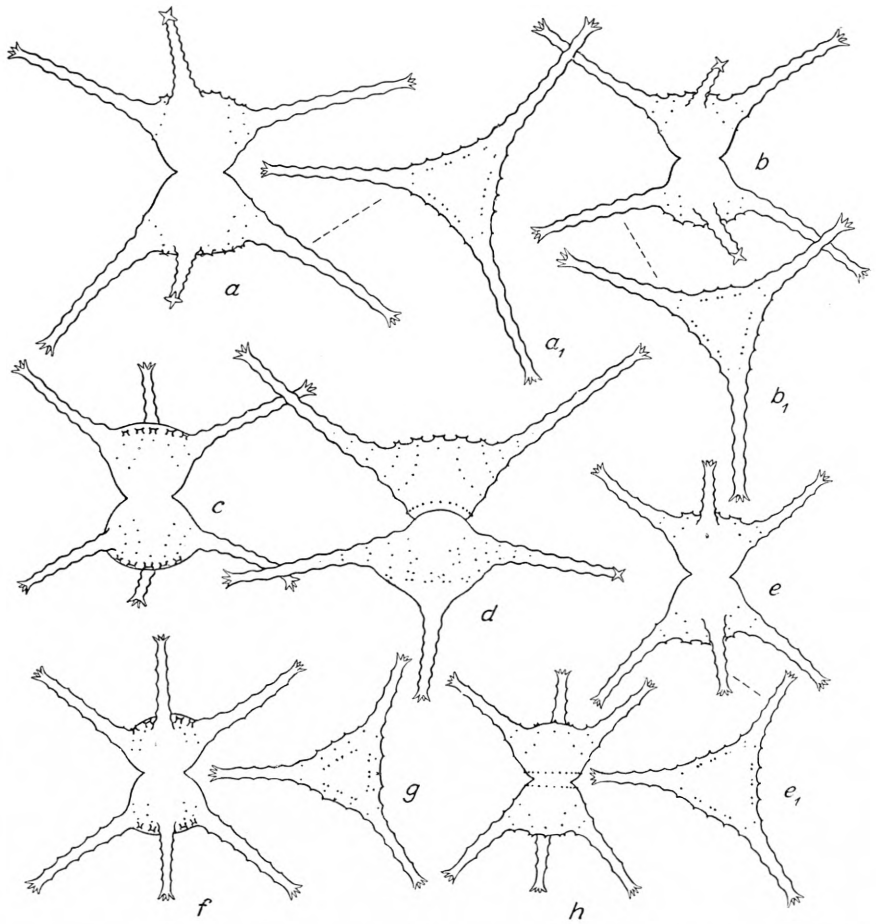


Fig. 38. *Staurastrum cingulum* G. M. Smith var. *inflatum* n. var.; *a*—a_1 from Salten Langsø, August 19th, 1929; *b*, b_1, *c* and *d* from Mossø, August 18th, 1929; *e*—e_1 from Hostrup Sø, June 23rd, 1925; *f*, *g* and *h* from Frederiksborg Slotssø, July 3rd, 1929. *a*, *b*, *c*, *e*, *f* and *h* front views, *d* oblique front view, a_1, b_1, e_1 and *g* vertical views. 800×.

samples containing it (in July, rare) the variety was observed between April and November at temperatures between 3.5 and 22° C., but not during the rest of the year.

Staurastrum cingulum var. *inflatum* thus seems to be periodical and eurythermic with a vegetation period during the warm half of the year. A distinct maximum was not observed.

Sociology. The variety was found in the following associations:

Hostrup Sø.

June 23rd, 1925: *Api fl*-association with *Coo Nä* as subdominant (the variety rare); see Table II.

Salten Langsø.

Aug. 19th, 1929: *Ste As-Mio aer ma*-association with *Api fl, Mel am, Mio fl ma* and *Mio pu* as subdominants (the variety very rare); see Table II.

Mossø.

Aug. 18th, 1929: *Api fl-Mio aer ma*-association with *Mio vi* and *Ste As* as subdominants (the variety very rare); see Table II.

Frederiksborg Slotssø.

June 11th, 1929: net plankton, *Ana in*-association with *Mio fl* + *Mio fl ma* as subdominants (see Table IV; the variety very rare). Nannoplankton, *Sce arm*-association (see Table IV; the variety very rare).

July 3rd, — : *Ana fl*-association with *Mio fl* and *Os Ag* as subdominants (the variety rare).

Aug. 21st—24th, 1929: *Os Ag*-association with *Sce arm* as subdominant (the variety very rare).

Sep. 2nd—6th, 1929: *Os Ag*-association with *Mio pu ra* as subdominant (the variety very rare).

Oct. 3rd—5th, 1929: *Os Ag*-association with *Mio pu ra* as subdominant (the variety very rare).

Oct. 22nd—25th, 1929: *Mio pu ra*-association with *Os Ag* and *Sce arm* as subdominants (the variety very rare).

Nov. 21st, 1929: *Sce arm*-association with *Mio pu ra* as subdominant (the variety very rare).

Apr. 22nd—25th, 1930: *Ste Ha*-association with *Sce arm* as subdominant (the variety very rare).

May 10th—13th, 1930: *Sce arm*-association with *Ste Ha* as subdominant (the variety very rare).

June 16th, 1930: *Sce arm*-association (the variety very rare).

In the great majority of cases *Staurastrum cingulum* var. *inflatum* occurs in associations of blue-green algae (*Aphanizomenon*, *Anabaena*, *Oscillatoria* and *Microcystis*), which incidentally constitute a great part of some of the following associations: diatom associations (*Stephanodiscus*) and green algae (*Scenedesmus*).

The most constant associates were *Microcystis flos aquae*, *Microcystis holsatica*, *Coelosphaerium Nägelianum* and *Dictyosphaerium pulchellum*, which were found in 100 % of the number (13) of samples that contained *Staurastrum cingulum* var. *inflatum*. *Microcystis aeruginosa* var. *major* and *Pediastrum Boryanum* (with varieties)

occurred in 92 % of the samples; *Microcystis flos aquae* var. *major*, *Anabaena flos aquae*, *Melosira granulata* and *Scenedesmus armatus* in 85 % and *Microcystis minutissima*, *Microcystis pulverea* var. *racemiformis*, *Microcystis viridis*, *Oscillatoria Agardhii*, *Stephanodiscus Hantzschii*, *Oocystis Marssonii* and *Pediastrum duplex* in 77 % of the samples.

It appears from this that *Staurastrum cingulum* var. *inflatum* sociologically is a most characteristic Desmid. Very few other *Staurastrum* species occur in associations that are pre-eminently dominated by blue-green algae, and the constant associates of which in the great majority of cases are also blue-green algae, particularly *Microcystis* species.

Staurastrum cingulum var. *inflatum* thus seems to be a decidedly characteristic form of eutrophic waters. As a *Staurastrum* species it is moreover interesting by the fact that it is able to thrive in contaminated water.

Ecology. All the lakes containing *Staurastrum cingulum* var. *inflatum* are decidedly eutrophic, only the rather lime-deficient Hostrup Sø of the mixotrophic phase. As will appear from Tables I and III the compound quotient for Mossø was $\frac{35}{6} = 5.8$ on August 18th, 1929, for Salten Langsø $\frac{35}{4} = 8.75$ on August 19th, 1929 and for Hostrup Sø $\frac{32}{6} = 5.3$ on June 23rd, 1925. In accord with the fact that its water is somewhat contaminated the small lake Frederiksborg Slotssø reached slightly higher values of the compound quotient: on June 11th, 1929 $\frac{24}{3} = 8$ for the net plankton and $\frac{36}{4} = 9$ for the nannoplankton; on September 23rd, 1929 $\frac{40}{4} = 10$.

A few other data of the ecology of *Staurastrum cingulum* var. *inflatum* are: pH 7.6—9.4, CaO about 12—71 mg/l, consumption of $KMnO_4$ 39—53 mg/l, contents of PO_4-P 0.005—1.5 mg/l, NH_3-N 0.1—1.25 mg/l, NO_3-N 0—0.25 mg/l and Fe 0.01 mg/l.

Staurastrum cingulum G. M. Smith var. **obesum** G. M. Smith.

1922, p. 354, t. 12, figs. 3—5.—*Fig. nostra* 39 *a*—a_1, *b*—b_1 and *d*.

The Danish individuals had ± highly divergent arms tipped with 4 or 5 small spines. Vertical view triangular with sides of cell body slightly concave and always denticulate; cell body with an intramarginal row of granula bigemina (= the verrucae in front view); from each of these pairs of granules a row of granules always proceeds at right angles to the sides of the cell body. Length with processes 39—59 μ, without processes 31.5—37 μ, breadth with processes 59—71 μ, breadth of isthmus 8.5—10 μ.

Distribution: In the plankton of Tissø and Hampen Sø.

Systematics. In G. M. Smith's specimens the verrucae were apparently reduced into simple, acute granules. Among the observed, verrucate individuals of var. *obesum* in the plankton of Tissø, however, I found a single specimen (*Fig. nostra* 39 *c*) that should undoubtedly be referred to var. *tortum* G. M. Smith; its breadth with processes was 54—58 μ.

Periodicity. *Staurastrum cingulum* var. *obesum* was found only on September 23rd, 1929 in Hampen Sø and on July 13th, 1929 in Tissø. In both samples it was very rare.

Sociology. The variety was found in a *Ta fe-Ana Ha ma*-association and an *Asi fo - Mel gr*-association, respectively. The qualitative composition of these two associations is given in Table II.

Ecology. Hampen Sø is a clear, oligotrophic lake; Tissø a large, typically eutrophic lake. Their phytoplankton quotients are found in Table I; the compound quotients in Hampen Sø reached the values $\frac{6}{13} = 0.5$, $\frac{2}{5} = 0.4$, $\frac{5}{10} = 0.5$ and $\frac{9}{13} = 0.7$, in Tissø the values $\frac{40}{8} = 5$ and $\frac{26}{6} = 4.3$. In Hampen Sø a few analyses for lime gave the values 4—6.5, in Tissø 107.8—125.6 mg CaO per litre.

Staurastrum cingulum var. *obesum* was found at the pH values 7.2 and 8.4, contents of PO_4-P 0 mg/l, NH_3-N 0.1 mg/l, and NO_3-N 0 mg/l.

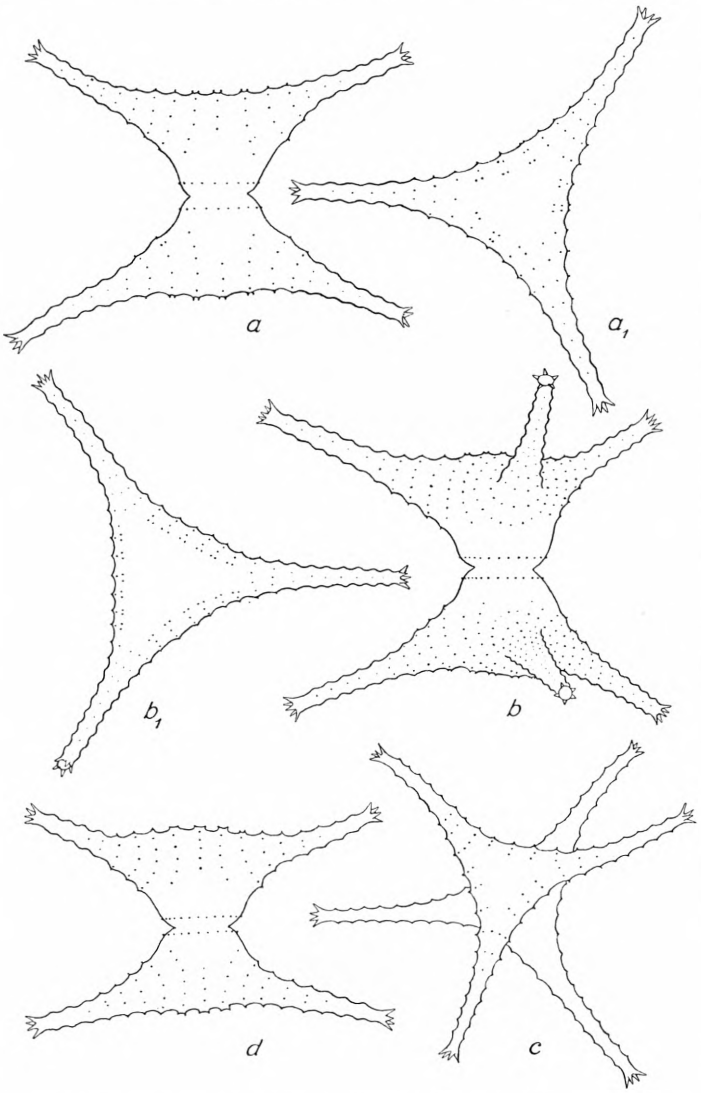


Fig. 39. *Staurastrum cingulum* G. M. Smith; *a*, a_1, *b* and b_1 var. *obesum* G. M. Smith from Tissø, July 13th, 1929; *d* var. *obesum* from Hampen Sø, September 23rd, 1929; *c* var. *tortum* G. M. Smith from Tissø, July 13th, 1929. *a*, *b* and *d* front views, a_1, b_1 and *c* vertical views. 800×.

Staurastrum Smithii

Teiling

var. **verrucosum** nov. var.

Fig. nostra 40.

Diagnosis. A typo in hoc modo differt: corpus semicellulae a vertice visum 4 verrucis parvis instructum, duabus in utroque latere. Processus 8—14 denticulis et 3 vel 4 spinis terminalibus ordinatus. Longitudo cum processibus 62—68 μ, sine processibus 13—16 μ, latitudo cum processibus 54—70 μ, latitudo isthmi 6—7.5 μ, crassitudo 8—9 μ.

Hab. In Tissø, Selandia, Dania, libere natans.

In 1921 GRÖNBLAD (p. 61, t. 5, figs. 31—32) described a *Staurastrum tetracerum* var. *biverruciferum*. This variety differs from *Staurastrum tetracerum* by the same characteristics as var. *verrucosum* from *Staurastrum Smithii* (G. M. SMITH 1924, p. 98,

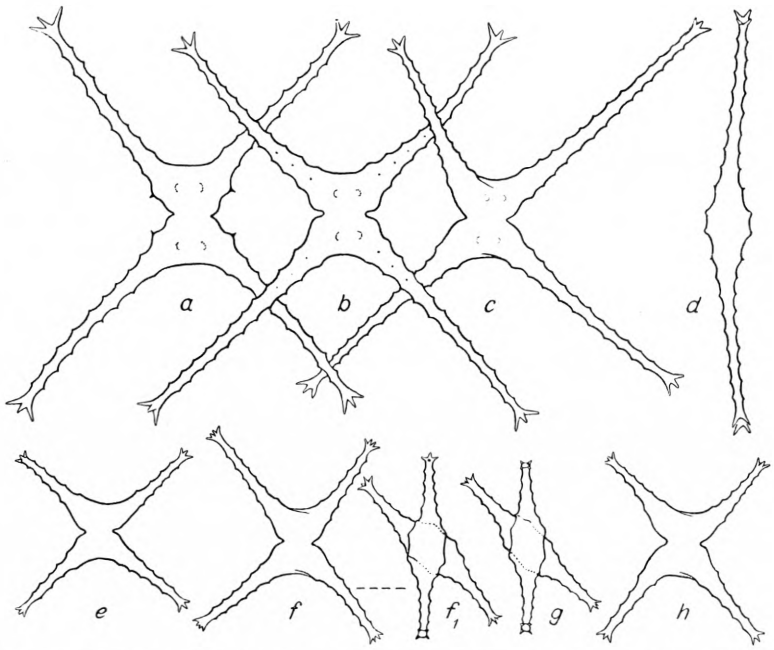


Fig. 40. *a—d*: *Staurastrum Smithii* Teiling var. *verrucosum* n. var. from Tissø, August 10th, 1927, and July 13th, 1929; *a—c* front views, *d* vertical view, 800×. *e—h*: *Staurastrum tetracerum* Ralfs var. *biverruciferum* Grönbl. from Blankeborg I, August 18th, 1928; *e*, *f* and *h* front views, f_1 and *g* vertical views, 800×.

t. 76, figs. 17—20, sub nomine *St. contortum* Smith). The last mentioned species has up to 10 denticulations per process, var. *verrucosum* 8—14 denticulations. *Staurastrum tetracerum* and its varieties have only 4—6 denticulations per process.

The variety was found in the plankton of Tissø on August 10th, 1927 and on July 13th, 1929; in both samples it was rare.

It occurred in a *Ly li*-association with *Os Ag* as subdominant and in an *Asi fo-Mel gr*-association; the qualitative composition of these two associations appears from Table II.

Tissø is a typically eutrophic, large lake, the phytoplankton quotients of which are found in Table I; on the two dates mentioned the compound quotient was $\frac{40}{8} = 5$ and $\frac{26}{6} = 4.3$. A few chemical data also appear from Table I; it remains to be added that *Staurastrum Smithii* var. *verrucosum* was found at the pH values 8.4 and 8.8, CaO 125.6 mg/l, PO_4-P 0 mg/l, NO_3-N 0 mg/l.

Staurastrum crenulatum Näg. var. **britannicum** Messik.

Messikommer 1927, p. 107, t. 5, fig. 8, t. 6, figs. 1—2; 1943, t. 15, fig. 3.

Forma 1 (*Fig. nostra* 41). Corpus semicellulae a fronte visum subfusiforme, margine ventrali convexiore quam est margo dorsalis, cum processibus crassis, brevibus, parallelis, 2—3-undulatis, terminaliter cum 4 spinis; a basi visum cum 6 spinis isthmalibus; a vertice visum triangulatum, cum lateribus laevibus atque cum 2 verrucis intra quodque latus. Quisque processus in parte proximali et dorsali cum 2 verrucis plusminusve longis et angustis, ceterum cum 1—3, saepe 2 seriebus con-

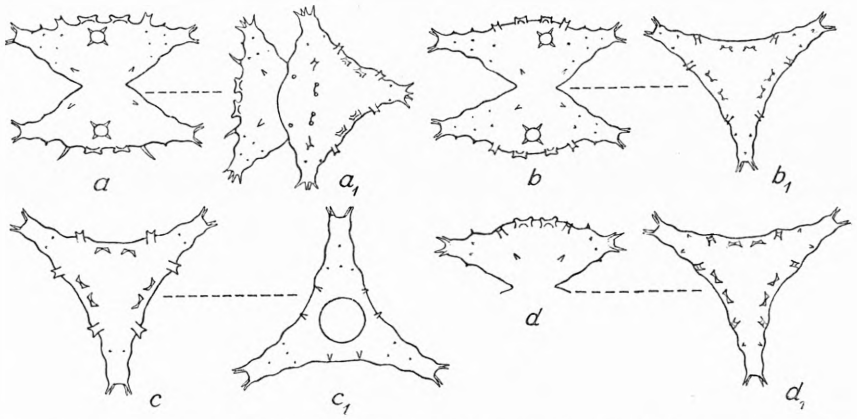


Fig. 41. *Staurastrum crenulatum* Näg. var. *britannicum* Messik. forma 1 from Blankeborg I, August 6th, 1929 (*c* and c_1, however, from August 18th, 1928). *a*, *b* and *d* front views, a_1 oblique front view, b_1, *c* and d_1 vertical views, c_1 basal view. 800×.

centricis granulorum parvorum. Longitudo cellularum 22—23 μ, latitudo 30—35 μ, latitudo isthmi 6.5—7 μ.

Hab. In Blankeborg I, Fionia, Dania, libere natans.

Forma 2 (*Fig. nostra* 42). Corpus semicellulae a fronte visum plusminusve cyathiforme cum apice plano vel convexo, raro subfusiforme, margine ventrali convexiore quam est margo dorsalis, cum processibus subangustis, brevibus vel mediocris, 4-undulatis, convergentibus vel parallelis, terminaliter cum 3 spinis; a basi visum cum 2—4 granulis isthmalibus et parvis apud basem cujusque processus; a vertice visum triangulatum, cum 2 (4) verrucis parvis vel 2 spinis intra quodque latus laeve. Quisque processus, cum 3—4 seriebus concentricis granulorum parvorum, raro inarmatus. Longitudo cellularum 16—23.5 μ, latitudo 24.5—40 μ, latitudo isthmi 4—5.5 μ.

Hab. in Blankeborg I, Fionia, Klitsø prope Højsande, Læsø, Vedsted Sø, Jutlandia meridionali, Furesø, Selandia, Dania, libere natans.

Systematics. To begin with I believed in the specimens of *Fig. nostra* 42 *d* to have found a new variety of *Staurastrum oxyacantha* Archer; however, renewed

examinations proved that in certain individuals the spines were replaced by granula bigemina (Fig. 42 *a*) and in others (Fig. 42 *b*) there were both spines and granula bigemina on one and the same semicell.

In forma 1 the two characteristic, long verrucae at the basis of each arm may be transformed into long spines, as demonstrated in Fig. 41 *a*; but in this form I have never observed that the verrucae on the apex of the cell body may be transformed into spines.

The specimens from Blankeborg I (*forma* 2) measured 19—23.5 μ in length, 24.5—40 μ in breadth, 5—5.5 μ in breadth of isthmus.

The specimens from Vedsted Sø, Furesø and dune lake at Højsande measured 16—18 μ in length, 25—30 μ in breadth, 4—5 μ in breadth of isthmus.

So it seems that within the form cycle of *Staurastrum crenulatum* var. *britannicum* there exist at any rate 2 forms (possibly 3, including the one from Vedsted Sø, Furesø and dune lake at Højsande). However, I do not venture to characterize them as named forms because they are difficult to delimit and because intermediary forms apparently exist. Such a form was described and pictured by GRÖNBLAD (1920, p. 60, t. 3, figs. 62—63); this individual is quite like *forma* 2, but it has 6 isthmal spines like *forma* 1. From the material of the Sunda Expedition KRIEGER (1932, t. 19, fig. 10) further depicts a form that is quite like *forma* 1 though the 6 isthmal spines are lacking. However, it is not totally excluded that KRIEGER's form is identical with *forma* 1 because the isthmal spines are difficult to see if the contents of the cell are preserved. Compare also MESSIKOMMER 1928, p. 210, t. 9, fig. 18 (*Staurastrum oxyacantha*).

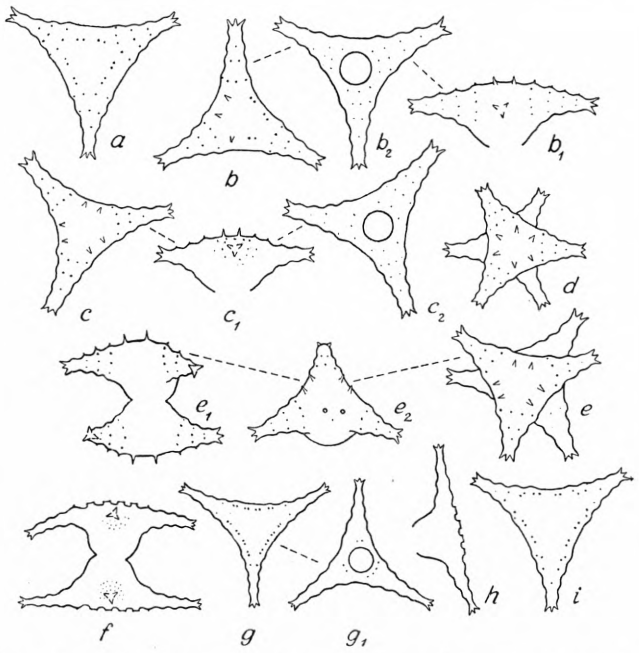


Fig. 42. *Staurastrum crenulatum* Näg. var. *britannicum* Messik. forma 2; *a*, *b*, b_1, b_2, *c*, c_1, c_2, *d*, *e*, e_1, e_2 and *i* from Blankeborg I, August 18th, 1928 (*i*, however, from August 6th, 1929); *f*, *g*, g_1 and *h* from Vedsted Sø, July 27th, 1926. *a*, *b*, *c*, *d*, *e*, *g*, and *i* vertical views, e_2 oblique vertical view, b_1, c_1, e_1, *f* and *h* front views, b_2, c_2 and g_1 basal views. All figures 800× with exception of *d*, 430×.

Periodicity. *Staurastrum crenulatum* var. *britannicum* was found only in June, July and August (temp. 16.5—19.5° C.) as will appear from the section on sociology. It was very rare in all samples.

Sociology. The species was found in the following associations:

Dune lake at Højsande.

June 30th, 1925: *Tsp Ny*-association with *El ge* as subdominant.

Vedsted Sø.

July 27th, 1926: *Ce hi si*-association with *Ana te lo* as subdominant.
— 2nd, 1927: *Ce hi si*-association.

Blankeborg I.

Aug. 16th, 1925: *Per Vo*-association with *Ce hi* as subdominant.
— 15th, 1926: *Ce hi*-association.
— 17th, 1927: net plankton, *Ce hi*-association; nannoplankton, *Cos pu - El ge bi*-association.
— 18th, 1928: net plankton, *Din di*-association; nannoplankton, association of an indeterminable green alga with *Mio mi* as subdominant.
— 6th, 1929: *Din di*-association.
June 10th, 1930: association of an indeterminable *Chrysophycea* with *Cyc co* and *Teë mi* as subdominants.

Furesø.

Aug. 21st, 1943: *Mel gr an*-association.

The qualitative compositions of all these associations appear from Tables II and IV. The species accordingly occurred in dinophycean associations of *Ceratium* and *Peridinium*, chlorophycean associations of *Elakatothrix*, *Tetraspora* and the Desmid *Cosmarium*, chrysophycean association of *Dinobryon* and a diatom association of *Melosira*.

The most constant associates were *Ceratium hirundinella*, which occurred in 100 % of the number (12) of samples that contained *Staurastrum crenulatum* var. *britannicum*; *Oocystis Marssonii* occurred in 92 % of the samples, *Botryococcus Braunii*, *Pediastrum Boryanum*, *Dinobryon divergens*, *Asterionella formosa* and *Glenodinium munusculum* in 75 % of the samples.

Ecology. The dune lake at Højsande and Vedsted Sø are oligotrophic, oligohumic lakelets, Blankeborg I a slightly eutrophic turf pit of the mixotrophic phase while Furesø is a large, moderately eutrophic, oligohumic lake. The plankton quotients of these localities appear from Tables I and III. This very limited material seems to show that *Staurastrum crenulatum* var. *britannicum* is confined to oligotrophic—mesotrophic—moderately eutrophic waters, both small bodies of water and larger lakes.

Staurastrum crenulatum var. *britannicum* was found at pH values between 5.7 and 8.2, consumption of $KMnO_4$ 49—81 mg/l, NO_3-N 0 mg/l.

Furesø, however, is clear (14 mg/l of $KMnO_4$ observed), and the two oligotrophic lakes are even clearer. In Furesø the content of lime according to Brønsted

& WESENBERG-LUND (1912, p. 453) varied between 54.5 and 65.4 mg/l of CaO, and in Blankeborg I a couple of analyses gave the values 82.3 and 91 mg/l (NYGAARD 1938, p. 671, 673). Both Vedsted Sø and particularly the dune lake at Højsande are undoubtedly much poorer in lime.

Staurastrum curvatum West f. **brevispina** n. f.

Fig. nostra 43.

A typo spinis brevioribus differt. Longitudo cellularum sine aculeis 19—28 μ, cum aculeis 30—44 μ, latitudo sine aculeis 23—28.5 μ, cum aculeis 35—42 μ, latitudo isthmi 6—8 μ, longitudo aculeorum 6.5—12.5 μ.

Hab. In Klitsø prope Højsande, Læsø, Dania, libere natans.

The form is characterized by its short spines, those of the main species being 20—23 μ long according to WEST and CARTER (Monograph V, 1923, p. 19, t. 130, figs. 15—16). Moreover the spines of f. *brevispina* often seem to form right, sometimes even obtuse angles *inter se* (the cell seen in front view) whereas the spines apparently always form acute angles in the main species.

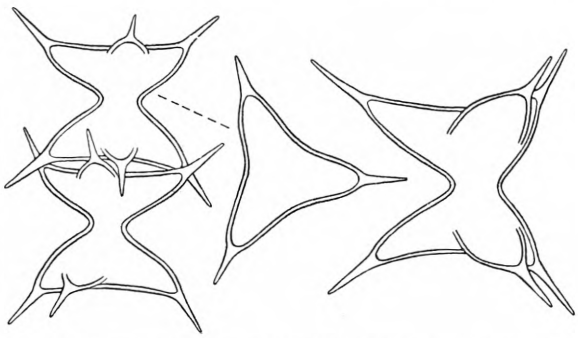


Fig. 43. *Staurastrum curvatum* West f. *brevispina* n. f. from Klitsø at Højsande, June 30th, 1925. 800×.

Only a few specimens of the form were observed in the oligotrophic dune-lake at Højsande on June 30th, 1925. As will be seen from Table III the compound quotient on this date was $\frac{15}{18} = 0.8$. The form occurred in a *Tsp Ny*-association with *El ge* as subdominant; its qualitative composition is given in Table IV.

Staurastrum cuspidatum Breb. var. **acuminatum** n. var.

Fig. nostra 44.

Diagnosis. A typo semicellulis (a fronte visis) latioribus, subfusiformibus vel raro subtriangularibus differt. Longitudo sine aculeis 28—34 μ, cum aculeis 29—51 μ, latitudo sine aculeis 30—39 μ, cum aculeis 58—73.5 μ, latitudo isthmi 5.5—6.5 μ, aculei recti, leviter incurvati vel recurvati, 14—24 μ longi sunt.

Hab. In Hampen Sø, Jutlandia, Dania, libere natans.

Systematics. In *Staurastrum cuspidatum* and its varieties (see WEST and CARTER, Monograph V, 1923, pp. 23—26, tt. 132—133) it is a distinctive feature that

the length without spines is a little greater than the breadth without spines. This is also true of G. M. Smith's North American specimens (1924, p. 74, t. 68, figs. 27—34) in spite of the fact that their spines are 15—20 μ long and at times somewhat divergent. In var. *acuminatum* nov. var., however, the length without spines is always smaller

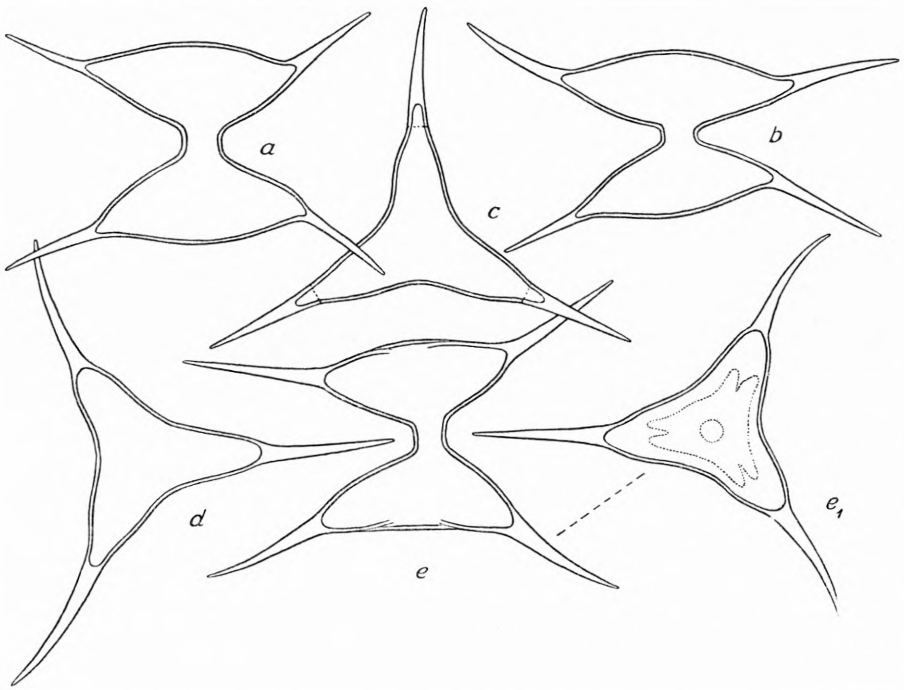


Fig. 44. *Staurastrum cuspidatum* Breb. var. *acuminatum* n. var. from Hampen Sø, *a* from May 17th, 1929, *b* and *c* from August 15th, 1927, *d*, *e* and e_1 from June 23rd, 1929; *a*, *b* and *e* front views, *c*, *d* and e_1 vertical views. 800×.

than the breadth without spines so that the semicells are often fusiform in front view. Consequently, the variety should therefore perhaps be considered a new species.

From *Staurastrum curvatum* West var. *elongatum* G. M. Smith (1924, p. 73, t. 69, figs. 10—15) var. *acuminatum* differs by its semicells, which in front view show a convex shape of sides and apex while var. *elongatum* Smith in front view has triangular semicells with nearly straight sides and a level or concave apex.

Periodicity. In Hampen Sø the variety was only found in May, June, August and September (there are no plankton samples from July) as will appear from the following section; it was very rare in these months except in June when it was not infrequent.

Sociology. *Staurastrum cuspidatum* var. *acuminatum* occurred in the following associations, the qualitative composition of which appears from Table II.

Aug. 15th, 1927: *Ta fe as - Ma ca*-association with *Ar cr lo* and *Coo Nä* as subdominants (variety very rare).
May 17th, 1929: *Per bi - Ta fe as*-association with *Per Wi* as subdominant (variety very rare).
June 23rd, — : *Ura am*-association (variety not infrequent).
Sep. 23rd, — : *Ta fe as - Ana Ha ma*-association with *Ce hi* as subdominant (variety very rare).

The variety thus occurred in associations distinguished by diatoms (*Tabellaria*), *Chrysophyceae* (*Mallomonas, Uroglena*), *Dinophyceae* (*Peridinium*) and blue-green algae (*Anabaena*).

The associates that occurred in all the 4 samples that contained *Staurastrum cuspidatum* var. *acuminatum* were: *Eudorina elegans* forma, *Arthrodesmus triangularis, Staurastrum granulosum, Xanthidium antilopaeum, Ceratium hirundinella, Peridinium cinctum* and *Coelosphaerium Nägelianum*.

Ecology. As will appear from Table I Hampen Sø is an (approximately) oligotrophic lake; on the 4 dates mentioned under the sociology the compound quotient was $\frac{6}{13} = 0.5$, $\frac{2}{5} = 0.4$, $\frac{5}{10} = 0.5$ and $\frac{9}{13} = 0.7$, respectively. pH varied between 5.4 and 8.5, but mostly ranged about the neutral point. The water was clear, the consumption of $KMnO_4$ in 2 analyses was 17 and 21 mg/l. Moreover the water was very poor in lime, 4—6.5 mg CaO per litre; its paucity in nutrients appears from the figures: PO_4-P 0 mg/l, NH_3-N 0.05—0.1 mg/l, NO_3-N 0—0.01 mg/l (the results of an analysis from February are found in Table I).

Staurastrum danicum n. sp.

Fig. nostra 45.

Diagnosis. Cellulae mediocres, longitudine cum processibus minore quam est latitudo cum processibus, profunde constrictae, sinu valde dilatato, rectangulato vel subrectangulato, cum lateribus rectis vel subrectis. Corpus semicellulae a fronte visum late coniforme cum lateribus fere rectis vel levissimis convexis; apice plano vel vix convexo, seriebus spinarum vel granulorum bigeminorum instructo. Anguli semicellulae sensim in processus divergentes et 5—8-denticulatos producti; processus terminaliter 4 spinis satis robustis et basaliter seriebus concentricis granulorum parvorum et acutorum ordinati. Corpus semicellulae a vertice visum triangulum, lateribus leviter concavis raro rectis; membrana intra margines undique serie 4 (raro 2—3) spinarum (terminalium interdum robustiorum quam mediarum) vel 4 (raro 2—3) granulorum bigeminorum ornata. Longitudo sine processibus 23—27 μ, cum processibus 37—41 μ, latitudo cum processibus 48—63 μ, latitudo isthmi 7—9 μ, spinae apicales ad 3 μ longae.

Hab. In Holmsø, Jutlandia occidentali, Dania, libere natans.

Systematics. This species is characterized by the rectangular or subrectangular sinus, the lateral sides of the body being straight or slightly convex. The 3 corners of the body taper into the straight and highly divergent arms. The apical ornamentation is variable, either exclusively with 4 spines in each intramarginal

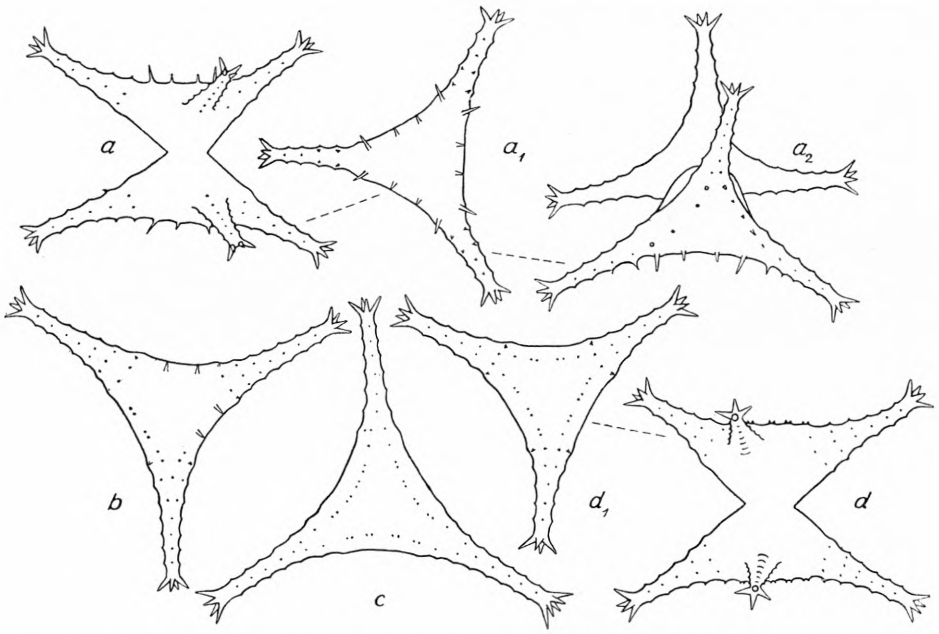


Fig. 45. *Staurastrum danicum* n. sp. from Holmsø, June 26th, 1930; *a* and *d* front views, a_1, *b*, *c* and d_1 vertical views, a_2 oblique vertical view. 800×.

series (see *Fig. nostra* 45 a_1) or with 4 granula bigemina in each series (see *Fig. nostra* 45 *c*) or with a mixture of these two characters (see *Fig. nostra* 45 *b*).

Periodicity and Sociology. The species was very rare in a *Per Wi*-association in Holmsø on June 26th, 1930 (temp. 17.5° C.).

Ecology. According to Table II this maximally 2 m. deep, clear heath lake, which is very rich in *Lobelia Dortmanna*, is oligotrophic of the acidotrophic phase. On the date mentioned the compound quotient was only $\frac{4}{10} = 0.4$, and pH was 4.6.

Staurastrum danicum n. sp. forma.

Fig. nostra 46.

Diagnosis. Hoc modo a typo differt: granula apicis semper valde reducta, aut simplicia aut trigemina; spinae terminales processuum robustiores quam in typo. Longitudo sine processibus 25—26 μ, cum processibus 44—50 μ, latitudo cum processibus 58—63 μ, latitudo isthmi 8—10 μ.

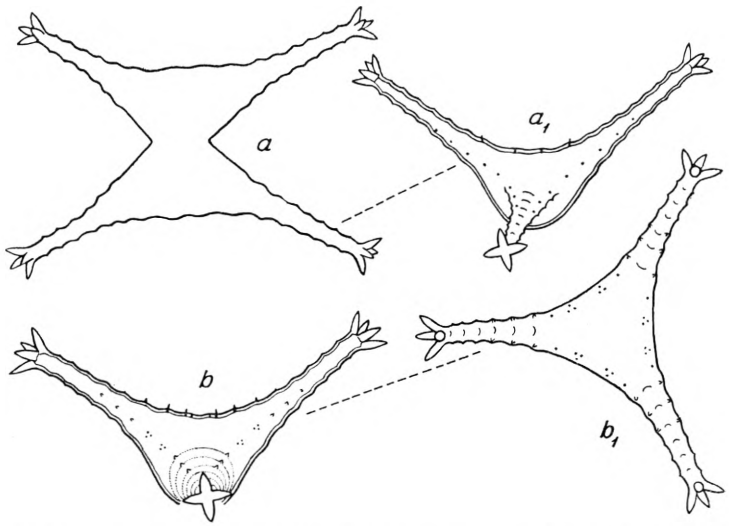


Fig. 46. *Staurastrum danicum* n. sp. forma from turf pit S of Store Jenshøj, June 25th, 1930; *a* front view, b_1 vertical view, a_1 and *b* oblique front views. 800×.

Hab. In stagno turfaceo prope Store Jenshøj, Jutlandia occidentali, Dania, libere natans.

Systematics. The strong endspines and the simple or trigeminate granules show that the individuals are hardly quite identical with those from Holmsø.

Periodicity and Sociology. The form was rare in an *Aso su-Oe It*-association on June 25th, 1930 (temp. 18° C.).

Ecology. The large, shallow turf pit S. of Store Jenshøj at Oxbøl is distinctly oligotrophic of the dystrophic phase. The compound quotient for the date mentioned was as low as $\frac{1}{10} = 0.1$, and pH was 4.0.

Staurastrum dejectum Breb. f. **mediocris** n. f.

Fig. nostra 47.

Diagnosis. A typo aculeis mediocribus differt. Longitudo cellularum sine aculeis 17—20 μ, cum aculeis 21—26 μ, latitudo sine acu-

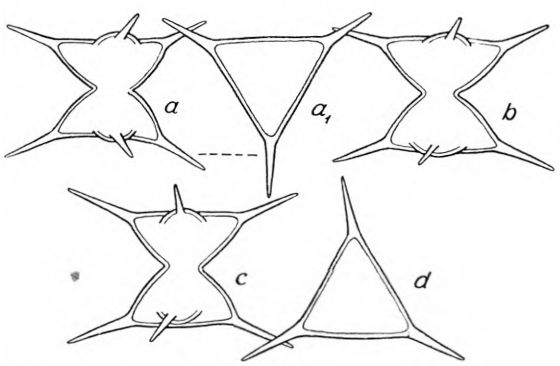


Fig. 47. *Staurastrum dejectum* Breb. f. *mediocris* n. f. from turf pit NE of Skaansø, July 4th, 1938; *a*, *b* and *c* front views, a_1 and *d* vertical views. 800×.

leis 16—19 μ, cum aculeis 30—38 μ, latitudo isthmi 5.5—6.5 μ, longitudo aculeorum 7.5—12 (saepe 9—11) μ.

Hab. In Bøndernes Mose II, Selandia, et stagno turfaceo prope Skaansø, Jutlandia boreali, Dania, libere natans.

f. **longispina** n. f.

Fig. nostra 48.

Diagnosis. A typo aculeis longis differt. Longitudo cellularum sine aculeis 19—20 μ, cum aculeis 25—31.5 μ, latitudo sine aculeis 18.5—22 μ, cum aculeis 39—53 μ, latitudo isthmi 6—6.5 μ, longitudo aculeorum 13—18 μ.

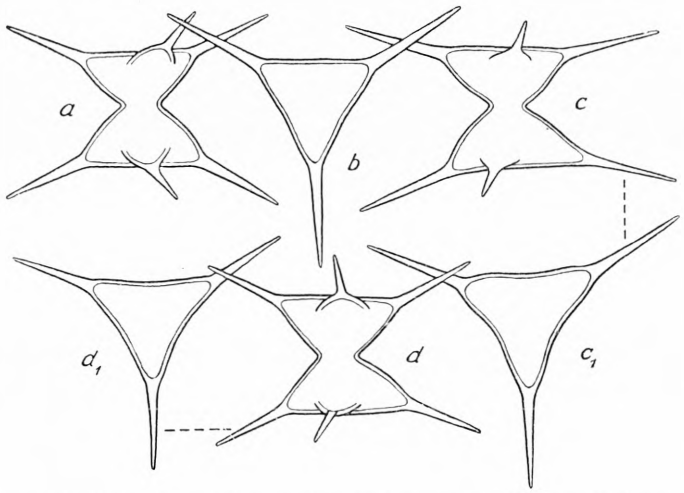


Fig. 48. *Staurastrum dejectum* Breb. f. *longispina* n. f. from Holmsø, June 26th, 1930; *a*, *c* and *d* front views, *b*, c_1 and d_1 vertical views. 800×.

Hab. In Holmsø, Grovsø et stagno turfaceo prope Store Jenshøj, omnes apud Oxbøl, Jutlandia occidentali, et in "Cirkelsø", Jutlandia meridionali, Dania, libere natans.

Systematics. West and Carter (Monograph V, 1923, p. 7, t. 129, figs. 9—12) have included different forms under the species *Staurastrum dejectum*; the measurements given are: longitudo sine aculeis 18—27 μ, latitudo sine aculeis 17—27 μ, latitudo isthmi 5—8 μ, longitudo aculeorum 3—8 μ. It must be supposed that these measurements refer to the main species (fig. 9), which accordingly must have short spines.

In Holmsø the comparatively rich material showed the length of the spines, according to 24 measurings, varied between 13 and 18 μ. The few individuals occurring in the turf pit at Store Jenshøj, which is situated in the same tract as the following locality, had a length of spines of 13—16 μ, while the spines of the Grovsø individuals had a length of 14—16 μ.

In Bøndernes Mose II and the turf pit NE. of Skaansø the spines of nearly all the individuals measured had a length of 9—11 μ (30 measurings).

I have found no transition stages between the spine lengths of these two form groups, and so I consider it proper to distinguish between them taxonomically. No doubt they are 2 local races, but ecologically they seem to present no very great difference.

Also Borge mentions a form (1930, p. 43, t. 2, fig. 39) in which the longitudo sine spinis = latitudo sine spinis = 21—22 μ; longitudo cum spinis 28—29 μ, latitudo

cum spinis 43 μ; latitudo isthmi 7 μ. This form is much like fig. 10 in WEST and CARTER (*loc. cit.*); its length of spines is not stated, but—as far as can be judged from the drawing fig. 39—the individual should be referred to f. *mediocris*.

Periodicity. In the said three localities near Oxbøl *Staurastrum dejectum* f. *longispina* was found in small quantities in June 1920 (temp. 17.5—18° C.) as will appear from the following section. F. *mediocris* occurred rather abundantly in the turf pit NE. of Skaansø in July 1938 (temp. 18.5° C.). In the regularly (fortnightly) examined Bøndernes Mose II it was observed in very small quantities throughout the period June 18th—October 29th, 1929 (temp. 8—24° C.); it did not reappear until June 16th, 1930 (temp. 21° C.).

Staurastrum dejectum f. *mediocris* thus seems to be periodical and meso- to polythermic (temp. 8—24° C.) with its vegetation period within the time of June—October.

Sociology. *Staurastrum dejectum* occurred in the following associations:

The Sphagnum bog "Cirkelsø".

July 23rd, 1926: *Sta po di*-association (f. *longispina* very rare).

Holmsø.

June 26th, 1930: *Per Wi*-association (f. *longispina* rare); see Table IV.

Turf pit at Store Jenshøj.

June 25th, 1930: *Aso su - Oe It*-association (f. *longispina* very rare); see Table IV.

Grovsø.

June 27th, 1930: *Ar in ex*-association (f. *longispina* very rare).

Turf pit NE. of Skaansø.

July 4th, 1938: *Sta br*-association with *Sta de me* as subdominant (rather common); see Table IV

Bøndernes Mose II.

June 18th, 1929
July 5th, —
— 17th, —
Aug. 12th, —
— 22nd, —
Sep. 7th, —
— 22nd, — } *Crym ov cu*-association (f. *mediocris* very rare).

Oct. 9th, — : *Crym ov cu*-association with *Tra vo* as subdominant (f. *mediocris* very rare).

— 29th, — : *Tra vo*-association (f. *mediocris* very rare).

June 16th, 1930: *Crym ov cu*-association with *Tra vo* as subdominant (f. *mediocris* very rare); see Table IV.

In other words *Staurastrum dejectum* was found in associations dominated by *Dinophyceae* (*Peridinium*), *Chlorophyceae* (*Asterococcus*, *Oedogonium*, the desmids *Staurastrum* and *Arthrodesmus*), *Cryptophyceae* (*Cryptomonas*) and *Euglenineae* (*Trachelomonas*).

The most constant associates were *Arthrodesmus incus* var. *extensus* f. *minor* and *Cryptomonas ovata* var. *curvata*, which occurred in 73 % and 80 %, respectively, of the number (15) of samples that contained *Staurastrum dejectum*.

Ecology. As will appear partly from Table III and p. 15, all the 6 ponds mentioned are oligotrophic, the clear Holmsø of the acidotrophic phase (compound quotient $\frac{4}{10} = 0.4$), the other 5 of the dystrophic phase, Grovsø (compound quotient $\frac{7}{18} = 0.4$), turf pit at Store Jenshøj (compound quotient $\frac{1}{10} = 0.1$), turf pit NE. of Skaansø (compound quotient $\frac{3}{10} = 0.3$), Bøndernes Mose II (compound quotient $\frac{5}{8} = 0.6$), and the Sphagnum bog "Cirkelsø" (compound quotient $\frac{2}{5} = 0.4$).

Accordingly, *Staurastrum dejectum* mostly occurred in highly acid, brown turf pits in raised bogs.

A few ecological data of the species: pH 4.0—5.4, CaO 2.9 mg/l, consumption of $KMnO_4$ 114—202 mg/l (in Holmsø hardly above 15 mg/l), contents of PO_4-P 0 mg/l, NH_3-N 0.9—1.25 mg/l, NO_3-N 0 mg/l, and Fe 0.25 mg/l.

Staurastrum Iversenii n. sp.

Fig. nostra 49.

Diagnosis. Cellulae mediocres, quarum longitudo cum processibus multo minor quam latitudo cum processibus est, profunde constrictae, sinu aperto, sed intime acuto. Corpus semicellulae a fronte visum late obconicum cum lateralibus valde undulatis (interdum cum spinis in tumoribus); apice plano 4 verrucis parvis instructo, quarum duae mediae robustiores quam sunt duae extremae; sub illis verrucis corpus cum serie horizontali 4 granulorum robustorum et acutorum, interdum cum duabus seriebus inter se parallelis et horizontalibus, 4 granula pro serie. Anguli

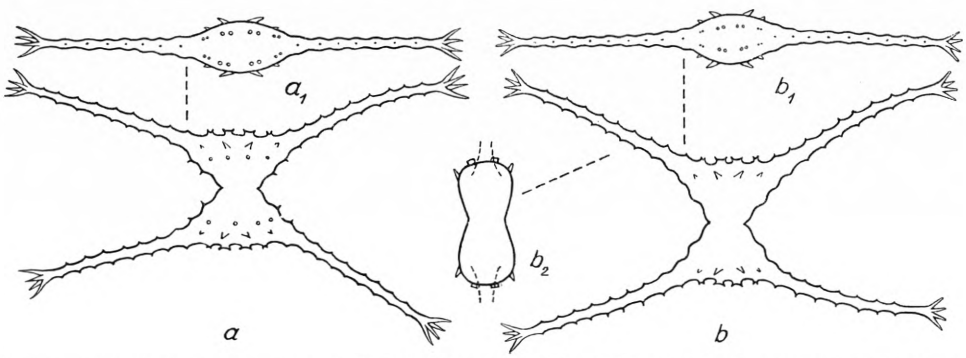


Fig. 49. *Staurastrum Iversenii* n. sp. from Vedsted Sø, July 27th, 1926; *a* and *b* front views, a_1 and b_1 vertical views, b_2 lateral view. 800×.

superiores corporis in processus longos, aculeatos vel 7—9-denticulatos, valde divergentes, leviter recurvatos, raro rectos producti. Corpus semicellulae a latere visum obconicum vel subobovatum, apice convexo; a vertice visum bibrachiale, fusiforme, duabus seriebus verrucarum intramarginalium (4 pro serie) et 4 granulis margi-

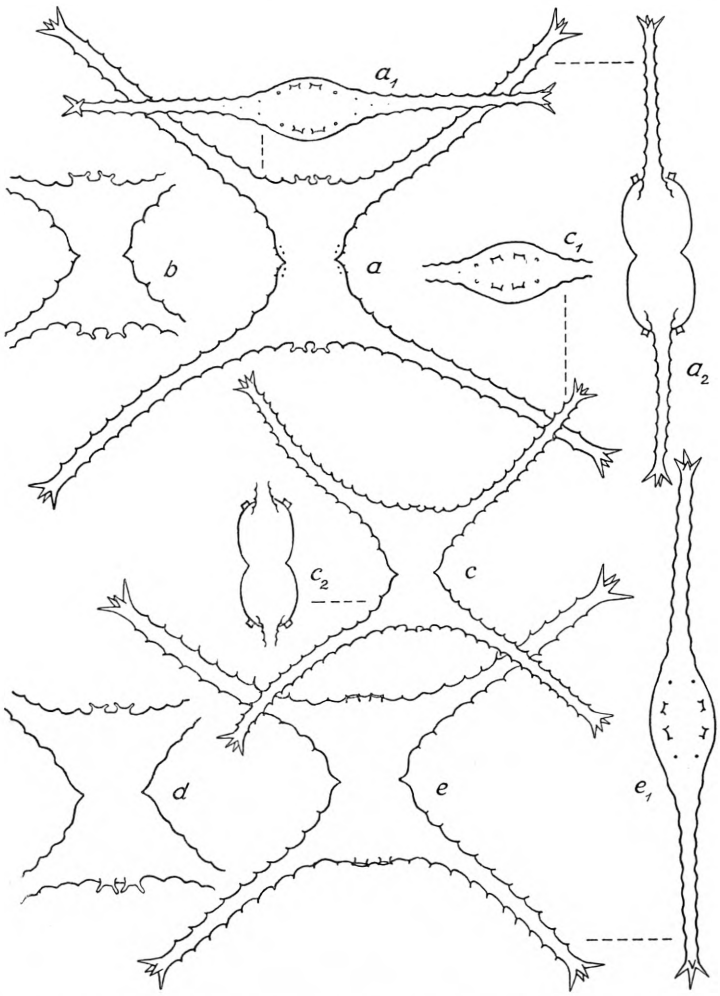


Fig. 50. *Staurastrum Bullardii* G. M. Smith var. *alandicum* Teiling; *a*, a_1, a_2, *b*, *c*, c_1 and c_2 from Slaaen Sø, September 4th, 1929; *d*, *e* and e_1 from Tissø, August 10th, 1927. *a*, *b*, *c*, *d* and *e* front views, a_1, c_1 and e_1 vertical views, a_2 and c_2 lateral views. All figures 800× except *c*, c_1 and c_2 560×.

nalibus, robustis et acutis ordinatum; duae mediae verrucae robustiores sunt quam duae extremae et retroflexae a medio lateris corporis. Uterque angulus in processum longum, tenuem, 7—9-undulatum, rectum productus, terminaliter cum 4 spinis satis longis, introflexis vel rectis. Longitudo sine processibus 20—21.5 μ, cum processibus

38—47 μ, latitudo 70—76 μ, crassitudo 9 μ, latitudo isthmi 5.5—6 μ, longitudo spinarum terminalium 3—4.5 μ.

Hab. In Vedsted Sø, Jutlandia meridionali, Dania, libere natans.

Systematics. The species bears some resemblance to *Staurastrum Bullardii* G. M. Smith var. *alandicum* Teiling (1942, p. 213, figs. 6—7), which is also biradiate and, in lateral view, has the same shape of body (the Danish specimens of Teiling's variety, however, in lateral view show an elliptical-cylindrical corpus with hemispherical ends, and besides this these individuals have incurved processes, see *Fig. nostra* 50. However, the processes of *Staurastrum Iversenii* are slightly recurved (or straight) while the processes of var. *alandicum* are slightly incurved (or straight), and the one or two horizontal series of pointed granules on the frontal part of corpus, which are found in *Staurastrum Iversenii*, are totally absent in *Staurastrum Bullardii* var. *alandicum*. Moreover the new species in all dimensions is smaller than var. *alandicum*.

Periodicity and Sociology. On the periodicity nothing can be stated but the fact that the species was found in the plankton of Vedsted Sø (collected by Dr. Johs. Iversen) on July 27th, 1926 and July 2nd, 1927.

Both samples, in which it was very rare, were dominated by *Ceratium hirundinella* f. *silesiacum* associations, the qualitative composition of which appears from Table II.

Ecology. Vedsted Sø at Haderslev is a clear, acid (ph 5.7—6.0), small but 15 m deep lake, approximately oligotrophic. Johs. Iversen has given an account of its vegetation of hydrophytes (1929, p. 312). Table I shows that the compound quotient was $\frac{9}{9} = 1$ and $\frac{3}{6} = 0.5$ on the two dates mentioned.

Staurastrum longiradiatum West forma.

Fig. nostra 51.

Diagnosis. Differs from the original specimens in having the divergent processes tipped with 4 end-spines and in showing a deeper crenation or dentation of the upper than of the lower margin of processes. Length without processes 32 μ, with processes 42 μ, breadth with processes 82 μ, breadth of isthmus 7 μ.

Hab. In Blankeborg I, Funen, Denmark, limnetic.

Systematics. The found individual comes nearest to West's original specimens from North America (1896, p. 267, t. 17, fig. 23), which measured 25—30 μ in length, 67—77 μ in breadth (incl. processes), the breadth of the isthmus being 6—7.5 μ. G. Morgan Smith's North American individuals, which together with the Australian specimens from the Yan Yean Reservoir should be regarded as a special variety, are much larger, measuring 41—49 μ in length, 73—108 μ in breadth (incl. processes)

and 8.5—10 μ in breadth of the isthmus; but their special characteristic is the more elongate cell-body (G. M. Smith 1924, p. 90, t. 74, figs. 5—11). The species seems to be rare; the Wests do not mention it in their Monograph of the British Desmidiaceae.

Periodicity. The species occurred in only one of the 95 examined samples from Blankeborg I, which were collected regularly between 1926 and 1930. In spite of renewed examinations of further plankton material from August 17th, 1927 (temp. 19.5° C.) I only managed to find the individual pictured here.

Sociology. The said specimen was found in a *Ce hi*-association with *Din di* as subdominant. In Table IV we find the qualitative composition of this association.

Ecology. Blankeborg I is a slightly eutrophic turf-pit of the mixotrophic phase (see Table III, which i. a. gives its phytoplankton quotients). On August 17th, 1927 the compound quotient of the net plankton was $\frac{21}{12} = 1.75$. On the same day pH was 7.6, and on August 5th of the same year the consumption of $KMnO_4$ was 81 mg/l. According to 2 analyses the calcium content of Blankeborg I was 82.3 and 91 mg CaO per litre.

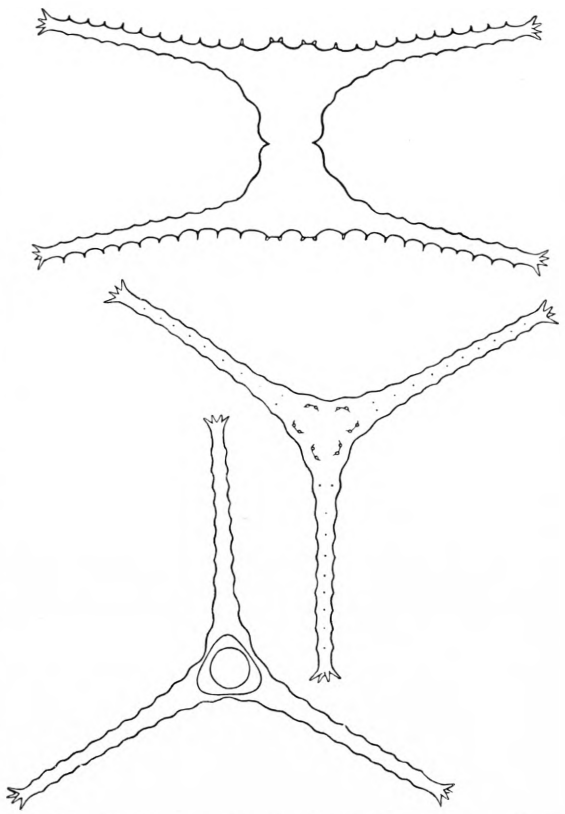


Fig. 51. *Staurastrum longiradiatum* West forma from Blankeborg I, August 17th, 1927. 800×.

Staurastrum pendulum n. sp.

Fig. nostra 52.

Diagnosis. Cellulae mediocres, quarum longitudo cum processibus minor quam latitudo cum processibus est, profunde constrictae; sinus extrorsum valde ampliatus, apice acutiore vel fere sublineari; isthmus angustus. Semicellulae inter se contortae, a fronte visae corpore obsemicirculari, apice concavo vel subplano sunt. Anguli semicellulae in processus trispinosos, sublongos, leviter vel distincte attenuatos producti sunt cum margine superiore dentatiore quam margo inferior et margines laterales; processus divergentes extremitatibus recurvatis. A vertice visae semicellulae triangulares, marginibus corporis rectis vel concavis, undulatis vel den-

tatis, quisque margo seriebus duabus spinarum simplicium parvarum ordinatus; in medio apice 6 puncta minutissima in sexangulo regulari ordinata. Longitudo cellularum sine processibus 20—21 μ, cum processibus 30—32 μ, latitudo cum processibus 42—54 μ, latitudo isthmi 6—6.5 μ.

Hab. In Hostrup Sø, Jutlandia meridionali, Dania, libere natans.

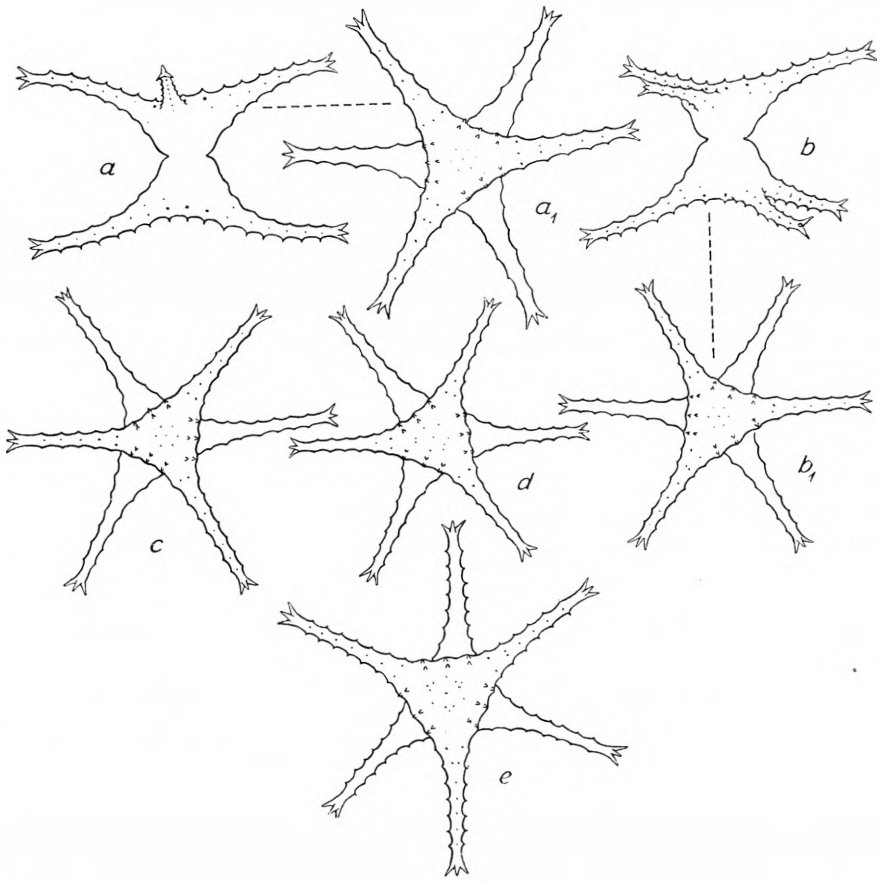


Fig. 52. *Staurastrum pendulum* n. sp. from Hostrup Sø, July 24th, 1926 (*a*, a_1, *b*, b_1), and July 5th, 1927 (*c*, *d* and *e*). *a*—*b* front views, the other figures vertical views. 800×.

Systematics. The species is characterized by its divergent, near the point recurvate processes and by the two parallel series of 3 spines at each side on the apex of the semicell; the semicells were always twisted at the isthmus. Every second of the tiny points in the hexagon in the middle of apex may be trebled (see Fig. 52e).

The species is closely related to *Staurastrum saltator* Grønblad (1938, p. 56, fig. 2, 4) which has the same habit and size, but quite another apical ornamentation (only 6 intramarginal spines in all) and show smooth, convex sides of the semicell

body in vertical view; further the arms of *Staurastrum saltator* are tipped with 4 minute spines.

Periodicity. The species was found in Hostrup Sø on July 24th, 1926, July 5th, 1927 and May 21st, 1929. In these samples it was rare with the exception of the 1927 sample where it was not infrequent.

Sociology. *Staurastrum pendulum* occurred in the following associations, the qualitative composition of which appears from Table II:

July 24th, 1926: *Fra cr*-association with *Trb tae* as subdominant (the species very rare).
— 5th, 1927: *Coo Nä*-association (the species not infrequent).
May 21st, 1929: *Trb tae*-association (the species rare).

The species thus occurred in a diatomaceous (*Fragilaria*), a myxophycean (*Coelosphaerium*) and a xanthophycean association (*Tribonema*).

Ecology. The about 7 m deep Hostrup Sø is a eutrophic lake of the mixotrophic phase. As shown in Table I the compound quotient reached the values 6.4—3.3—4.5—4.5. The lake is lime-deficient, according to Johs. Iversen (1929, p. 315) with 12 mg CaO per litre; the same author mentions that pH varied between 6.4 and 8.8. On July 24th, 1926 pH was 7.3 and the consumption of $KMnO_4$ 50 mg/l.

Staurastrum pingue Teiling var. **tridentata** n. var.

Fig. nostra 53.

Diagnosis. Hoc modo a typo differt: apex semicellulae 3 spinis et 3 granulis bigeminis sic instructus, ut ad quodque latus semicellulae (a vertice visae) una spina et unum granulum bigeminum sint. Processus cum 3—5 spinis terminalibus. Corpus semicellulae ad basem cum granulis nonnullis. Semicellulae binae semper inter se contortae. Longitudo cellularum sine processibus 29—31.5 μ, cum processibus 40—63 μ, latitudo cum processibus 56—75 μ, latitudo isthmi 7 μ.

Hab. In Nors Sø, Jutlandia septentrionali, Dania, libere natans.

Systematics. This variety is conspicuous by the fact that every second *granulum bigeminum* of the apex is developed into a rather strong spine and by its constantly twisted semicells. In quite a few individuals (cp. Fig. 53d) there are but 2 spines but 4 *granula bigemina* on the apex; in such an individual, however, the proximal spines of the processus situated immediately beside the reduced spine are more developed than in the other two processes.

Periodicity. The variety was found only in the summer months: on July 18th, 1925 (temp. 21° C.) when it was common in the plankton of Nors Sø, and on August 18th, 1939 (*legit* Sig. Olsen) when it was very rare.

Sociology. The variety was found in the following 2 associations:

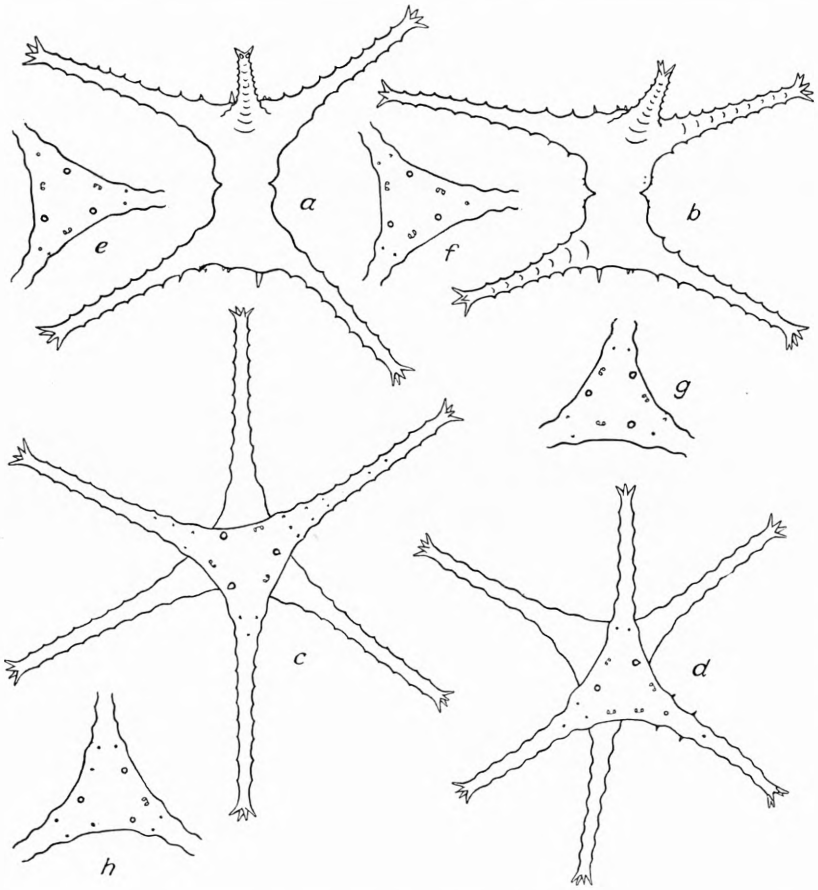


Fig. 53. *Staurastrum pingue* Teiling var. *tridentata* n. var. from Nors Sø, July 18th, 1925. *a*—*b* front views, *c*—*d* vertical views, *e*—*h* 4 other semicells in vertical view showing the apical ornamentation. 800×.

July 18th, 1925: *Ana ci - Mio fl ma*-association with *Ce hi* and *Eut gl* and the variety in question as subdominants.

Aug. 18th, 1939: *Mio fl ma - Ana fl*-association with *Coo Kü* as subdominant (the variety very rare).

The qualitative composition of these two associations appears from Table II.

Like the main species (Teiling 1942, p. 66, figs. 3—5) *Staurastrum pingue* var. *tridentata* thus occurs in associations characterized by blue-green algae (*Microcystis* and *Anabaena*).

Ecology. Nors Sø is a slightly eutrophic ("mesotrophic") lake situated on a substratum of cretaceous deposits (see Table I). The calcium content, however, is not very great, according to 2 analyses only 43.1—52 mg CaO per litre. The measured pH values range between 8 and 8.3. On July 18th, 1925 the compound quotient reached the value $\frac{27}{12} = 2.25$, on August 18th, 1939 the value $\frac{24}{12} = 2.0$.

Staurastrum polymorphum Breb. var. **divergens** nov. var.

Fig. nostra 54.

Diagnosis. Cellulae parvae, tam longae quam latae vel longitudine (cum processibus) paulo minores quam latitudine (cum processibus), profunde constrictae; sinus apertus, saepe rectangulus, cum apice acuto vel subacuto. Semicellulae a fronte

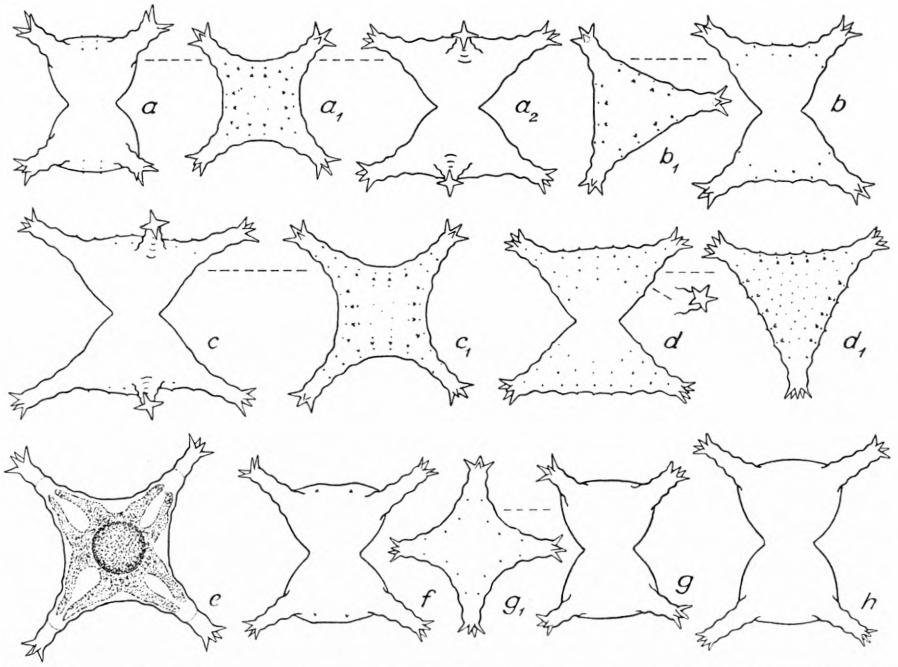


Fig. 54. *Staurastrum polymorphum* Breb. var. *divergens* n. var.; *a*, a_1, a_2, *b*, b_1, *c* and c_1 from turf pit NE of Skaansø, July 4th, 1938; *d* and d_1 from Bøllemosen, September 5th, 1946; *e* and *f* from a dystrophic turf pit near Eggesø, Salling, July 4th, 1938; *g* and g_1 from "Cirkelsø," July 23rd, 1926; *h* from Bøndernes Mose II, September 7th, 1929. *a*, a_2, *b*, *c*, *d*, *f*, *g* and *h* front views, a_1, b_1, c_1, d_1, *e* and g_1 vertical views. 800×.

visae cum corpore cyathiformi vel subconiformi; margo dorsalis subconvexus, raro fere planus, levis vel tenuiter denticulatus, margines laterales leviter ad valde convexi; angulis superioribus in processus breves interdum brevissimos, bi- ad quadrinodulosos, valde divergentes productis, terminaliter cum 4, raro 5 spinis satis robustis et brevibus. Semicellulae a vertice visae quadriradiatae, interdum triradiatae; latera corporis concava, raro recta, leves vel tenuiter denticulata; apex corporis levis vel cum uno serie 8 punctulorum vel cum 2—4 seriebus marginalibus inter se parallelis granulorum minimorum et acutorum, interdum valde reductorum, serie interiore validissima; granulis etiam in series breves et radiatae ordinatis; apex medius levis vel punctulatus. Longitudo sine processibus 22.5—28 μ, cum processibus 28—36 μ, distantia inter apices processuum proximorum 25—38 μ, inter apices processuum oppositorum 33—48 μ, latitudo isthmi 7—8.5 μ.

Hab. In Bøndernes Mose I et II, Bøllemosen, Selandia; in palude turfacea prope Skaansø et palude turfacea prope Hvidemose, Jutlandia septentrionali; in palude turfacea prope Krusaa Dam et "Cirkelsø" prope Søgaard, Jutlandia meridionali, libere natans.

Systematics. According to W. and G. S. West's Monograph (vol. 5, 1923, p. 125, t. 142, fig. 24, t. 143, figs. 1—3) *Staurastrum polymorphum* has converging or parallel processes with 3—4 very poorly developed terminal spines; further the apex of the semicells is distinctly convex. Messikommer (1943, p. 37, t. 15, fig. 2) also depicts *Staurastrum polymorphum* with parallel arms and highly convex apex; the drawing of the same author in the 1927 paper (t. 2, fig. 27) shows a specimen with slightly convex apex and very slightly divergent arms.

In my opinion it will therefore be legitimate to consider the individuals the arms of which are highly divergent and provided with 4—5 comparatively strong terminal spines as a special variety: var. *divergens* nov. var. The *Staurastrum polymorphum* depicted by A. Donat (1926a, t. 3, fig. 6) is most likely identical with this new variety. His individuals evidently have a smooth apex like the individual pictured in *figura nostra* 54 *h*. Compare also Grönblad 1921, p. 58, t. 5, figs. 17—20.

Periodicity. The variety seems to be periodical and to be a typical summer form: it was seen only during the period May—October at temperatures between 7° and 21.5° C. In the former of the two regularly examined turf pits Bøndernes Mose I and II it was observed only in June—August, in the latter, however, in May—October. It never occurred in the winter samples from these two localities. As will appear from the following section the variety may be rare or not infrequent in June—July, but is always very rare in May and August—October.

Sociology. The variety occurred in the following associations:

Bøndernes Mose I.

June 28th, 1929: *Crym ov cu*-association (the variety very rare), see Table IV.
Aug. 22nd, — : *Crym ov cu*-association with *Gos se* as subdominant (the variety very rare).

Bøndernes Mose II.

Aug. 22nd, 1929: *Crym ov cu*-association (the variety very rare), see Table IV.
Sep. 7th, — : *Tra vo*-association with *Crym ov cu* as subdominant (the variety very rare).
— 22nd, — : *Crym ov cu*-association (the variety very rare).
Oct. 29th, — : *Tra vo*-association (the variety very rare).
May 24th, 1930: *Crym ov cu*-association with *Tra vo* as subdominant (the variety very rare).
June 16th, — : *Crym ov cu*-association with *Tra vo* as subdominant (the variety rare), see Table IV.

Large turf pit 1 km W. of Hvidemose, Salling.

July 4th, 1938: *Sta al*-association (the variety rare).

Nearly overgrown turf pit NE. of Skaansø.

July 4th, 1938: *Sta br*-association with *Sta de lo* as subdominant (the variety rare), see Table IV.

Sphagnum bog ("Cirkelsø") S. of Søgaard Sø, North Sleswick.

July 23rd, 1926: *Sta po di*-association (the variety not infrequent).
July 16th, 1939: *Crym ov*-association (the variety very rare).

Large turf pit N. of the Krusaa Dam.

Aug. 18th, 1945: *Crym ov cu*-association (the variety very rare).

The variety thus occurs in cryptophycean (*Cryptomonas*), euglenine (*Trachelomonas*) and chlorophycean (*Staurastrum*) associations.

The most constant associate was *Cryptomonas ovata* (var. *curvata*), which occurred in 85 % of the samples (13) containing *Staurastrum polymorphum* var. *divergens*.

Ecology. All the localities mentioned are oligotrophic turf pits of the dystrophic phase. In all of them submerse *Sphagnum* species were growing (*Sphagnum cuspidatum*). Concerning the plankton quotients see Table III.

Of *Staurastrum polymorphum* A. Donat says, "Allgemein verbreitet und häufig in Sphagneten. Kosmopolit und Ubiquist." This characteristic possibly applies to the main species; according to the description given above var. *divergens* cannot at all be a ubiquist: on the contrary it seems to be confined to *Sphagnum* bogs with their brown, very acid water (pH < 4.5). The ecological demands of the variety are indicated by the following values: pH 3.7—4.4, CaO 2.9—5 mg/l, consumption of $KMnO_4$ 114—205 mg/l, PO_4-P 0 mg/l, NH_3-N 0.9—1.25 mg/l, NO_3-N 0 mg/l, Fe 0.25 mg/l.

Staurastrum Pseudosebaldii Wille var. **simplicius** West.

Monograph of the British Desmidiaceae, Vol. 5, 1923, t. 149, fig. 13.—*Fig. nostra* 55.

Systematics. This variety occurred in small quantities in the plankton from Holmsø, SW-Jutland, on June 26th, 1930. The individuals were 33 μ long, 35—42 μ broad; the breadth of isthmus was 8.5—9.5 μ. The spines were replaced by tiny sticks or even *granula bigemina*. The processes were tipped with 4, rarely 5 spines.

The association that contained the variety was dominated by *Peridinium Willei*; its qualitative composition appears from Table IV.

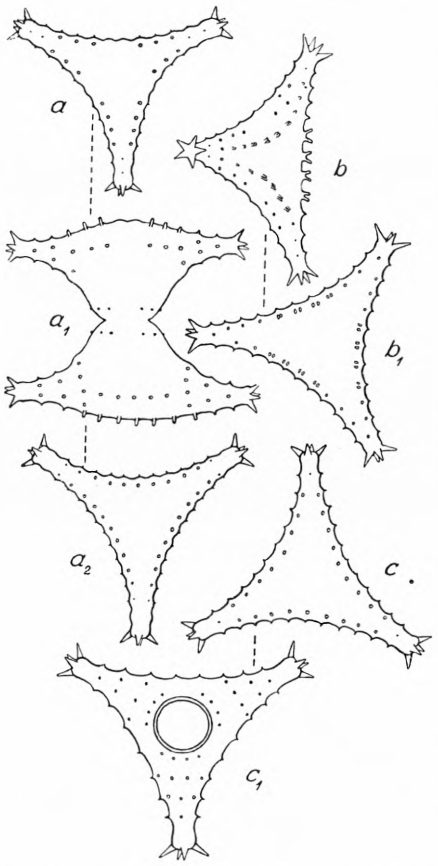


Fig. 55. *Staurastrum pseudosebaldii* Wille var. *simplicius* West from Holmsø, June 26th, 1930. *a*, a_2, b_1, and *c* vertical views, a_1 front view, c_1 basal view, *b* oblique vertical view. 800×.

Holmsø is an oligotrophic heath lake with colourless water; pH was 4.6. Its phytoplankton quotients are listed in Table III; let it be enough to mention that in the sample containing var. *simplicius* the compound quotient was $\frac{4}{10} = 0.4$.

Staurastrum Sebaldii Reinsch var. **ornatum** Nordstedt f. **planctonica** Teiling.

Teiling 1947, p. 227, fig. 20; Grönblad 1942, p. 42, figs. 1—3 and Messikommer 1942, p. 174, fig. 1, *sub nomine Staurastrum Manfeldtii* Delp. var. *planctonicum* Lütkemüller.—*Fig. nostra* 56.

Diagnosis. Cells fairly large, breadth with processes somewhat greater (1—1.5 times) than length with processes. Sinus widely open and acute-angled. Semicells cyathiform, rarely cylindrical at the base, dorsal margin flattened or slightly convex. Apex of semicell body with one row of tri- or bidentate verrucae along the margin, each edge with 2—4 verrucae. Angles of semicells continued into rather long, distinctly divergent processes with 7—8 (rarely 9) deep undulations, the dorsal ones being more prominent and stronger denticulate than the ventral ones; the processes are straight or slightly bent, gradually extending from the body and tipped with 3 (rarely 4) divergent spines. Lateral margins of the body furnished with 3 subbrachial and 3 isthmal granula groups or often only the latter. Vertical view triangular; the corpus smooth, sometimes finely punctate, with straight to very slightly concave, smooth, very rarely subundulate sides; processes in vertical view faintly undulate. Cells 41—50 μ long without processes, 60—83 μ long with processes, breadth with processes 72—96 μ, breadth of isthmus 9.5—13 μ.

Hab. In Lunz Untersee in Austria and Mossø, Furesø, Tissø, Esrom Sø, Salten Langsø and Vedsted Sø in Denmark, pelagic.

Systematics. Originally I intended to term the Danish individuals *Staurastrum planctonicum* Teil. f. *duplex* n. f. or *Staurastrum Sebaldii* var. *ornatum* f. *duplex* n. f. because Teiling (1947, p. 227) claims that "if Lütkemüller's taxonomical estimation is to be maintained, the biverrucate[1] form must be called *St. Sebaldii* var. *ornatum*

[1] Emphasized by me.

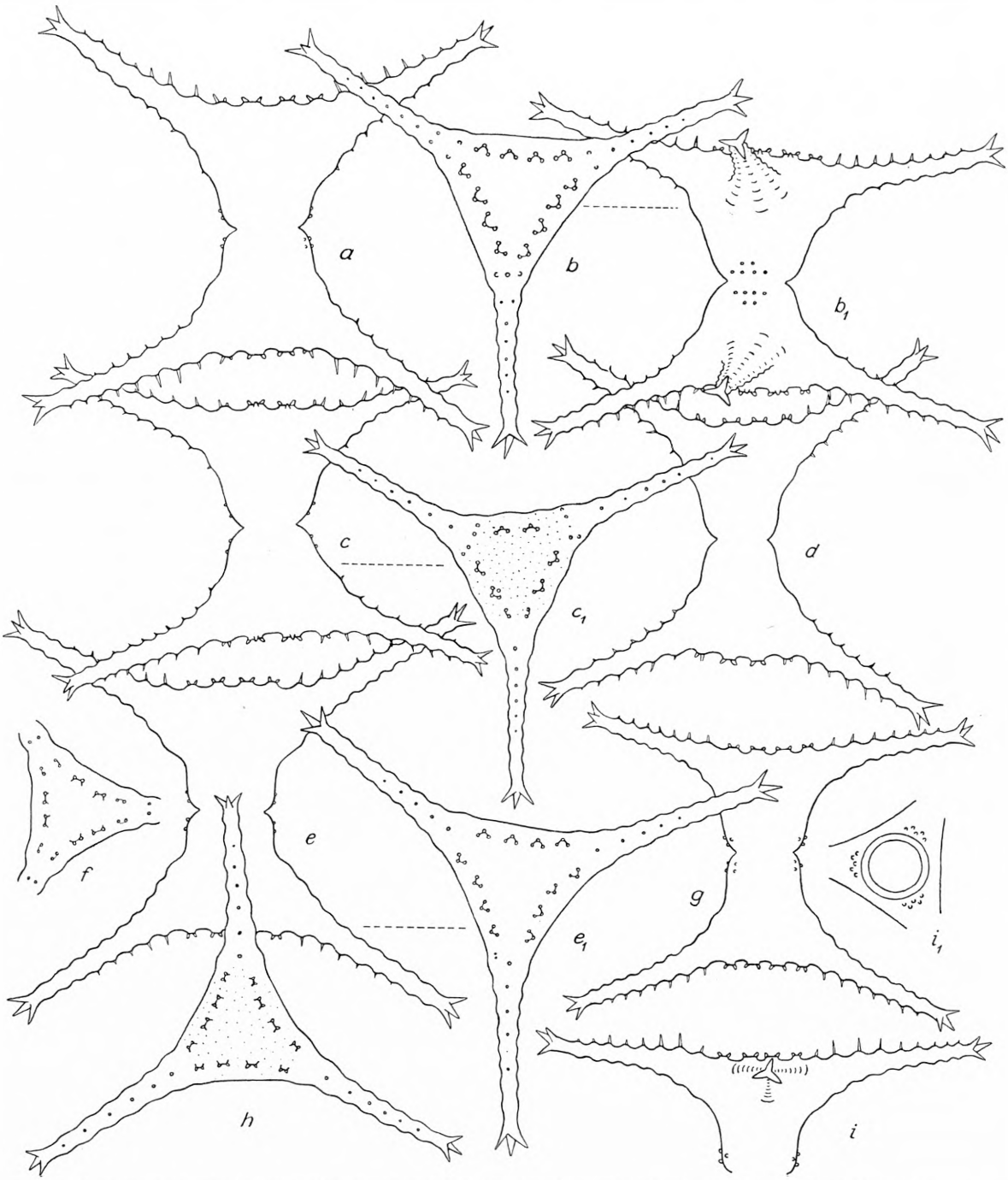


Fig. 56. *Staurastrum Sebaldii* Reinsch var. *ornatum* Nordst. f. *planctonica* Teiling; *a*, *b* and b_1 from Mossø, August 18th, 1929; *c*, c_1 and *d* from Tissø, August 10th, 1927; *e*, e_1 and *f* from Furesø, August 21st, 1943; *g*, *h*, *i* and i_1 from Vedsted Sø, July 2nd, 1927. *a*, b_1, *c*, *d*, *e*, *g* and *i* front views, *b*, c_1, e_1 and *f* vertical views, i_1 basal view. 800×.

forma *planctonica*." However, about fig. 20, which in the explanation of the text-figures is called *Staurastrum Sebaldii* var. *ornatum* f. *planctonica*, TEILING says "Most specimens (Fig. 20) possessed a cup-shaped semicell and a marginal row of four[1] forked spines (verrucae) towards the processes turning into simple spines." So there can be no doubt that LÜTKEMÜLLER's *Staurastrum Manfeldtii* var. *planctonicum*, pictured by TEILING and MESSIKOMMER in the places cited above, is identical with the Danish specimens; I have therefore defined this form and extended the diagnosis of *Staurastrum Sebaldii* var. *ornatum* f. *planctonica* to include individuals with 4 verrucae also. As will appear from the said drawing by MESSIKOMMER and my Fig. 56 c_1 and *f* the apical verrucae adjoining the processes may be more or less reduced. *Staurastrum planctonicum* Teiling (1946, p. 77, figs. 30, 32) comes very near to this pelagic form of *Staurastrum Sebaldii* var. *ornatum*.

The dimensions of the delineated Danish specimens are: length without processes 43—50.5 μ, with processes 60—83 μ, breadth with processes 75—96 μ, breadth of isthmus 9.5—12.5 μ.

In Esrom Sø all specimens were biverrucate and always furnished with isthmal granulation, but the corpus was mostly cylindrical near the isthmus, rarely cyathiform as in a slender individual of 50 μ in length. Otherwise the length was only 37—40 μ, with processes 57—61 μ; the breadth 78 μ with processes and the breadth of the isthmus 9 μ; 4 terminal spines.

Periodicity. In this country the species was found only in the months of July, August and September at temperatures between 16.5 and 20° C., but the material is too small for an establishment of its period of vegetation. The species always occurred in small quantities; besides in the plankton samples given in Table II it was found on July 29th and September 1st, 1947 in Furesø and on September 8th, 1929 in Esrom Sø.

Sociology. The species occurred in the following associations:

Esrom Sø.

Sep. 8th, 1929: *Ce hi*-association (the species rare).

Mossø.

Aug. 18th, 1929: *Api fl - Mio aer ma*-association with *Mio vi* and *Ste As* as subdominants (the species very rare).

Tissø.

Aug. 10th, 1927: *Ly li*-association with *Os Ag* as subdominant (the species very rare).

Furesø.

Aug. 7th, 1932: *Ana fl - Asi fo*-association (the species very rare).

Aug. 21st, 1943: *Mel gr an*-association (the species very rare).

Sep. 1st, 1946 (July 29th and Sep. 1st, 1947): *Ce hi*-association (the species very rare).

[1] Emphasised by me.

Vedsted Sø.

July 27th, 1926 and July 2nd, 1927: *Ce hi*-association (f. *silesiacum*, the species rare).

In other words the species occurs in associations characterised by blue-green algae (*Microcystis*, *Lyngbya*, *Oscillatoria*, *Aphanizomenon* and *Anabaena*), diatoms (*Melosira*, *Stephanodiscus* and *Asterionella*) and by *Ceratium hirundinella*.

The most constant associates were *Ceratium hirundinella*, which occurred in 100 per cent. of the samples (8 in all) that contained *Staurastrum Sebaldii* var. *ornatum* f. *planctonica*, *Dictyosphaerium pulchellum* in 88 per cent. of the samples and the following species in 75 per cent. of the samples: *Botryococcus Braunii*, *Microcystis flos aquae*, *Peridinium cinctum*, *Sphaerocystis Schroeteri* and *Stephanodiscus Astraea*.

Ecology. All the Danish lakes mentioned are eutrophic with the exception of the approximately oligotrophic Vedsted Sø. Tables I and II, respectively, show the plankton quotients and the qualitative composition of the plankton. Suffice it to mention here that the compound quotient for Vedsted Sø was $\frac{3}{6} = 0.5$ and $\frac{9}{9} = 1$, for the moderately eutrophic Furesø $\frac{42}{12} = 3.5$, $\frac{28}{8} = 3.5$ and $\frac{22}{5} = 4.4$, and for the 3 distinctly eutrophic lakes Tissø $\frac{40}{8} = 5$, Mossø $\frac{35}{6} = 5.8$ and Esrom Sø $\frac{19}{3} = 6.3$. In the last-mentioned lake the dominant *Ceratium hirundinella* reached an absolute frequency of 10 cells per ml on September 8th, 1929.

Staurastrum Sebaldii var. *ornatum* f. *planctonica* thus seems to be much more common in eutrophic than in oligotrophic lakes of this country, in which respect it is quite like *Staurastrum planctonicum* Teiling (1947, p. 222). It is questionable whether *Staurastrum Sebaldii* var. *ornatum* f. *planctonica* is so rare as supposed by Teiling (1947, p. 222).

Some data of the ecology of the form are: pH 5.7—8.8, CaO 125.6 mg/l, PO_4-P 0.005 mg/l, NH_3-N 0.2 mg/l, NO_3-N 0 mg/l. According to Brønsted and Wesenberg-Lund (1912, p. 478) Mossø contained 60 mg CaO per litre, Furesø (1912, p. 453) between 54.5 and 65.4 mg CaO per litre; no doubt Vedsted Sø is much poorer in calcium.

Staurastrum uniseriatum n. sp.

Fig. nostra 57.

Diagnosis. Cellulae mediocres, quarum latitudo cum processibus circiter 1.75 plo longior quam longitudo cum processibus est, profunde constrictae, sinu acut-angulo, mox ampliato. Corpus semicellulae a fronte visum cyathiforme vel sub-cylindricum in parte isthmali, apice vix convexo vel plano, cum 2, raro 4 verrucis parvis ordinato; anguli superiores semicellulae in processus breves vel mediocres, rectos, basaliter coniformes, 4- ad 7-undulatos, paralleles vel leviter divergentes, rarissime vix convergentes, terminaliter cum 4 spinis parvis, leniter producti; sub quoque processu granulum unum prope isthmum. Corpus semicellulae a vertice visum triangulum, lateribus glabris, leviter concavis vel rectis, undique 2, raro 4

verrucis intramarginalibus instructum; angulus unusquisque in processus 4- ad 7-undulatos productus. Longitudo sine processibus 22—29 μ, cum processibus 20—32 μ, latitudo cum processibus 33—51 μ, latitudo isthmi 5—6 μ.

Hab. In Hulsø, Store Dam, Badstue-Ødam et Frederiksborg Slotssø, Selandia; Blankeborg I, Fionia; Slaaen Sø, Jutlandia, Dania, libere natans.

Systematics. This species, which in lists of plankton is no doubt often given as *Staurastrum gracile*, is characterized by the facts that the body of semicell in vertical view has smooth sides without indications of undulations or granules and is provided

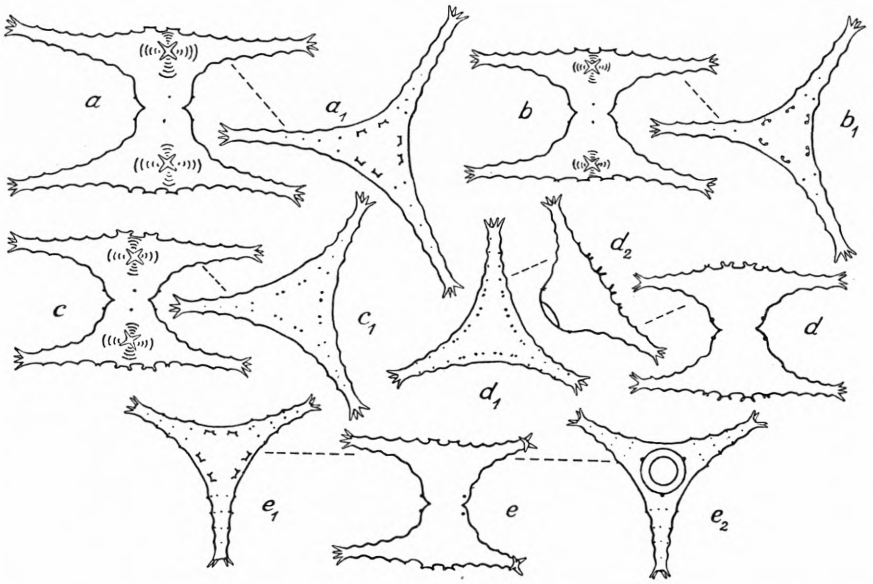


Fig. 57. *Staurastrum uniseriatum* n. sp.; a—a_1 from Slaaen Sø, September 4th, 1929; b—b_1 from Hulsø, August 8th, 1946; c—c_1 from Blankeborg I, August 16th, 1925; d, d_1 and d_2 from Eriophorum moor at Sorø, July 9th, 1947; e, e_1 and e_2 from Store Dam, August 17th, 1929. a—e front views, a_1—e_1 vertical views, d_2 oblique front view, e_2 basal view. 800×.

with but one row of 2, rarely 4 small verrucae within each lateral margin. The species is further recognizable by its parallel or slightly divergent, non-denticulate processes, under each of which there is only one granule near the isthmus.

Whether fig. 9D in G. M. Smith's paper on the phytoplankton of Wisconsin (1924, p. 88, *sub nomine Staurastrum gracile* Ralfs) is identical with *Staurastrum uniseriatum* cannot be decided because the specimen is not shown in front view; but as the number of verrucae is considerably higher than 2—4, this is hardly probable.

In Cedercreutz and Grönblad's paper on the *Desmidiaceae* of Åland (1936) the specimens pictured on t. 1, figs. 23—24 *sub nomine Staurastrum gracile formae* (possibly also 22, but not 21) are identical with *Staurastrum uniseriatum*.

In Nygaard's paper on the plankton of Lake Ohoitiel in the Key Islands and

Toba Lake on Sumatra (1926) the individuals from Lake Ohoitiel (*sub nomine Staurastrum gracile*, p. 212, t. 5, figs. 50—52) are typical specimens of *Staurastrum uniseriatum*. A re-examination of the plankton material has confirmed this view. Also figs. 74 and 76 (*sub nomine Staurastrum gracile*, from Toba Lake) of t. 7 are no doubt identical with *Staurastrum uniseriatum*, whereas fig. 75 is a special form, considerably broader in the body of semicell.

Also KRIEGER has found *Staurastrum uniseriatum* in Toba Lake and given a good illustration of it (1932, p. 200, t. 18, fig. 13) and described it as *Staurastrum gracile* var. *ornatum* Krieger. However, a *Staurastrum ornatum* Turner has previously been described, and so KRIEGER's name of variety cannot be made into a name of species.

There is hardly any doubt that also the individuals pictured by NORDSTEDT from New Zealand (1888, p. 38, t. 4, figs. 10—11) are identical with *Staurastrum uniseriatum*; this is also indicated by the measurements and the remark of the diagnosis on the slightly divergent or parallel processes.

In GRÖNBLAD's paper on the *Desmidiaceae* of Lappland (1942) an individual is described and pictured (p. 41, t. 4, fig. 22) *sub nomine Staurastrum gracile forma*(?), which should likewise be referred to *Staurastrum uniseriatum*.

"*Staurastrum gracile*" on t. 4, fig. 60 in "Dansk Planteplankton" (NYGAARD 1945) is identical with *Staurastrum uniseriatum*.

From these examples it will be seen that *Staurastrum uniseriatum* is a species with a very wide geographical distribution.

Periodicity. As will appear from the section Sociology the species was observed only during the period May—September at temperatures between 13 and 21.5° C.; it was always very rare. 4 of the 6 localities mentioned were examined regularly every fortnight for at least a whole year, and so it may be said with a rather high degree of certainty that *Staurastrum uniseriatum* is a periodical, meso- to polythermic desmid with its vegetation period in the summer half-year.

Sociology. The species was found in the following associations:

Hulsø.

Aug. 8th, 1946: *Rhi lo*-association with *Coo Nä*, *Mel am*, *Mel gr*, *Mio fl* as subdominants (the species very rare).

Slaaen Sø.

Sep. 4th, 1929: *Ce hi*-association (the species very rare).

Blankeborg I.

Aug. 16th, 1925: *Per Vo*-association with *Ce hi* and *Coo Nä* as subdominants (the species very rare).

Aug. 15th, 1926: *Ce hi*-association (the species very rare).

Badstue-Ødam.

June 6th, 1929: *Mel gr an*-association with *Sye ac an* as subdominant (the species very rare).

Aug. 23rd, 1929: *Frg cr*-association with *Ana af in te* and *Cyc st su* as subdominant (the species very rare).

Frederiksborg Slotssø.

Sep. 6th, 1929 — 17th, — — 23rd, — } *Os Ag*-association with *Mio pu ra* and *Sce arm* as subdominants (the species very rare).

May 13th, 1930: *Sce arm*-association with *Ste Ha* as subdominant (the species very rare).

Store Dam.

July 6th, 1929: *Gy ex*-association (the species very rare).

Aug. 17th, — : *Oo cr mi - Gy ex*-association (the species very rare; 20 individuals seen).

Sep. 21st, — : *Oo cr mi*-association with *Tra vo* as subdominant (the species very rare).

June 16th, 1930: *Tra vo*-association with *Gy ex* as subdominant (the species very rare).

In other words *Staurastrum uniseriatum* was found in diatomaceous (*Rhizosolenia*, *Melosira* and *Fragilaria*) and dinophycean associations (*Ceratium*, *Peridinium* and *Gymnodinium*); further in chlorophycean (*Scenedesmus*, *Oocystis*), myxophycean (*Oscillatoria*) and euglenine associations (*Trachelomonas*).

The most constant associate was *Trachelomonas volvocina*, which occurred in 78 % of the number (14) of samples that contained *Staurastrum uniseriatum*.

Ecology. All the localities mentioned are more or less eutrophic. The very clear lakelet Slaaen Sø is the least eutrophic, the compound quotient being $\frac{12}{11} = 1.1$ on September 4th, 1929; the contaminated lakelet Frederiksborg Slotssø is one of the most eutrophic of these waters, the compound quotient being $\frac{40}{4} = 10$ on September 23rd, 1929. Blankeborg I ("mesotrophic") and Hulsø are both eutrophic ponds of the mixotrophic phase; the compound quotient of the former was $\frac{16}{9} = 1.8$ on August 16th, 1925 and $\frac{22}{10} = 2.2$ on August 15th, 1926; in Hulsø it was $\frac{35}{5} = 7$ on August 8th, 1946. In the eutrophic pond Badstue-Ødam, which is approaching mixotrophy, the compound quotient was $\frac{20}{2} = 10$ on June 6th, 1929 and $\frac{38}{3} = 12.7$ on August 23rd, 1929. In the pond Store Dam, which is also transitional, the compound quotient was $\frac{7}{1} = 7$ on July 6th, 1929, $\frac{10}{5} = 2$ on August 17th and $\frac{13}{2} = 6.5$ on June 16th, 1930.

It must be emphasized here that in this country *Staurastrum uniseriatum* was found only in eutrophic and alkaline waters. *Staurastrum gracile*, however, was found both in oligotrophic waters (also those of the dystrophic phase) and in eutrophic waters (including those of the mixotrophic phase).

Moreover *Staurastrum gracile* to a much higher degree seems to be indigenous to lakes than *Staurastrum uniseriatum*, which is more properly an inhabitant of lake-

lets and ponds. However, the said occurrence of *Staurastrum uniseriatum* in the large and very deep Toba Lake on Sumatra shows that it is not always confined to smaller bodies of water.

On the basis of my limited Danish material (12 localities for *Staurastrum gracile*, 6 for *Staurastrum uniseriatum*) I venture to advance the opinion that the "ecological spectrum" of *Staurastrum gracile* is not so narrow as that of *Staurastrum uniseriatum* as regards both pH, contents of humic substances and the size and quantitative nutrition of the water bodies.

A few ecological data of *Staurastrum uniseriatum* are: pH 7.6—9.1, CaO 70.6—75.3 mg/l, consumption of $KMnO_4$ 54—65 mg/l, contents of PO_4-P 0.005—0.25 mg/l, NH_3-N 0.05—0.1 mg/l, NO_3-N 0—0.01 mg/l and Fe 0.03 mg/l.

f. **bicornis** n. f.

Fig. nostra 58.

A typo semicellulis bibrachiatis differt. Longitudo sine processibus 24—25 μ, cum processibus 26—33 μ, latitudo cum processibus 47—51 μ, latitudo isthmi 5.5 μ, crassitudo 9 μ.

Hab. In Hulsø, Selandia, Dania, libere natans.

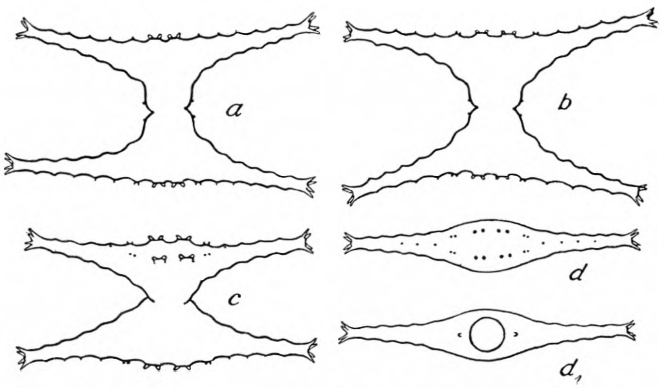


Fig. 58. *Staurastrum uniseriatum* n. sp. f. *bicornis* n. f. from Hulsø, August 8th, 1946; *a*—*b* front views, *c* oblique front view, *d* vertical view, d_1 basal view. 800×.

The form was found only in Hulsø on August 8th, 1946 in the association mentioned on p. 112 (see Table II). Hulsø is typically eutrophic of the mixotrophic phase.

Staurastrum vestitum Ralfs var. **parvum** nov. var.

Fig. nostra 59.

Diagnosis. A typo cellulis minoribus cum processibus quadridentatis et valde divergentibus differt. Longitudo sine processibus 15 μ, cum processibus 22 μ, latitudo cum processibus 31—33 μ, latitudo isthmi 5.5 μ.

Hab. In Holmsø prope Oxbøl, Jutlandia occidentali, Dania, libere natans.

The variety is easily distinguished from the main species (West and Carter: Monograph, vol. 5, p. 158, t. 151, figs. 9—11; t. 152, figs. 5—6) by its small cells

with highly divergent processes; the cells of the main species are 28—43 μ long (without proc.), 46—90 μ broad (with proc.) and its processes are convergent or parallel.

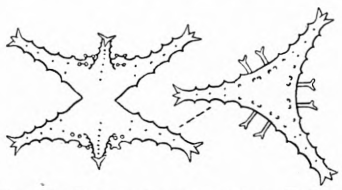


Fig. 59. *Staurastrum vestitum* Ralfs var. *parvum* n. var. from Holmsø, June 26th, 1930. 800×.

The new variety bears a greater resemblance to *Staurastrum vestitum* var. *subanatinum* West (*loc. cit.*, p. 159, t. 153, fig. 5), which also has divergent processes; but var. *subanatinum* has 7—9-dentate processes and cells of more than twice the size of the cells of var. *parvum*.

The variety was found in very small quantities in Holmsø (N. of Esbjerg) on June 26th, 1930 (temp. 17.5° C.). As will appear from Table III Holmsø is oligotrophic of the acidotrophic phase (pH 4.6); on the said date the compound quotient of this clear heath lake with its extremely poor plankton was only $\frac{4}{10} = 0.4$. The plankton association in which *Staurastrum vestitum* var. *parvum* occurred was dominated by *Peridinium Willei*; its qualitative composition appears from Table IV.

Sphaerozosma vertebratum Ralfs f. **quadrata** n. f.

Fig. nostra 60.

Diagnosis. A typo cellulis constrictioribus et quadratioribus differt. Longitudo cellulae 0.73—0.9 latitudinis. Sinus linearis; apex cellulae planus vel levissime convexus. Membrana disperse punctata. Longitudo cellularum 16—19 μ, latitudo 20—22 μ, crassitudo 12 μ, latitudo isthmi 7—9 μ.

Hab. In Hampen Sø, Jutlandia, Dania, libere natans.

Systematics. The form is characterized by its subquadratic cells with linear sinus. V. et P. Allorge's form (1930, p. 42, t. 31, fig. 10) is probably identical with f. *quadrata*. *Sphaerozosma vertebratum* var. *depressum* Grönblad (1920, p. 83, t. 1, figs. 2—4), however, is something quite different because its cells are about twice as broad as long (19 μ × 36—39 μ).

Periodicity. The form was observed only on August 15th, 1927 and June 23rd, 1929, but not in the April, May and September samples. So it is possibly a high summer form, which was always very rare in the plankton of Hampen Sø.

Sociology. *Sphaerozosma vertebratum* f. *quadrata* was found in the following 2 associations:

Aug. 15th, 1927: *Ma ca-Ta fe as*-association with *Ar cr lo* and *Coo Nä* as subdominants (the form very rare).

June 23rd, 1929: *Ura am*-association (the form very rare).

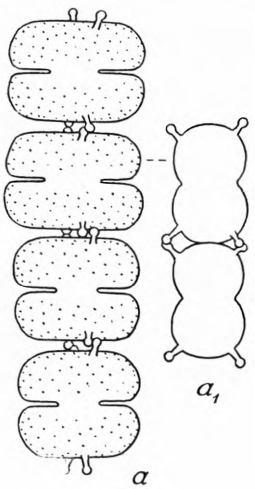


Fig. 60. *Sphaerozosma vertebratum* Ralfs f. *quadrata* n. f. from Hampen Sø, June 23rd, 1929. *a* front view, a_1 lateral view. 800×.

The form thus occurred in a chrysophycean association of *Uroglena* and a mixed association of the Chrysomonade *Mallomonas* and the Diatom *Tabellaria*.

Ecology. Hampen Sø is an approximately oligotrophic, lime-deficient (CaO 4—6.5 mg/l) and clear lake, the pH of which is subject to great and rapid variations; for further details see IVERSEN 1929, p. 314 and NYGAARD 1938, p. 685. On both days mentioned above the compound quotient was $\frac{6}{13} = 0.5$ and $\frac{5}{10} = 0.5$; see further Table I. On August 15th, 1927 JOHS. IVERSEN (1929, p. 286) found that pH near hydrophytes varied between 5.4 and 8.4; the open waters, however, were mostly slightly acid and rarely exceeded the neutral point. Other ecological data of *Sphaerozosma vertebratum* f. *quadrata* are: pH 6.9, CaO 6—6.5 mg/l, PO_4-P 0 mg/l, NH_3-N 0.05 mg/l and NO_3-N 0.01 mg/l.

Chrysophyceae.

Chrysomonadales.

Euchromulinaceae.

Chromulina pygmaea n. sp.

Fig. nostra 61.

Diagnosis. Cellulae solitariae, sphaericae vel late ellipsoideae, raro cylindricae apicibus rotundatis, submetabolicae. Periplastus delicatissimus et levis. Chromatophorus unus, brunneus, aut parvus, plusminusve apicalis et patellaris, aut major, parietalis, medianus et abrupte anuliformis, sine pyrenoide. Stigma longe ovale, in parte anteriori cellulae, saepe in margine chromatophori. Flagellum unum, $1\frac{1}{2}$ longitudinis cellulae. Cellulae 4—7 μ longae, 3—5 μ latae.

Hab. In Jægerbakke Dam prope Hillerød, Dania, libere natans.

Fig. 61. *Chromulina pygmaea* n. sp. from Jægerbakke Dam, February 17th, 1930. 750×.

Systematics. The species differs from the other *Chromulina* species described by its very small dimensions and its round —broadly ellipsoidical cells with one chromatophore. The two most closely related species, *Chromulina Rosanoffii* and *Chr. Woroniniana* (PASCHER 1913, p. 15, fig. 12; p. 15, fig. 11) have no stigma and show somewhat greater dimensions.

Periodicity. The species was seen for the first time under the ice on February 17th, 1930 (temp. 1° C.) when it was not infrequent just as on April 1st. On April 7th the species was common at a temperature of 6° C. During the rest of the month it was rather common or not infrequent, and on May 16th it was rare and then dis-

appeared from the plankton of Jægerbakke Dam. In the other months of the year it was never seen.

Accordingly, *Chromulina pygmaea* is eurythermic but apparently not perennial. Its vegetation period was February—May, and its maximum occurred at the beginning of April.

Sociology. The species was found in the following associations:

Feb. 17th, 1930: *Ki mi*-association with *Din cy al* as subdominant (the species not infrequent).

Apr. 1st, 7th, and 10th, 1930: *Din se pr*-association (the species respectively not infrequent, common and rather common).

Apr. 26th, 1930: *Ge mi*-association with *Din se pr* as subdominant (the species not infrequent).

May 16th, — : *Ank fa spa - Mio ho - Sce arm*-association (see Table IV; the species rare).

In other words *Chromulina pygmaea* was found in chlorophycean associations of *Kirchneriella*, *Geminella*, *Ankistrodesmus* and *Scenedesmus*, and in chrysophycean associations of *Dinobryon*; the associations are rarely characterized by blue-green algae (*Microcystis*).

The constant associates were *Ankistrodesmus falcatus* var. *spiralis*, *Scenedesmus armatus*, *Cryptomonas ovata* and *Anabaena tenericaulis*, which occurred in 100 % of the number (6) of samples that contained *Chromulina pygmaea*. *Chlamydomonas kakosmos*, *Scenedesmus falcatus*, *Geminella minor*, *Dinobryon bavaricum* and *Microcystis holsatica* were found in 83 % of the samples.

Ecology. Jægerbakke Dam is a small, highly eutrophic pond, sheltered from winds, conspicuous by its lime deficiency (see further Table III). For the ascertainment of the periodicity, sociology and the ecological data of *Chromulina pygmaea* only such samples were used in which the species was observed with certainty though it is very probable that it was also present in the month of March. pH 7.2—7.8, CaO 9—10.6 mg/l, consumption of $KMnO_4$ 27 mg/l, contents of PO_4-P 0.005—0.015 mg/l, NH_3-N 0.05—0.6 mg/l, NO_3-N 0—0.01 mg/l (Fe 0.45 mg/l on January 31st, 1930).

Kephyrion impletum n. sp.

Fig. nostra 61 *bis*.

Diagnosis. Loricae minimae, tenues, sine colore, fere tam longae quam latae, quarum pars basalis subconica sed postremus late rotundata, pars antica coniformis vel subcylindracea apice truncata et lateribus concavis est; in media lorica inflatio anularis et transversalis est. Protoplastus loricam fere ad oram implet, chromatophoro uno parietali et ochraceo; in medio protoplasto sphaera leucosini adest. Flagellum unum protoplasto 2—3-plo longius. Longitudo loricae 7.5—9.5 μ, latitudo 7—9 μ, latitudo orae 3.5—4.5 μ.

Hab. In stagno prope Sønderborg, Dania, libere natans.

Systematics. This new species is closely allied to *Kephyrion Rubri-claustri* Conrad (Huber-Pestalozzi 1941, p. 70, fig. 86A), likewise a coldwater form. The latter is, however, smaller, 5—7 $\mu \times 5$ μ, the houses are more elongated, and its protoplast does not fill up the house, the colour of which is yellow to pale brown.

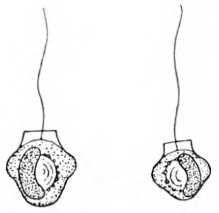


Fig. 61 bis. *Kephyrion impletum* n. sp. from a field pool north of Søndre Landevej in Sønderborg, February 27th, 1938. 1070×.

Kephyrion impletum was found under the ice on a field pool north of Søndre Landevej in Sønderborg, North Sleswick, on February 27th, 1938 by a temperature of 2.5° C. The plankton of this eutrophic pool was highly dominated of *Chlamydomonas Serbinowii*; of the other prominent constituents should be mentioned *Cryptomonas ovata*, *Mallomonas Teilingii* and *Mallomonas akromos* (both with cysts) and *Chlorogonium maximum*. On March 25th, 1945 pH was 8.4.

Mallomonadaceae.

Mallomonas areolata n. sp.

Fig. nostra 62.

Diagnosis. Cellulae cylindraceae apicibus rotundatis vel fusiformibus, tamen in statu cystophoro oviformibus, 23—38 μ longis, 6—11 μ latis. Squamis siliceis in series spirales axi longiore transverse ordinatis, 5—6.5 μ longis, 3.5—5 μ latis, v-descriptione et loco depresso cum seta affixa. Setis rectis vel leviter curvatis, in latere uno tenuiter denticulato, 20—45 μ longis, imprimis ad apicem anteriorem congregatis. Flagello cellulae longitudine aequilongo vel paulo longiore. Duobus chromatophoris luteo-brunneis instructis. Cystae ellipsoideae, perspicue punctatae, spinosae videntur, spinis verum ad superficiem extremam ordinatis, interdum collis brevissimis instructis, 13.5—18 μ longae, 11—15.5 μ latae. Protoplasma tota cellulae ad natum cystae consumitur.

Hab. In Gadevang Mose, Selandia, Dania, libere natans.

In Sortedam II on April 4th—10th, 1930, I found a *Mallomonas* species that is probably identical with *Mallomonas areolata* (Fig. 63). The cells were 24—25 μ in length, 11—13 μ in breadth (including, however, individuals containing spores). The scales, much like those of *Mallomonas areolata* in the v-shaped markings, were 6 μ long and 4 μ broad. The cysts were 13—15 μ long, 10—11.5 μ broad but with a denser punctuation than in the individuals from Gadevang Mose. The silicious bristles—if they be appurtenant—were straight or slightly curved, finely and unilaterally denticulate and 22—34 μ long. However, in the samples from April 4th and 10th the following species were found: *Mallomonas akrokomos*, *M. reginae*, *M. species*$_1$, *M. semiglabra* n. sp., *M. tessellata* and *M. tridentata* n. sp. or *Teilingii*, none of which

have denticulate bristles (except perhaps *M. sp*$_1$, the bristles of which are unknown); and so it is just possible that the bristle figured is appurtenant. However, the material is too sparse and heterogenous for a safe establishment whether or not this is a *Mallomonas areolata*.

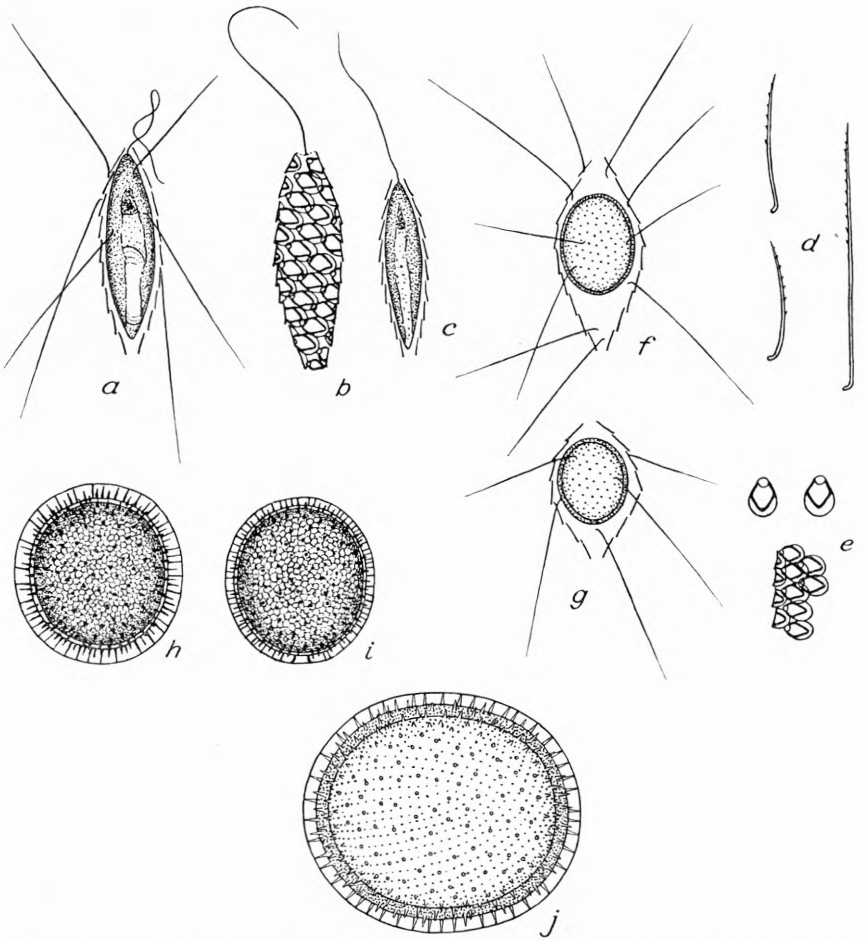


Fig. 62. *Mallomonas areolata* n. sp. from Gadevang Mose, April 28th, 1930. *a*, *c*, *f* and *g* are drawn after living material; *b*, *d* and *e* after material dried up on a cover-slip (all figures 800×). *h*, *i* and *j* cysts drawn after material heated on a cover-slip (*h*—*i* 1600×, *j* 2400×).

Systematics. *Mallomonas areolata* belongs to the *tonsurata* group on account of its ovate scales with v-shaped markings and the denticulate bristles, which are principally found at the anterior end of the cell. From *Mallomonas tonsurata*, *M. alpina* and *M. elongata* it differs by the shape, size and structure of the cysts, from the first two further by the shape of the cell and the larger scales, etc., from the last one further by its smaller dimensions, the relatively great length of the flagellum, the length of the bristles, etc.

Periodicity. In Gadevang Mose the species was first seen on March 15th, 1930 (temp. 5° C.), several individuals occurring. The rather high maximum was reached on April 1st (9° C.). The formation of cysts took place in April, especially during the latter half of the month, and at the beginning of May. After the middle of May the species had totally disappeared from the plankton. In Sortedam II it was observed at the beginning of April at temperatures of 3.5 and 8° C. In other words it is a typical spring organism (March—May), the limits of temperature being 3.5 and 18.5° C., and the maximum development occurring at temperatures below 10° C.

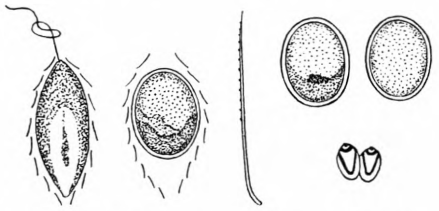


Fig. 63. *Mallomonas areolata* n. sp.? from Sortedam II, April 10th, 1930. 800×.

Sociology. In Gadevang Mose the species was found in the following associations:

Mar. 15th, 1930: Association of a unicellular green alga with *Ma ak* as subdominant (*M. areolata* not infrequent).
Apr. 1st, — : *Crym ov*-association with *Ma ak* as subdominant (*M. areolata* common).
— 7th, — : *Crym ov* - *Ste Ha* - association (*M. areolata* not infrequent).
— 10th, — : *Ste Ha*-association with *Crym ov* as subdominant (*M. areolata* rare).
— 22nd, — : *Crym ov*-association with *Ste Ha* as subdominant (*M. areolata* rare).
— 28th, — : *Ste Ha*-association (*M. areolata* not infrequent).
May 1st, — : *Ste Ha*-association (*M. areolata* rare).
— 10th, — : *Ste Ha*-association (*M. areolata* rare).

In Sortedam II the species presumably occurred in the following associations:

Apr. 1st, 1930: *Ank fa se el* - *Crym ov*-association (*M. areolata* very rare).
— 10th, — : *Crym ov*-association with *Chla ac* as subdominant (*M. areolata* rare).

In other words *Mallomonas areolata* occurs in flagellate associations of *Cryptomonas*, in diatom associations of *Stephanodiscus* and in green algae associations, *i. a.* of *Ankistrodesmus*.

The most constant associates were *Cryptomonas ovata* and *Stephanodiscus Hantzschii*, which occurred in 100 % of the number of samples (10) that contains *Mallomonas areolata*; *Mallomonas akrokomos* and *Chlamydomonas Reinhardii* (+var. *minor*) reached 80 %.

Ecology. In spite of the enormous *Stephanodiscus Hantzschii* maximum in spring the somewhat contaminated and a little overshadowed Gadevang Mose is not a quite typically mixotrophic pond (see Table III). After its abundant development

of plankton in April when the plankton shows a totally "eutrophic" character it becomes distinctly acid during early summer and develops no trace whatever of water bloom of blue-green algae in summer or autumn but an enormous maximum of *Ceratium hirundinella*. Data of the ecology of *Mallomonas areolata* are: pH 7.1—8.6, calcium content 15.6—15.9 mg of CaO per litre, consumption of $KMnO_4$ 72 mg/l, contents of NH_3-N 0.2—0.35 mg/l, NO_3-N 0—0.16 mg/l, PO_4-P 0.11—0.175 mg/l and Fe 0.3 mg/l.

Mallomonas heterothricha n. sp.

Fig. nostra 64.

Diagnosis. Cellulae ellipsoideae, duplo longiores quam latiores, 16—21 μ longae, 8—10 μ latae. Squamis siliceis rotundatis—late ovalibus, levibus, parvis, 2—2.5 μ longis, in lineis spiralibus satis praecipiter ascendentibus superficie cellulae locatis. Setae formarum duarum: vel 18—25 μ longae, rectae, mobiles, interdum apicaliter paulo recurvatae; vel 7—13 μ longae, curvae, immobiles. Quae leves atque omnes ad apicem cellulae aggregatae et tantum hic occurrentes sunt. Numerus setarum longarum plerumque 8, numerus brevium 5—8. Flagellum $\frac{1}{3}$—$\frac{1}{2}$ corporis longitudinis. Duobus chromatophoris luteo-brunneis instructae sunt. Cystae ignotae.

Hab. In Teglgaard Sø, Selandia, Dania, libere natans.

Systematics. When alive this species is easily distinguished from all other *Mallomonas* species by its 2 kinds of bristles. The small curved ones stand like the stretchers of a put-up umbrella from the anterior end of the cell and are rather immovable; the mobility of the long straight bristles amounts to nearly 90°. In swimming individuals nearly all the long bristles are standing almost parallel to the longitudinal axis of the cell whereas in resting individuals they are directed obliquely sidewards so as to stand nearly square to the longitudinal axis. If these observations under the coverslip apply in the free natural bodies of freshwater, we have here a *Mallomonas* species which to a special degree is able to vary its sinking rate (as compared to its active motion) when not swimming actively.

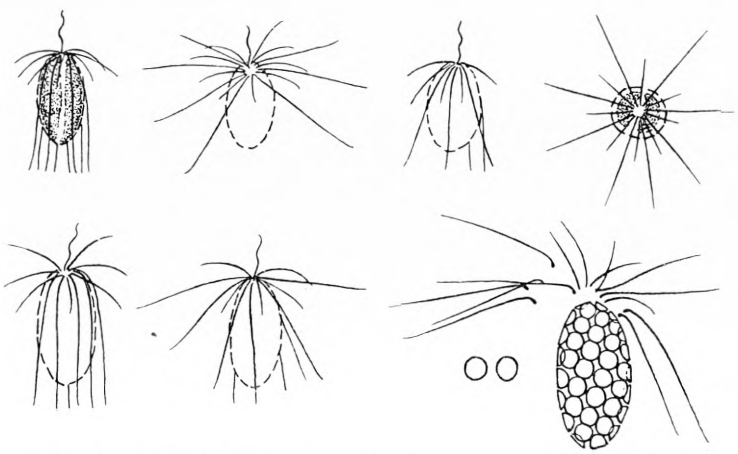


Fig. 64. *Mallomonas heterothricha* n. sp. from Teglgaard Sø, October 7th, and 14th, 1929. Last figure 1070×, the others 850×.

Periodicity. A few specimens appeared on October 3rd, 1929 (temp. 12° C.) in Teglgaard Sø, and the species was last seen on November 30th, 1929 (temp. 6° C.). The highest frequency of *Mallomonas heterothricha* occurred on October 23rd—25th (temp. 8.5° C.), the species, however, being in no way predominant. This *Mallomonas* was never observed in any of the other ten months of the year. It must therefore be considered an oligo- to mesothermic autumnal form with an amplitude of temperature between 4 and 12° C. and with a maximum development at the end of October at 8.5° C.

Sociology. The species occurred in the following associations:

Oct. 3rd, 1929: *Chry mi*-association (*M. heterothricha* very rare).
— 7th, — : *Din di*-association (*M. heterothricha* rare).
— 14th, — : *Chry mi*-association (*M. heterothricha* very rare).
— 23rd, — : *Chry mi*-association (*M. heterothricha* not infrequent).
— 25th, — : *Ste Ha*-association (*M. heterothricha* rather common).
Nov. 2nd, — : *Chry mi*-association (*M. heterothricha* not infrequent).
— 16th, — : *Crym ov*-association (*M. heterothricha* rare).
— 28th, — : *Ste Ha*-association (*M. heterothricha* not infrequent).
— 30th, — : *Crym ov*-association (*M. heterothricha* very rare).

Mallomonas heterothricha thus occurs in flagellate associations of *Chrysococcus*, *Cryptomonas* and *Dinobryon* and in a diatom association of *Stephanodiscus*.

The most constant associates were *Chrysococcus minutus*, *Scenedesmus armatus* and *Stephanodiscus Hantzschii*, which occurred in 100 % of the samples (9) that contained *Mallomonas heterothricha*; *Cryptomonas ovata* reached 90 %.

Ecology. The eutrophic pond Teglgaard Sø is situated in open land and nearly overgrown with reed swamps. Both inlets and outlets are present. The species occurred at pH values between 7.4 and 7.6, at a calcium content of 53.4—55.7 mg of CaO per litre and a consumption of 37 mg $KMnO_4$ per litre. Other data are: NH_3-N 0.2 mg/l, NO_3-N 0—0.01 mg/l, PO_4-P 0,01 mg/l; on January the Fe content was 0.45 mg/l.

Mallomonas oviformis n. sp.

Fig. nostra 65.

Diagnosis. Cellulae late oviformes, 23—24 μ longis, 19—20 μ latis. Squamis siliceis ovalibus, inter se semitectis, in lineis spiralibus axi longiore transverse ordinatis, levibus et prope duplo longioribus quam latioribus, 6—7 μ longis, 3—4 μ latis. Setis rectis, levibus, satis paucis, in superficie cellulae dispersis, $\frac{1}{4}$—1 cellulae longitudinis, 6—25 μ longis. Flagello corpori aequilongo, ab apice subacuto cellulae exoriente. Duobus chromatophoris luteofuscis instructae. In parte posteriore cellulae globulum leucosini et vacuola contractilia observata sunt. Cystae ignotae.

Hab. In Rønhavegaard Dam, Alsia, Dania, libere natans.

Systematics. This new species differs from *Mallomonas ovum* Schiller (1926, p. 15, fig. 7; incomplete description) in the shape of the cells and the location of the scales, possibly also in their shape, which is not described by Schiller. The species should also be compared with *Mallomonas semiglabra* n. sp. (p. 124), in which, however, the flagellum of half the length of the body is situated in the broadly rounded part of the cell, and the scales of which are smaller with half their surface punctate, the smooth part having only a slight depression in which the bristle is fixed.

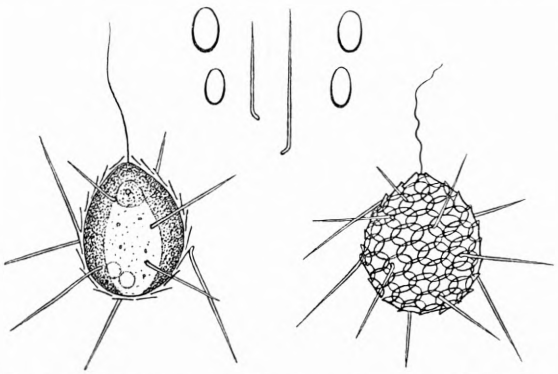


Fig. 65. *Mallomonas oviformis* n. sp. from Rønhavegaard Dam, March 12th, 1944. 800×.

The species was represented by a few individuals in Rønhavegaard Dam on March 12th and 19th, 1944 (temp. 4.5 and 6° C.) and is possibly a cold water form like *Mallomonas semiglabra*. On March 8th and 22nd, 1945 the species failed to reappear.

Mallomonas oviformis was very rare in the following two associations:

Mar. 12th, 1944: *Chrom No mi*-association with *Chla Re* as subdominant.
— 19th, — : *Chrom No mi*-association with *Ste Ha* as subdominant.

Rønhavegaard Dam is a highly eutrophic pond, which is polluted *i. a.* by swimming birds. Such an enormous development of plankton is rare in March; the water had an intense and deep blue-green colour from the large quantities of *Chroomonas* and *Chlamydomonas*. At the said time pH was 8.2 at 3 p. m.

Mallomonas pediculus Teiling var. **echinospora** n. var.

Fig. nostra 66.

Diagnosis. Cellulae late ellipsoideae vel oviformes, 18—26 μ longae, 14—17 μ latae, 1.25—1.6 plo longiores quam latiores. Squamae siliceae in lineis spiralibus, oviformes, 6 μ longae, 4 μ latae, ad apicem anteriorem loco depresso et hic seta affixa est, ceterum leves cum v-descriptione (cellulae vivae squamis rhombeis tectae videntur). Setis acutis, retroflexis, corpore aequilongis, per superficiem totam cellulae extendentibus, 14—24 μ longis, valde arcuatis, in apicibus non recurvatis, in latere convexo serie spinarum tenuissimarum instructae. Flagello $\frac{1}{2}$—$\frac{3}{4}$ longitudinis cellulae, raro cellulae longitudine aequilongo. Duobus chromatophoris luteo-brunneis instructis. Cystis globosis, spinis tenuibus tectis, 17—18 μ in diametro, foramine $2\frac{1}{2}$ μ lato.

Hab. In Badstue-Ødam, Selandia, Dania, libere natans.

Systematics. This variety, the silicious bristles of which lie close to the cell when it swims is distinguished from *Mallomonas acaroides* Perty by the character of the bristles, the relative length of the flagellum and the size and structure of the cysts. According to W. KRIEGER (1930, p. 292, Fig. 35) the bristles of *Mallomonas acaroides* are recurvate at the tip and have only 2 denticles near the apices; the flagellum is as long as the body, and the verrucose cysts are 20—22 μ in diameter. It is well-known that the *Mallomonas tonsurata* group (*M. tonsurata*, *M. alpina* and *M. elongata*), the scales of which have the same characteristic v-shaped markings, includes species with denticulate bristles. These species, however, are conspicuous by having the greater part of their bristles directed forward fountain-like; moreover only the front half or two thirds of the cell are covered with bristles.

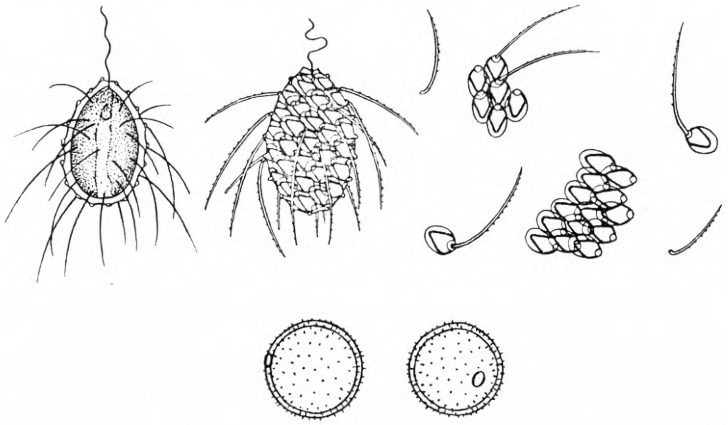


Fig. 66. *Mallomonas pediculus* Teiling var. *echinospora* n. var. from Badstue-Ødam, May 6th, 1931. 800×.

After this part of the manuscript had been terminated and translated, Dr. EINAR TEILING sent me his paper "Zur Phytoplanktonflora Schwedens", 1946. When I had studied more closely the *Mallomonas* species described in his paper, it became clear to me that my "*Mallomonas Mülleri*" n. sp. was closely related to *Mallomonas pediculus* Teiling. According to TEILING's information to me the latter species has smooth cysts, and so the Danish individuals have been classed as a new variety of *Mallomonas pediculus*.

Periodicity. *Mallomonas pediculus* var. *echinospora* was observed for the first time on April 3rd, 1930 in Badstue-Ødam. In this month it was sometimes very rare or absent, sometimes common. Between May 10th and 31st (temp. 12—20.5° C.) it was rather common in the plankton of the pond, particularly on May 21st (temp. 17° C.). Already on June 16th it was absent. The formation of cysts took place during the latter half of May (temp. 17—20.5° C.). In the plankton sample taken with townet on May 6th, 1931 the species was common.

Mallomonas pediculus var. *echinospora* thus seems to be eurythermic, in April and May occurring within an interval of 6—20.5° C. The maximum development of this spring form took place in May (temp. about 17° C.).

Sociology. The variety was found in the following associations:

Apr. 3rd, 1930: *Ste Ha*-association with *As fo* and *Sye ac an* as subdominants (*Mallomonas* not infrequent).

Apr. 22nd, 1930: *Sye ac an*-association with *Ura vo* as subdominant (*Mallomonas* very rare).
— 25th, — : *Din so - Sye ac an*-association (*Mallomonas* common).
May 10th, — : *Ste Ha - Sye ac an - Ura vo*-association (*Mallomonas* not infrequent, about 1.700 individuals per ml).
— 16th, — : *Ura vo*-association (*Mallomonas* not infrequent).
— 21st, — : *Ura vo*-association (*Mallomonas* common).
— 31st, — : *Cy st su*-association (*Mallomonas* rather common).
— 6th, 1931: *Sye ac an*-association with *Dia el* and *Syu Pe* as subdominants (*Mallomonas* common).

In other words *Mallomonas pediculus* var. *echinospora* mainly occurs in diatom-associations of *Cyclotella*, *Stephanodiscus* and *Synedra*, but also in flagellate associations of *Dinobryon* and *Uroglena*.

The most constant associates were *Synedra acus* var. *angustissima* and *Uroglena volvox*, which occurred in 100 % of the number of samples that contained *Mallomonas pediculus* var. *echinospora*. *Anabaena incrassata*, *Asterionella formosa*, *Chrysococcus minutus*, *Cyclotella Meneghiniana*, *Glenodinium edax*, *Scenedesmus armatus*, *Stephanodiscus Hantzschii*, *Trachelomonas intermedia* and *Trach. volvocina* occurred in 88 %, *Cryptomonas ovata* and *Peridinium palatinum* in 75 % of the samples.

Ecology. Badstue-Ødam is somewhat overshadowed, has inlets and outlets and ranges between the eutrophic and the mixotrophic types of water. A synopsis of the ecology of *Mallomonas pediculus* var. *echinospora*: pH 8.4—9.4, consumption of $KMnO_4$ 44—57 mg/l, contents of CaO 81.4—82.2 mg/l, Fe 0.02 mg/l, NO_3-N 0—0.35 mg/l, NH_3-N 0.05—0.1 mg/l, and PO_4-P 0.005—0.01 mg/l.

Mallomonas semiglabra n. sp.

Fig. nostra 67.

Diagnosis. Cellulae obovatae, saepe ad partes posteriores subacutatae, 20—$22\frac{1}{2}$ μ longae, 14—17 μ latae. Squamis siliceis ovalibus, in lineis spiralibus ordinatis, ascensu parvo, 4—$4\frac{1}{2}$ μ longis, $2\frac{1}{4}$—3 μ latis, tantum in parte dimidia punctatis; pars levis in apice locum depressum parvum habet, in quo seta fixa est. Setis levibus, rectis, 9—21 μ longis, in superficie omni cellulae dispersis. Flagello $\frac{1}{2}$ cellulae longitudinis. Duobus chromatophoris luteo-brunneis instructae. Cystis oviformibus, tenuiter punctulatis, magnitudine cellularum. Protoplasma totum cellulae ad natum cystae consumitur.

Hab. In Spejldam, Hesteskodam et Sortedam II, Selandia, Dania, libere natans.

Systematics. This species differs from all those formerly described by its characteristic scales. Moreover the cell seems to be set with round, punctate scales

because the smooth part of one scale is situated immediately above the punctate part of the neighbouring scale. In this way the species gets a superficial resemblance to *Mallomonas reginae* Teil., but it will always be possible to see the true structure of the scale from dry-slides. Besides this the scales of the latter species are larger: 5.5—7.5 μ long and 4—5.5 μ broad.

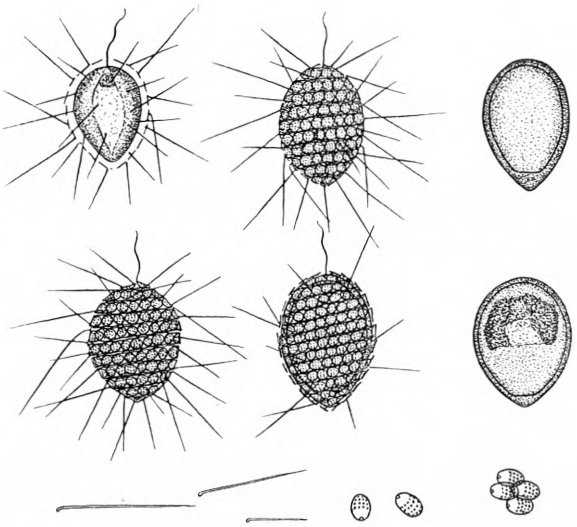


Fig. 67. *Mallomonas semiglabra* n. sp. from Spejldam, March 15th, and April 1st, 1930. 800×.

Periodicity. *Mallomonas semiglabra* appeared in Spejldam on November 22nd, 1929 when the temperature had fallen to 4° C. During the following winter months it was extremely rare and was even lacking in several of the samples. A more frequent occurrence was not observed until the beginning of March 1930, and particularly on March 15th (temp. 3° C.), when the ice was going to melt, the individuals were so numerous that they prevailed in the plankton. Most of them were finishing the formation of spores. Already at the beginning of April (temp. 4.5—6° C.) the species had disappeared from Spejldam; in the examination of the living plankton only one egg-shaped cyst was observed on April 4th (temp. 4.5° C.). In Hesteskodam, however, which drains directly into Spejldam, a few specimens were seen on April 4th (temp. 5° C.). In Sortedam II it did not appear until March 15th, 1930 (temp. 4.5° C.) when it was comparatively frequent. At the beginning of April (temp. 3.5—8° C.) it was rare; the last occurrence was observed on April 10th. The species was never found during the warm half of the year.

Accordingly, *Mallomonas semiglabra* must be characterised as typically oligothermic or a stenothermic cold water form because it was found only at temperatures between 0.5 and 8° C. Its maximum occurred in March (temp. 3—4.5° C.) during the breaking of the ice.

Sociology. The species was observed in Spejldam in the following associations:

Nov. 22nd, 1929: *Ma ak - Tra vo*-association (*M. semiglabra* very rare).
Feb. 17th, 1930: *Crym ov - Chla ac*-association (*M. semiglabra* very rare).
Mar. 1st, — : *Chla ac*-association with *Mallomonas* sp_1 as subdominant (*M. semiglabra* rare).
— 15th, — : *Ma se*-association with *Ank fa se br* as subdominant (*M. semiglabra* common).

Apr. 4th, 1930: *Ank fa se br*-association (*M. semiglabra* very rare).

In Hesteskodam it was only present in this association:

Apr. 4th, 1930: *Mio ho* with *Ank fa se br* as subdominant (*M. semiglabra* very rare).

In Sortedam II the species occurred in the following associations:

Mar. 15th, 1930: *Mallomonas* sp_1-association with *Crym ov* and *Ma ak* as subdominants (*M. semiglabra* rather common).

Apr. 4th, — : *Crym ov - Ank fa se el*-association (*M. semiglabra* not infrequent).

This means that the species mostly occurs in flagellate associations of *Cryptomonas*, *Mallomonas* and *Trachelomonas*, more rarely in green algae associations of *Chlamydomonas* and *Ankistrodesmus* and in a blue-green algae association of *Microcystis*.

The most constant associates were *Ankistrodesmus falcatus* var. *setiformis*, *Glenodinium edax*, *Chlamydomonas acidophila*, *Mallomonas akrokomos* and *Trachelomonas volvocina*, which all occurred in 75 % of the number of samples (8) that contained *Mallomonas semiglabra*.

Ecology. Both Spejldam and Hesteskodam are rather overshadowed ponds draining into Frederiksborg Slotssø. Hesteskodam in particular is polluted (mem. *Euglena sanguinea*), and both of them are eutrophic—mixotrophic with their great maximum of *Cyanophyceae* in late summer (Spejldam: *Aphanizomenon flos aquae*; Hesteskodam: *Microcystis aeruginosa* + *Anabaena Viguieri*). Sortedam II is a typical mixotrophic, greatly overshadowed pond. A synopsis of the ecology of the species: pH 6.8—8.0, consumption of $KMnO_4$ 37—84 mg/l, contents of CaO 36.4—42.9 mg/l, Fe 0.17 mg/l, NO_3-N 0.06—0.43 mg/l, NH_3-N 0.08—0.55 mg/l and PO_4-P 0.015—0.03 mg/l.

Mallomonas sphagnicola n. sp.

Fig. nostra 68.

Diagnosis. Cellulae magnae, cylindricae vel longe ellipsoideae apicibus rotundatis vel subacutis, 3.1—4.7 plo longiores quam latiores. Laminis tegumenti magnis, 1.5—1.8 plo longioribus quam latioribus, 7—9 μ longis, 4—5.5 μ latis, ellipticis, raro subcuneatis, cum v-descriptione et margine striatulo, 10—12 striis pro 4 μ, medio indistincte punctulatis vel striatulis, in series spirales axi longiore transverse ordinatis. Superficies tota cellulae setis numerosis, glabris vel indistincte denticulatis, rectis vel leviter curvatis, 19—43 μ longis tecta. Chromatophori bini, luteo-brunnei, parietales et longi. Nucleus in parte anteriore cellulae. Flagellum breve, $\frac{1}{3}$—$\frac{1}{2}$ longitudinis cellulae, 20—25 μ longum. Vacuola contractilia quattuor in parte posteriore cellulae, raro vacuolum unum in parte anteriore. Longitudo cellularum 56—69 μ, latitudo 13—20 μ.

Hab. In Bøndernes Mose I et II prope Hillerød, Selandia, stagno turfaceo prope Skaansø, Jutlandia, Dania, libere natans.

Systematics. The species differs from all other previously described *Mallomonas* species by its big scales with marginal striation and a v-shaped marking, and so it might just as well be termed *Mallomonas megalepis* n. sp. The scales of most species seem to be 2—5 μ in size, a few of them (*M. Teilingii* and *M. tridentata* n. sp.)

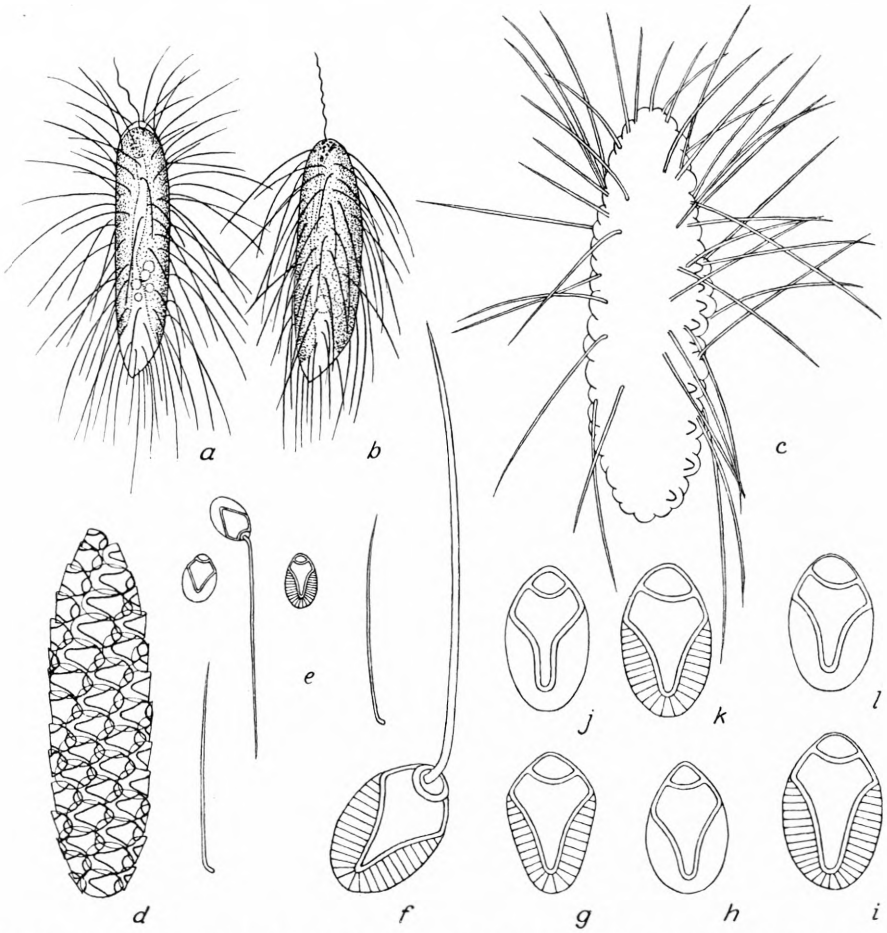


Fig. 68. *Mallomonas sphagnicola* n. sp. from Bøndernes Mose II; *a*—*b* are delineated from living material, September 7th, 1929, 550×; *c*—*l* from dried-up material, June 16th, 1930; *e*—*l* silicified scales and bristles. *c*, *d* and *e* 800×, *f*—*l* 2400×.

have densely punctate scales of 6—8 μ; only *M. caudata* have scales of the same dimensions as *Mallomonas sphagnicola*, but it is well-known that the scales of the former are completely smooth and nearly round.

After this part of the manuscript had been finished and translated I received Bourrelly's interesting paper (1947) on the algae of la Forêt de Fontainebleau. In this paper Bourrelly has described *Mallomonas Leboimii* (p. 4, t. 3, figs. 12—16),

a very characteristic species with scales which as to form and structure are quite similar to those of *Mallomonas sphagnicola* n. sp.; they are, however, considerably larger (10—12 $\mu \times 6$—7 μ) than the scales of *Mallomonas sphagnicola*. *Mallomonas Leboimii* further differs in having relatively shorter cells (35—50 $\mu \times 10$—22 μ), strongly dentate bristles and a flagellum of the same length as the cell.

Periodicity. During the examination of the living plankton from Bøndernes Mose I and II the species was found in Bøndernes Mose II in all months of the year (1929) except February, March and April, *i. e.* not during and immediately after the freezing-up of the pond. It reached its highest frequencies in the September samples and the sample from June 1930 without ever being very conspicuous. In this locality the species was eurythermic, occurring at temperatures between 2.5 and 21° C.

In Bøndernes Mose I, however, the species was distinctly periodical: it was seen only in the September samples at temperatures of 15.5 and 11.5° C.

In the turf pit NE of Skaansø the species was not infrequent on July 4th, 1938 (temp. 18,5° C.).

In contrast to several *Mallomonas* species, the maxima of which occur about the time when the ice breaks in the ponds, *Mallomonas sphagnicola* thus seems to reach its optimum development in September at temperatures between 11.5 and 16.5° C. If this eurythermic species is diacmic, its second vegetation period most probably occurs in June.

Sociology. The species occurred in the following associations:

Bøndernes Mose II.

July 5th, 1929: *Crym ov cu*-association with *Tra vo* as subdominant (the species rare).
Aug. 22nd, — : *Crym ov cu*-association (the species very rare).
Sep. 7th, — : *Tra vo*-association with *Crym ov cu* as subdominant (the species not infrequent).
— 22nd, — : *Crym ov cu*-association (the species not infrequent).
Oct. 9th, — : *Crym ov cu*-association with *Tra vo* as subdominant (the species rare).
— 29th, — : *Tra vo*-association (the species rare).
Nov. 24th, — : *Crym ov*-association (the species rare).
Dec. 16th, — : *Crym ov*-association (the species very rare).
Jan. 15th, 1930: *Tra vo*-association with *Eug pr* as subdominant (the species very rare).
May 24th, — : *Crym ov cu*-association (the species very rare).
June 16th, — : *Crym ov cu*-association with *Tra vo* as subdominant (the species not infrequent).

The qualitative composition of the associations from August 22nd, 1929 and June 16th, 1930 appears from Table IV.

Bøndernes Mose I.

July 5th, 1929: *Crym ov cu*-association with *Gos se* as subdominant (the species very rare).

Sep. 7th, 1929: *Crym ov cu*-association with *Gos se* as subdominant (the species not infrequent).

— 22nd, — : ditto.

Turf pit NE of Skaansø.

July 4th, 1938: *Sta br*-association with *Sta de lo* as subdominant (the species not infrequent).

In other words the species occurs in Flagellate associations (*Cryptomonas* and *Trachelomonas*) and a desmid association of *Staurastrum*.

The most constant associates were *Cryptomonas ovata* (var. *curvata*), which occurred in 93 % of the number of samples (15) that contained *Mallomonas sphagnicola*; *Goniostomum semen* occurred in 80 % and *Trachelomonas volvocina* in 73 % of the samples.

Ecology. Bøndernes Mose I and II are two small oligotrophic turf-pits of the dystrophic phase, situated in a raised bog of Gribskov. The turf pit NE of Skaansø is quite similar. They have quaking bog of *Sphagnum cuspidatum*. The following are dates from the ecology of *Mallomonas sphagnicola*: pH 4.1—4.4, CaO 0.8—5 mg/l, consumption of $KMnO_4$ 176—202 mg/l, content of PO_4-P 0 mg/l, NH_3-N 0.9—1.6 mg/l, NO_3-N 0 mg/l, and Fe 0.25 mg/l.

Mallomonas tessellata Nyg.

Nygaard 1945, p. 52, fig. 18.—*Fig. nostra* 69.

Diagnosis. The *setae* are not dispersed over the surface of the cell as stated in the original diagnosis. An examination of living cells from the *Eriophorum* moor at Sorø and Store Gribsø showed that they were found only on the front end of the cell and in a number of 4—5; they are always more or less curved, and their length is about $^3/_4$ that of the cell.

According to 40 measurings of cells, both sterile and carrying cysts, the cells are 18—44 μ long, 10—18 μ broad, ratio of axes 1.7—3 (average 2.26). 24 measurings of cysts proved them to be 17—23 μ long, 11—15 μ broad, ratio of axes 1.2—1.8 (average 1.5), shape ellipsoidical. 20 measurings of the thick, more or less curved, pointedly oval scales gave lengths of 4—9.5 μ, breadths of 2—4.5 μ (mostly 6—8 $\mu \times$ 3—4 μ) with 3—9 points along each side.

Distribution. Sortedam II, Hesteskodam, Store Gribsø and *Eriophorum* moor, Seeland, Store Øxsø and Løvenholm Langsø, Jutland, pelagic.

Systematics. Bourrelly (1947, p. 5, t. 4, figs. 17—20) has emendated Conrad's description of *Mallomonas lychenensis* (see Huber-Pestalozzi 1941, p. 94, fig. 111 A), now including individuals with 5—7 apical siliceous bristles. Both *Mallomonas lychenensis* and *Mallomonas tessellata* have the apical scales ("Oralschuppen") in common, see Fig. nostra 69 A. The reason why I have not referred *Mallomonas*

tessellata as a synonym to *Mallomonas lychenensis* is that a renewed examination of more than 100 cysts from the Danish material has proved that the cysts never possess a 6—9 μ broad collar as demonstrated in HUBER-PESTALOZZI's and BOURRELLY's text-figures cited above. The exactly ellipsoidical cysts of *Mallomonas tessellata* are

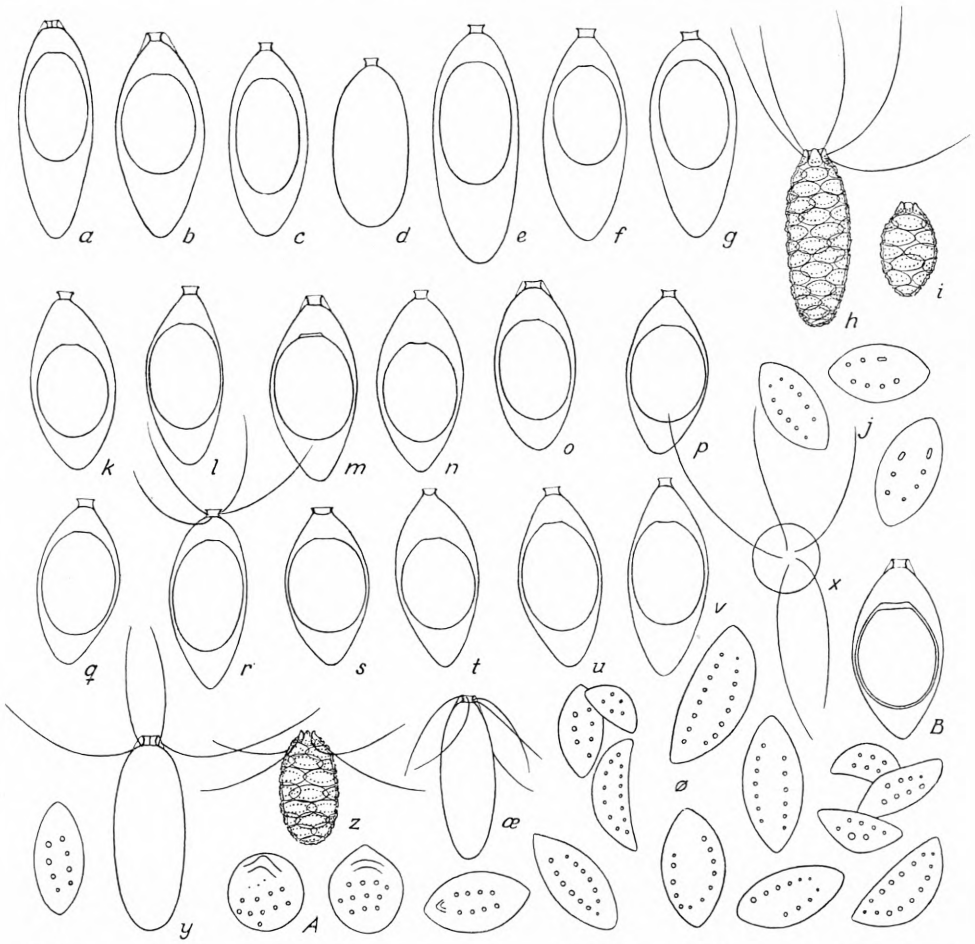


Fig. 69. *Mallomonas tessellata* Nyg.; *a*—*j* from Store Øxsø, May 23rd, 1929; *k*—*ø* and *A* from Eriophorum moor, *k*—*v* and *æ* from March 20th, 1948, *x*, *y* and *z* from January 10th, 1948; *B* from Sortedam II, April 1st, 1930. Only the outlines of the cells are drawn except *h*, *i* and *z*, *A* apical scales ("Oralschuppen"), *j* and *ø* scales, *x* vertical view. Magnification of the cells 710×, of the scales 2140×.

only provided with a 3—4.5 μ broad aperture in the apical part; very rarely they are slightly thickened around this aperture.

Periodicity. Among the localities mentioned above Sortedam II was examined fortnightly for a whole year and the *Eriophorum* moor monthly for 12 months. In Sortedam II the species was totally absent from June 1929 till the beginning of March 1930. It did not appear until March 15th when the ice was beginning to break, and the

temperature was 4.5° C., and at the beginning of April (temp. 3.5—8° C.) a few individuals carrying cysts were found in the plankton. It was seen for the last time on April 10th.

In the *Eriophorum* moor it was lacking in all samples from July—November 1947, but a few specimens appeared on December 13th (temp. 3° C.). On January 10th, 1948, when the moor was about to freeze up (temp. 1° C.), it was rather common, and on February 21st, when the ice was 8 cm thick and the temperature 2° C., it was common, and now a few individuals were beginning to form cysts. On March 20th, when the moor was free from ice and the temperature had risen to 7.5° C., the species was common, too, and most of the individuals were carrying cysts. On April 17th (temperature 15.5° C) *Mallomonas tessellata* was rare; the specimens contained cysts. On May 14th, June 13th, and July 13th the species was not observed.

As will appear from the following section the species also occurred in May and September and even in August (temp. 27° C.).

Accordingly, *Mallomonas tessellata* must be characterized as eurythermic, occurring at temperatures between 1 and 27° C. Its maximum development, during which it may be the dominant form of the plankton, falls within the period between January and the beginning of April at temperatures between 1 and 8° C.; even under the ice it may be common. The formation of cysts was observed from February to the beginning of April.

Sociology. The species occurred in the following associations:

Sortedam II.

Mar. 15th, 1930: *Ma* sp_1-association with *Ma ak* and *Crym ov* as subdominants (the species rare).
Apr. 1st, — : *Crym ov*-association (the species very rare).
— 4th, — : *Crym ov - Ank fa se el*-association (the species very rare).
— 10th, — : *Crym ov*-association with *Chla ac* as subdominant (the species very rare).

Eriophorum moor.

Dec. 13th, 1947: *Gle Lo - Per Wi*-association (the species very rare).
Jan. 10th, 1948: *Gle Lo*-association (the species rather common).
Feb. 21st, — : *Ma te*-association with *Gle Lo* as subdominant (the species common).
Mar. 20th, — : *Syu Pe - Ma te*-association (the species common).
Apr. 17th, — : *Chrysococcus*-association (the species rare).

Hesteskodam.

Apr. 4th, 1930: *Ank fa se br*-association (the species not infrequent).

Store Øxsø.

May 23rd, 1929: *Asi fo*-association (the species rare).

Store Gribsø.

June 18th, 1929: *Crym ov*-association (the species very rare).
Jan. 4th, 1947: *Ma ak*-association (the species very rare).

Løvenholm Langsø.

Sep. 9th, 1929: *Ma ca*-association (the species rare).

Aug. 1st, 1948: *Bo Br*-association (the species very rare).

Mallomonas tessellata thus occurred in cryptophycean associations of *Cryptomonas*, chrysophycean associations of *Mallomonas* and *Synura*, more rarely in dinophycean associations of *Glenodinium* and *Peridinium*, chlorophycean associations of *Ankistrodesmus* and diatom associations of *Asterionella*.

The most constant associates were *Synura Petersenii* and *Euglena acus*, which occurred in 70 % of the number (13) of samples that contained *Mallomonas tessellata*.

Ecology. The species is uncommonly adaptive, at least to the same degree as *Mallomonas caudata*. All the waters that contain *Mallomonas tessellata* are more or less rich in humus, the smallest amount of which is perhaps found in Hesteskodam whereas Løvenholm Langsø contains quite extraordinary quantities (see Table I). The species was found in an extremely eutrophic pond with brownish water (Hesteskodam), in a highly eutrophic pond of the mixotrophic phase (Sortedam II) and in 3 oligotrophic lakes of the dystrophic phase (Løvenholm Langsø, Store Øxsø and Store Gribsø). The *Eriophorum* moor is more difficult to place within the system (see p. 166 where *i. a.* its plankton composition is given), but it is a fact that its water was brown when *Mallomonas tessellata* occurred in it and that it is contaminated by cattle. The plankton quotients of the 3 oligotrophic lakes appear from Table I, those of Hesteskodam are mentioned on p. 211, and the quotients of Sortedam II are found in Table III.

The following data speak of the very different environments in which *Mallomonas tessellata* lives: pH 4.1—7.5, content of CaO 3—42.9 mg/l, consumption of $KMnO_4$ 86—several hundred mg/l, contents of PO_4-P 0—0.03 mg/l, NH_3-N 0.4—0.55 mg/l, NO_3-N 0—0.43 mg/l; on January 31st, 1930 Sortedam II contained 0.35 mg Fe per litre.

Mallomonas tridentata n. sp.

Fig. nostra 70.

Diagnosis. Cellulae cylindricae vel longe ellipsoideae, in parte posteriore saepe subacutae, 50—81 μ longae, 16—20 μ latae, in natione cystae turgidae, ad 24 μ latae. Squamis siliceis ovalibus vel rotunde angulatis, tenuiter punctatis, in series spirales axi longiore transverse ordinatis, $4^1/_2$—$6^1/_2$ μ longis, 3—5 μ latis. Setis levibus, satis parcis, ad apices cellulae restrictis, 17—33 μ longis. Flagello corpori aequilongo vel paulo longiore. In parte anteriore cellulae nucleus submagnus situs. Duobus chromatophoris instructis, prope ad partem posteriorem cellulae attinentibus. Cystis longe obovatis vel fusiformibus, in parte posteriore acutis, in parte anteriore subtruncatis, et hic tribus verrucis instructis, 41—57 μ longis, 17—21 μ latis. Protoplasma et chromatophori cellulae a nata cysta prorsus non consumuntur.

Hab. In Vandingsdam et Sortedam II prope Hillerød, Dania, libere natans.

Systematics. In the vegetative state this species differs from *Mallomonas Teilingii* Conrad (1927, p. 465, Fig. 19; KRIEGER 1930, p. 286, Fig. 28) in the cell dimensions being a little larger and the scales smaller. When carrying cysts, however, the two species could not possibly be mistaken. For the rest both species were found together in Sortedam II in the plankton from the month of March.

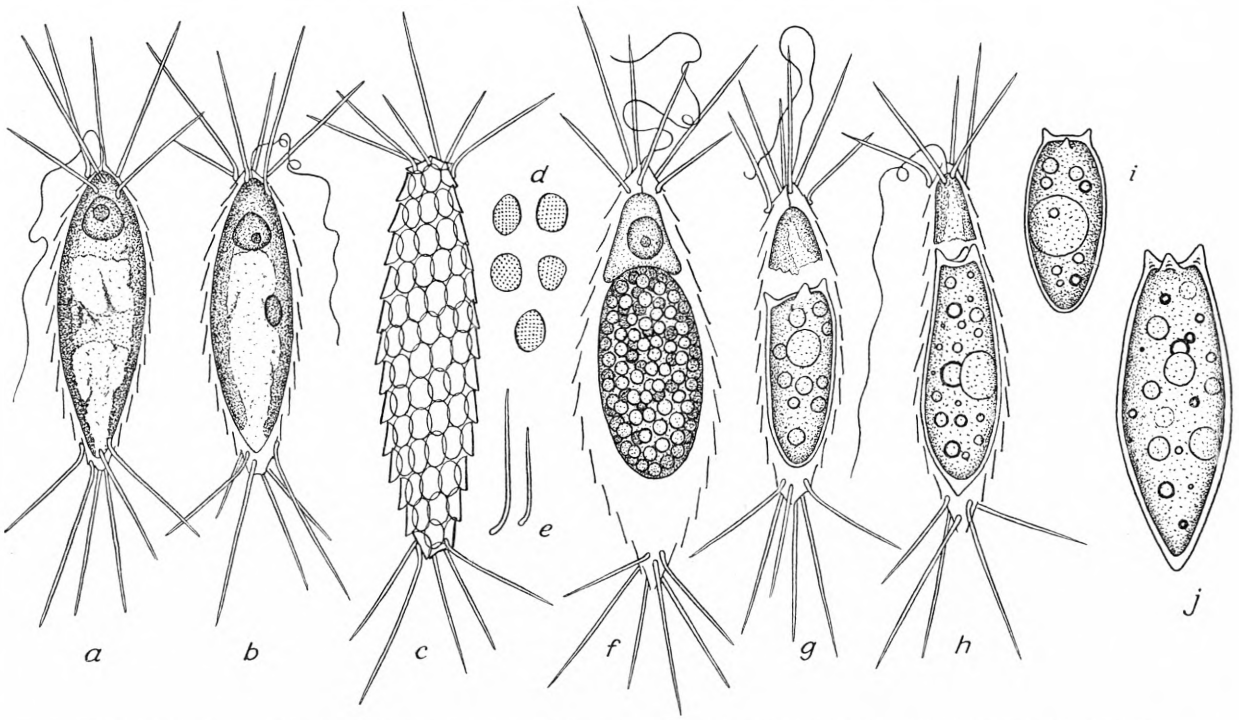


Fig. 70. *Mallomonas tridentata* n. sp.; *a*—*e*, g—*j* from Vandingsdam, March 15th, 1930; *f* from Sortedam II, March 15th, 1930. The punctulations of the silicified scales (*d*) are not delineated in fig. *c*. *g*—*h* are cells carrying cysts, *i*—*j* isolated cysts. *a*—*f* and *j* 800×, *g*, *h* and *i* 640×.

Periodicity. In Vandingsdam the species was observed only within the period between January 15th and April 1st, 1930. During the whole month of January it was extremely rare but gradually grew more and more frequent until it reached its highest development on March 15th (temp. 0° C.), at which time it was rather common in the plankton (48 individuals per ml). On April 1st it was rare again and was not found in the living plankton examined on April 7th. It failed to appear during the other months of the year. The formation of spores was observed for the first time on March 15th when a few individuals (3 %) carried spores. On April 1st only 2 individuals were found to carry spores and further 2 free spores were seen in the plankton of the pond. At the end of the vegetative period nearly all the *Mallomonas tridentata* individuals had apparently formed spores. In Sortedam II (where also *Mallomonas Teilingii* was present) a sure occurrence of the species in the plankton

was established on March 15th, 1930 only (temp. 4.5° C.), at which time a few specimens containing cysts occurred.

In other words the species is a stenothermic cold water form or distinctly oligothermic because it was observed only at temperatures between 0 and 4.5° C.

Sociology. The species occurred in the following associations in Vandingsdam:

Jan. 15th, 1930: *Tra vo*-association with *Sce arv* as subdominant (*M. tridentata* very rare).
— 31st, — : *Tra vo*-association with *Sce arv* as subdominant (*M. tridentata* very rare).
Feb. 17th, — : *Tra vo*-association (*M. tridentata* not infrequent).
Mar. 1st, — : *Tra vo*-association (*M. tridentata* not infrequent).
— 15th, — : *Chla ac - Chla ps*-association (*M. tridentata* rather common).
Apr. 1st, — : Indeterminable flagellate—*Tra vo*-association (*M. tridentata* rare).

In Sortedam II it was found only in the following association:

Mar. 15th, 1930: *Mallomonas* sp_1-association with *Crym ov* and *Ma ak* as subdominants (*M. tridentata* rare).

In other words *Mallomonas tridentata* principally occurred in flagellate associations of *Trachelomonas* and *Mallomonas* and in a green algae association of *Chlamydomonas*. In Sortedam II it occurred together with a number of *Mallomonas* species on March 15th, 1930: *M. akrokomos*, *M. semiglabra*, *M.* sp_1, *M. tessellata*, *M. Teilingii* and an indeterminable species of the *M. alpina* group.

The most constant associates were *Chlamydomonas pseudoplatyrhyncha* and *Trachelomonas volvocina*, which occurred in 86 % of the number of samples (7) that contained *Mallomonas tridentata*.

Ecology. Sortedam II is a typically eutrophic pond of the mixotrophic phase and highly overshadowed, while the polluted pond Vandingsdam, which has no inlets or outlets should rather be considered a transition stage between pronounced eutrophy and mixotrophy. Some ecological data of the species are: pH 6.6—7.1, consumption of $KMnO_4$ 67—87 mg/l, contents of CaO 18.7—42.9 mg/l, NH_3-N 0.25—0.4 mg/l, NO_3-N 0—0.55 mg/l, PO_4-P 0.018—0.04 mg/l and Fe 0.35—0.85 mg/l (the figures for iron basing only on the analyses from January).

Mallomonas sp_1.

Fig. nostra 71.

Cells spindle-shaped or vase-shaped with pointed posterior end, often curved, 15—29 μ long, 5—8 μ broad. Scales about 3 μ in size, form and structure unknown. Bristles also unknown. Flagellum $^1/_2$—$^3/_4$ time length of body. 2 brown chromatophores present. Cysts ellipsoidical or narrowly obovate, 9.5—13 μ long, 6—6.5 μ

broad, smooth; position of the cyst in posterior end of the cell. Only part of the protoplasm is used for the formation of the cyst.

In Spejldam, Sortedam II and Teglgaard Sø, NE-Seeland, pelagic.

Originally I intended to call this new *Mallomonas* species *Mallomonas curvata*, but both bristles and scales are so little known, that I consider it more correct to give it the provisional name of *Mallomonas* sp_1. In spite of reiterated attempts with several dry-slides I never managed to establish the exact character of the scales. They are

Fig. 71. *Mallomonas* sp_1; upper row: cells from Spejldam, March 1st, 1930; lower row: cells from Sortedam II, April 1st, 1930. 800×.

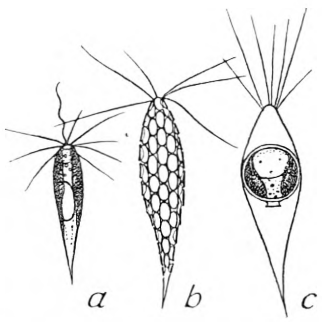


Fig. 71 bis. *Mallomonas akrokomos* Ruttner; *a* from Gadevang Mose, September 21st, 1929; *b* from field pool N of Søndre Landevej, Sønderborg, February 27th, 1938; *c* from Badstue-Ødam, March 15th, 1930. *a* and *c* 750×, *b* 1070×.

probably pyriform or ovate, in the latter case with a v-shaped marking. These 2 types of scales were found close to the dry individuals of *Mallomonas* sp_1, but it remains an open question which of the types is appurtenant.

For the sake of comparison some drawings of *Mallomonas akrokomos* Ruttner are given in Figura nostra 71 bis. The siliceous scales are elliptical not triangular as Conrad has stated (see Huber-Pestalozzi 1941, p. 93, fig. 109), their margins are touching each other and the measurements are 2 $\mu \times 1$ μ. Further the collar of the cyst is often antapically directed.

Periodicity. In Spejldam the species occurred only in March 1930: it was common on March 1st (temp. 1.5° C.) and rare on March 15th (temp. 3° C.). Both times cysts were observed. In Sortedam II a few individuals of the species appeared on February 17th, 1930 (temp. 1° C.); on March 1st (temp. 1.5° C.) it was common but the great maximum was not reached until March 15th (temp. 4.5° C.) when cysts were observed. After this it decreased in frequency, and the last few specimens were observed on April 10th (temp. 8° C.). In Teglgaard Sø a few individuals occurred

throughout November 1929; the species showed a somewhat higher frequency in March 1930 with an inconsiderable maximum on March 15th (temp. 2.5° C.). In this locality the last individuals were seen on April 22nd (temp. 7° C.).

In other words the species is decidedly oligothermic with a temperature amplitude of 0.5—8° C. and a distinct maximum with formation of cysts in March at temperatures between 0.5 and 4.5° C.

Sociology. The species occurred in Spejldam in the following associations:

Mar. 1st, 1930: *Chla ac*-association (*Mallomonas* sp_1 common).
— 15th, — : *Ma se*-association with *Ank fa se br* as subdominant (*Mallomonas* sp_1 very rare).

In Sortedam II the species occurred in these associations:

Feb. 17th, 1930: phytoplankton very scarce, association perhaps dominated by *Gle Lo* and *Ma Te* (*Mallomonas* sp_1 very rare).
Mar. 2nd, — : *Ma* sp_1-association (*Mallomonas* sp_1 common).
— 15th, — : *Crym ov - Ma* sp_1-association with *Ma ak* as subdominant (*Mallomonas* sp_1 very common).
Apr. 1st, — : *Crym ov*-association (*Mallomonas* sp_1 rather common).
— 4th, — : *Crym ov - Ank fa se el*-association (*Mallomonas* sp_1 rare).
— 10th, — : *Crym ov*-association with *Chla ac* as subdominant (*Mallomonas* sp_1 rare).

In Teglgaard Sø the species was seen in the following associations:

Nov. 2nd, 1929: *Chry mi*-association (*Mallomonas* sp_1 very rare).
— 16th, — : *Crym ov*-association (*Mallomonas* sp_1 very rare).
— 30th, — : *Crym ov*-association (*Mallomonas* sp_1 very rare).
Mar. 1st, 1930: *Ank fa se br*-association (*Mallomonas* sp_1 very rare).
— 15th, — : *Chry mi - Crym ov - Ste Ha*-association (*Mallomonas* sp_1 not infrequent).
Apr. 22nd, — : *Crym ov - Syu Pe - Syu ec*(?)-association (*Mallomonas* sp_1 very rare).

The species thus principally occurred in flagellate associations dominated by *Cryptomonas*, *Mallomonas*, *Synura* and *Chrysococcus*, more rarely in green algae associations of *Ankistrodesmus* and *Chlamydomonas*.

The most constant associates were *Cryptomonas ovata* and *Stephanodiscus Hantzschii*, which occurred in 86 and 79 % resp., of the number of samples (14) that contained *Mallomonas* sp_1.

Ecology. Both Spejldam and Sortedam II are greatly overshadowed ponds of some coolness in summer; Teglgaard Sø lies in open land. All of them have inlets and outlets. Spejldam stands between eutrophy and mixotrophy, Sortedam II is typically eutrophic of the mixotrophic phase and Teglgaard Sø is a eutrophic pond, partly overgrown with reed swamp. Some data of the ecology of the species: pH 6.8—

8.0, consumption of $KMnO_4$ 49—89 mg/l, contents of CaO 40—59.5 mg/l, NH_3-N 0.15—0.6 mg/l, NO_3-N 0.01—2.5 mg/l, PO_4-P 0.01—0.055 mg/l, Fe 0.35 mg/l in Sortedam on January 31st and 0.45 at the same time in Teglgaard Sø.

Coccolithophoridaceae.

Hymenomonas stagnicola Kampt.

Kamptner 1930, p. 150; Conrad 1928, p. 64, figs. 6—7 *sub nomine Pontosphaera stagnicola* Chodat et Rosillo.—*Fig. nostra* 72.

Cells spherical, about 20 μ in diameter, with a yellowish brown patelliform chromatophore. The envelope with numerous, close-set, oval coccoliths, about 2 μ long and 1 μ broad.

Distribution. Badstue-Ødam and Teglgaard Sø, Seeland; Flødegaardens Dam, Funen, pelagic.

Systematics. As the coccoliths are numerous and densely situated on the surface of the envelope, the correctness of the determination is hardly dubious though no flagella were observed in the Danish specimens. All determinations were made with living plankton material. A renewed examination of the most important samples and of the quantitative slides gave a negative result, presumably because the coccoliths had been decomposed by the formic acid of the formalin.

Periodicity. *Hymenomonas stagnicola*, which was originally found by Chodat and Rosillo in a pond near Geneva in 1925, is rare in this country where it was observed only in April-June at temperatures between 12.5 and 24° C. and in September (temp. 18.5° C.). The 3 localities mentioned above were examined regularly every fortnight for at least one year and so it may be said with some degree of certainty that the species is periodical and meso- to polythermic.

Sociology. The species was found in the following associations:

Badstue-Ødam.

Sep. 5th, 1929: *Ana af in te*-association with *Os li ac* as subdominant (the species not infrequent).

Apr. 26th, 1930: *Din so - Sye ac an*-association with *Ma pe ec* as subdominant (the species very rare).

May 16th, — : *Ura vo*-association (694 colonies per ml; the species very rare).

June 16th, — : *Crym ov*-association with *Ana af in te* and *Cyc st su* as subdominant (the species very rare).

Flødegaardens Dam.

June 10th, 1930: association of indeterminable green alga with *Chry mi* as subdominant (the species very rare).

Teglgaard Sø.

Apr. 29th, 1930: *Din di*-association with *Chry mi*, *Sye ac an* and *Syu Pe - Syu ec*(?) as subdominant (the species very rare).

In other words the species primarily occurred in associations characterized by *Chrysophyceae* (*Dinobryon*, *Uroglena*), further in diatomaceous (*Synedra*), myxophycean (*Anabaena*), chlorophycean and cryptophycean (*Cryptomonas*) associations.

The most constant associate was *Trachelomonas intermedia*, which occurred in 100 % of the number (6) of samples that contained *Hymenomonas stagnicola*; the following were found in 83 % of the samples: *Cyclotella Meneghiniana*, *Stephanodiscus Hantzschii*, *Asterionella formosa*, *Synedra acus* var. *angustissima*, *Glenodinium edax* and *Trachelomonas volvocina*.

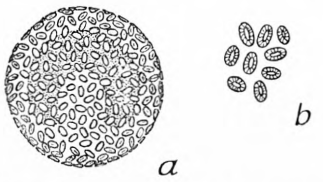


Fig. 72. *Hymenomonas stagnicola* Kampt. from Badstue-Ødam, September 5th, 1929. *a* 1070×, *b* 2140×.

Ecology. Flødegaardens Dam is a small, polluted, very highly eutrophic pond, always alkaline and rich in lime; Badstue-Ødam is also eutrophic, alkaline and rich in lime, but not nearly so polluted; see further Table III. Teglgaard Sø is a comparatively large, shallow and alkaline pond, overgrown with reed swamps; the following data speak for its eutrophy: On June 22nd, 1929 the plankton consisted of a *Rhi lo - Ste Ha*-association (65 species) with the myxophycean quotient $\frac{1}{3}$, the chlorophycean $\frac{21}{3}$, the diatom $\frac{5}{6}$, the euglenine $\frac{13}{22}$ and the compound quotient $\frac{40}{3} = 13.3$. On August 23rd, 1929: *Pa mo*-association with *Mel am* and *Ank co mi* as subdominants (40 species); the plankton quotients mentioned in the same order as above were $\frac{2}{4} - \frac{11}{4} - \frac{3}{6} - \frac{6}{13} - \frac{22}{4} = 5.5$. On June 16th, 1930: *Crym ov*-association (34 species) with the plankton quotients $\frac{2}{1} - \frac{7}{1} - \frac{6}{9} - \frac{2}{9} - \frac{17}{1} = 17$.

A few data of the ecology of *Hymenomonas stagnicola* are: pH 7.7—8.8, CaO 59.5—82.2 mg/l, consumption of $KMnO_4$ 44—57 mg/l, contents of PO_4-P 0—0.01 mg/l, NH_3-N 0.05—0.1 mg/l, NO_3-N 0—0.01 mg/l, Fe 0.02 mg/l,

Synuraceae.

Synura.

In my 1945 paper (Dansk Plante-Plankton, p. 24, Fig. 17) *Synura uvella* Ehrb. var. *punctata* Awerinzew is given as a characteristic form of oligotrophic localities of the dystrophic phase. This form is identical with *Synura sphagnicola* Korshikov (1929, p. 287; 1927, p. 450, t. 7 *sub nomine Skadowskiella sphagnicola* Korshikov) and in the living state is recognizable by the small haematochrome granules in the peripheral part of the cell. On May 24th, 1930 living colonies from Bøndernes Mose I were placed in osmic acid: the red granules did not change their colour. If they had in fact been oil-droplets as stated in Pascher's Süsswasserflora, Heft 2, 1913, p. 51, they would have turned black.

Synura Petersenii Korshikov (1929, p. 283, t. 11, figs. 54—58, text-figure A) is widely distributed both in large Danish lakes and in Danish ponds; this is also true of *Synura sphagnicola* (see Tables II and IV). *Synura spinosa* Korshikov (1929, p. 281, t. 11, figs. 38—41) is comparatively common, but I have only found it in ponds (see Table IV). *Synura echinulata* Korshikov and *Synura glabra* Korshikov (1929, p. 282 and p. 285, t. 11, figs. 42—53 and figs. 59—65) I have only seen in the *Eriophorum* moor on March 20th, 1948 when they occurred sparsely together with large amounts of *Synura Petersenii* colonies and smaller quantities of *Synura spinosa* colonies (see further under *Mallomonas tessellata* p. 131).

On April 22nd, 1930 Teglgaard Sø contained *Synura Petersenii* and a form of *Synura echinulata*, the scales of which, however, were of the same size as those of *Synura spinosa* and were furnished with 2—3 minute apical teeth.

Certain colonies of this sample had red granules in the anterior part of the living cells, but in the dry slide no scales of *Synura sphagnicola* were found. So it seems that beside this species one (or some) of Korshikov's other *Synura* species may have haematochrome granules in the peripheral part of the cells.

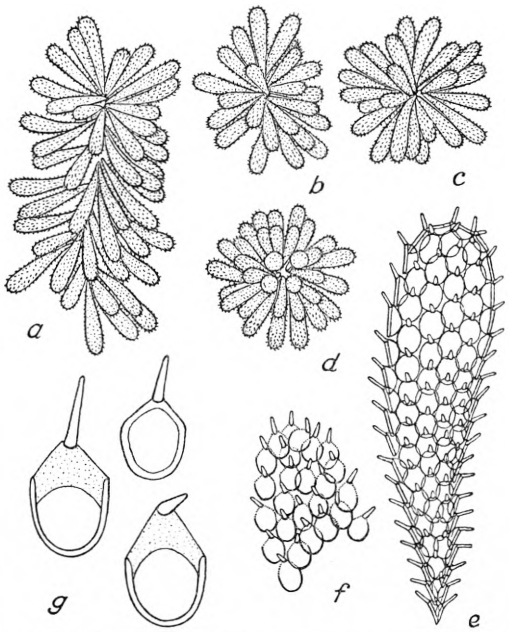


Fig. 72 bis. *Synura Adamsii* G. M. Smith from Ryven Sjön, Sweden; *a*—*d* four colonies fixed in formalin, *e* a single cell (only the scales are drawn), *f*—*g* scales from material dried up on a cover-slip. *a*—*d* 260×, *e*—*f* 1200×, *g* 3600×.

Dr. Einar Teiling kindly sent me a Swedish plankton sample containing *Gemellicystis neglecta*. In this sample, where *Tabellaria fenestrata* var. *asterionelloides* and *Mallomonas caudata* Krieger (non Iwanoff) were the dominating organisms, colonies of the rare *Synura Adamsii* G. M. Smith were found (see Huber-Pestalozzi 1941, p. 144, fig. 200). Some of these colonies were isolated by means of my micro-manipulator. Each of the cells had two chromatophores, but also the basal part of the cell was provided with short spines. As the structure of the scales is unknown I give a figure (Fig. nostra 72 bis) of this interesting species from Ryven Sjön, Sweden. The dimensions of the scales were 3—4.5 $\mu \times 2.3$—3 μ, length of spines 1.5—2.7 μ. As distinct from the spines of the closely related species *Synura spinosa* Korsh. the spines of *Synura Adamsii* are not situated in the scale plane as shown in Fig. nostra 72 bis *e*. In the sample I found 36 species; the myxophycean quotient was $\frac{9}{6} = 1.5$, the chlorophycean $\frac{5}{6} = 0.8$, the diatom $\frac{4}{3} = 1.3$, the euglenine $\frac{0}{14} = 0$ and the compound quotient $\frac{18}{6} = 3$ which indicates moderate eutrophy.

Bacillariophyceae.

Centrales.

Discoideae.

Cyclotella Meneghiniana Kg. emend. Nyg.

Syn.: *Cyclotella Meneghiniana* Kg. var. *spinifera* Nygaard, Dansk Plante-Plankton, 1945, p. 52, t. 1, fig. 21.—*Fig. nostra* 73 and 73 *bis*.

To the original diagnosis should be added: typus spinis parvis inter costas instructus.

Distribution. Sandbjerg Sø at Alssund, Miang Dam on Als, Flyndersø in North Jutland, pond at Sønder Landevej, Sønderborg, all in Jutland; Flødegaardens Dam at Nyborg, Funen; Badstue-Ødam, Vandingsdam, Hesteskodam, Frederiksborg Slotssø, Badstue-Dam, Hulsø and pond in Fælledparken, København, all in North-East Seeland.

Systematics. In the beginning I considered the spines an optical illusion but after having reverted to the problem several times in the process of time I am now certain that there are in fact spines on *Cyclotella Meneghiniana*. At high focussing they are seen as small black dots, but they sometimes appear with the greatest distinctness in girdle-view or on obliquely situated shells. The fact that experienced scientists like van Heurck, Grunow, A. Schmidt, Fr. Hustedt a. o. observed no such spines seemed to indicate that they are not present, and so it was presumably legitimate to put up var. *spinifera* Nyg. A close examination of slide No. 478 in Henri Van Heurck's Types du Synopsis de Diatomées de Belgique, has shown, however, that minute spines are really present on the individuals of *Cyclotella Meneghiniana* (see Fig. nostra 73 bis).

On August 28th, 1926 *Cyclotella Meneghiniana* with long bristles (Fig. 73) were observed in the plankton of Flødegaardens Dam. This is the first time that such bristles have been observed in singly living *Cyclotella* species!

Periodicity. In Sandbjerg Sø it reached a very great maximum in the plankton on September 4th, 1938 (temp. 17° C.). This was not the case on September 4th, 1937 or on September 3rd, 1939 though the species was present. On August 6th, 1939 and August 26th, 1944 it was common or rather common. In Badstue-Ødam, which was examined regularly, it was probably perennial though extremely rare in the winter months and not present in all the winter samples. A distinct maximum occurred on September 23rd, 1929 (temp. 13.5° C.); the species was also comparatively common on October 3rd—12th (temp. 12.5—10° C.) occurring in short chains with up to 4 individuals in each! In Flødegaardens Dam, where *Cyclotella*

Meneghiniana was periodical, it reached a distinct maximum on August 28th, 1926; in 1927 there was no maximum, but in 1928 there was one on September 21st (temp. 14° C.). In 1929 the highest frequency of the species was found on September 15th.

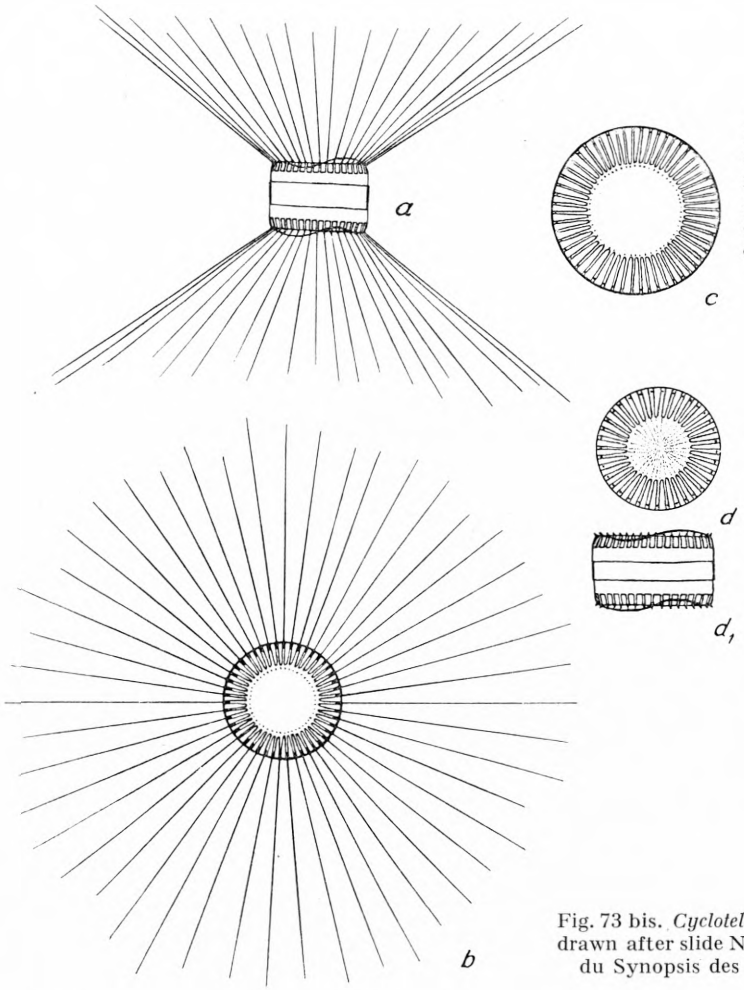


Fig. 73. *Cyclotella Meneghiniana* Kg. emend. Nyg.; *a*—*b* individuals carrying silicified bristles from Flødegaardens Dam, August 28th, 1926; *c* from Flyndersø, July 3rd, 1938; *d*—d_1 from Sandbjerg Sø, September 4th, 1938. 800×.

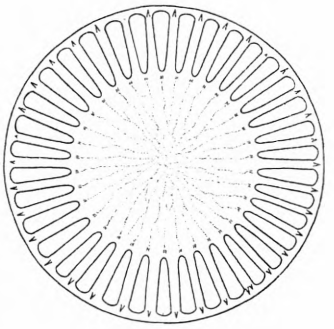


Fig. 73 bis. *Cyclotella Meneghiniana* Kg. emend. Nyg. drawn after slide No. 478 in Henri van Heurck: Types du Synopsis des Diatomées de Belgique. 2400×.

In Frederiksborg Slotssø very small quantities were seen in the autumn and the beginning of the winter of 1929.

Altogether we may conclude that the optimal development of *Cyclotella Meneghiniana* normally falls in September at temperatures between 13.5 and 17° C. It is sometimes common also in July-August and in October. It seems to occur somewhat sporadically or rather to be facultatively periodical, being perennial in certain localities and periodical through several years in others. The species must be considered eurythermic with a temperature amplitude of 2.5—26.5° C.

Sociology. *Cyclotella Meneghiniana* was found in 92 samples. The following is a survey of the associations because it would be unpractical to give them in the usual way:

Associations containing *Cyclotella Meneghiniana*.

The relative frequencies of *Cyclotella* and the dates of the samples are given parenthetically.

Bacteria	*Flagellatae*	*Myxophyceae*	*Diatomeae*	*Chlorophyceae*
La hy (rr, $^{5}/_{9}$-29)	*Chry ma* (r, $^{28}/_{10}$-29)	*Ana fl* (rrr, $^{30}/_{7}$-27)	*Cyc Me* (c, $^{28}/_{8}$-26)	*Ank fa sp* (rrr, $^{5}/_{6}$-28)
La hy (r, $^{15}/_{9}$-29)	*Chry ma* (rrr, $^{23}/_{11}$-29)	*Api fl* (rr, $^{6}/_{7}$-38)	*Cyc Me* (ccc, $^{4}/_{9}$-38)	*Ank co mi*—*Mio ho* (+, $^{23}/_{9}$-29)
La hy — *Teë mi* (rrr, $^{4}/_{10}$-29)	*Chry ma* (rr, $^{15}/_{1}$-30)	*Mio ho* (rrr, $^{20}/_{7}$-27)	*Cyc st su* (rr, $^{21}/_{5}$-39)	*Ank fa se br* (rrr, $^{4}/_{4}$-30)
	Crym ov (rr, $^{12}/_{9}$-29)	*Mio ho* — indeterm. *Chlorophyceae* (rrr, $^{13}/_{7}$-28)	*Cyc st su* (rr, $^{10}/_{8}$-29)	*Ank fa sp* (rrr, $^{29}/_{10}$-26)
	Crym ov (rrr, $^{23}/_{10}$-29)	*Mio ho* (r, $^{20}/_{7}$-28)	*Cyc st su* (rr, $^{17}/_{8}$-29)	*Chla Re mi* (rr, $^{15}/_{8}$-27)
	Crym ov (r, $^{16}/_{6}$-30)	*Mio ho* (r, $^{2}/_{8}$-28)	*Cyc st su* (rr, $^{3}/_{9}$-29)	*Chla Re mi* (rr, $^{30}/_{8}$-27)
	Din di (c, $^{28}/_{7}$-26)	*Mio ho* (rrr, $^{2}/_{9}$-28)	*Cyc st su* (r, $^{31}/_{5}$-30)	*Chla Re mi* (rr, $^{23}/_{10}$-27)
	Din so (r, $^{18}/_{9}$-29)	*Mio ho* (rrr, $^{7}/_{9}$-28)	*Dia vu gr* (rrr, $^{21}/_{2}$-44)	Indeterm. *Chlorophyceae* (rr, $^{2}/_{7}$-29)
	Din so — *Cyc co* (r, $^{16}/_{5}$-30)	*Mio ho* (rr, $^{15}/_{9}$-28)	*Frg ca* (rr, $^{19}/_{6}$-25)	Indeterm. *Chlorophyceae* (rrr, $^{10}/_{6}$-30)
	Din so — *Sye ac an* (r, $^{25}/_{1}$-30)	*Mio ho* — *Ni ac* (r+, $^{21}/_{9}$-28)	*Frg cr* (rrr, $^{23}/_{8}$-29)	*Dic pu* — *Din di* (rr, $^{1}/_{7}$-26)
	Din so am (rrr, $^{14}/_{6}$-28)	*Mio ho* — *Tra hi* (rrr, $^{9}/_{9}$-29)	*Mel gr* (+, $^{1}/_{10}$-38)	*Ul pe* — *Mio ho* (rrr, $^{5}/_{7}$-28)
	Tra vo (rrr, $^{1}/_{12}$-27)	*Os Ag* (rrr, $^{6}/_{9}$-29)	*Mel gr an* (rr, $^{6}/_{6}$-29)	*Ul pe* (rrr, $^{2}/_{6}$-29)
	Ura vo (r, $^{1}/_{5}$-30)	*Os li* (rr, $^{4}/_{9}$-37)	*Mel gr an* (rrr, $^{21}/_{8}$-43)	*Ki mi* — *Mio ho* — *Ni ac* (rrr, $^{1}/_{10}$-28)
	Ura vo (r, $^{16}/_{5}$-30)		*Mel gr* + *an* (c, $^{6}/_{8}$-39)	*Ki mi* — *Mio ho* — *Ni ac* (rrr, $^{10}/_{10}$-28)
	Ura vo (r, $^{21}/_{5}$-30)		*Ni ac* (rrr, $^{2}/_{8}$-40)	*Pa mo* (rr, $^{14}/_{8}$-38)
			Rhi lo (r, $^{20}/_{6}$-29)	*Sce arm* (rrr, $^{21}/_{11}$-29)
			Rhi lo (r, $^{1}/_{7}$-29)	*Sce arm* (rr, $^{16}/_{12}$-29)
			Rhi lo (r, $^{5}/_{7}$-29)	*Sce arm* (rr, $^{15}/_{1}$-30)
			Rhi lo (r, $^{17}/_{7}$-29)	*Sce arm* — *Teë mi* (rr, $^{23}/_{10}$-29)

Bacteria	*Flagellatae*	*Myxophyceae*	*Diatomeae*	*Chlorophyceae*
			Rhi lo (rrr, $^{26}/_{7}$-29)	*Sce arv — Dic pu* (rrr, $^{19}/_{6}$-29)
			Ste du (rrr, $^{16}/_{6}$-25)	*Sce ec* (+, $^{26}/_{8}$-44)
			Ste Ha (rrr, $^{17}/_{4}$-27)	*Se ca* (rrr, $^{9}/_{11}$-27)
			Ste Ha (rrr, $^{1}/_{5}$-27)	*Spc Sc* (rr, $^{12}/_{7}$-40)
			Ste Ha (rr, $^{2}/_{6}$-27)	*Teë mi* (rr, $^{21}/_{10}$-29)
			Ste Ha (rrr, $^{18}/_{11}$-28)	*Tet st* (rrr, $^{17}/_{5}$-27)
			Ste Ha (c+, $^{15}/_{9}$-38)	
			Ste Ha (r+, $^{3}/_{10}$-29)	
			Ste Ha — Cyc Me (c, $^{5}/_{10}$-29)	
			Ste Ha (r+, $^{12}/_{10}$-29)	
			Ste Ha (rrr, $^{15}/_{3}$-30)	
			Ste Ha (rrr, $^{1}/_{4}$-30)	
			Ste Ha (rrr, $^{3}/_{4}$-30)	
			Ste Ha (rrr, $^{2}/_{4}$-29)	
			Ste Ha — Sye ac an — Ura vo (rr, $^{22}/_{4}$-30)	
			Ste Ha — Sye ac an — Ura vo (r, $^{10}/_{5}$-30)	
			Sye ac an (rr, $^{22}/_{4}$-30)	

As will be seen the species was found in 36 Diatom associations of *Cyclotella*, *Diatoma*, *Fragilaria*, *Melosira*, *Nitzschia*, *Rhizosolenia*, *Stephanodiscus* and *Synedra*, 25 green alga associations of *Ankistrodesmus*, *Chlamydomonas*, *Dictyosphaerium*, *Ulothrix*, *Kirchneriella*, *Pandorina*, *Scenedesmus*, *Sphaerocystis*, *Tetraëdon* and *Tetrastrum*, 15 Flagellate associations of *Chrysococcus*, *Cryptomonas*, *Dinobryon*, *Trachelomonas* and *Uroglena*, 13 blue-green alga associations of *Anabaena*, *Aphanizomenon*, *Microcystis* and *Oscillatoria* and 3 bacterial associations of *Lampropedia*. Among the

36 Diatom associations no less than 11 are dominated by *Stephanodiscus Hantzschii*, which in high production is characteristic of eutrophy, and among the 13 blue-green alga associations 6 are dominated by *Microcystis holsatica*, which in high production indicates a high degree of eutrophy; if regard is paid to mixed associations, the former is found in 14, the latter in 13 associations.

The most constant associates were *Scenedesmus armatus* and *Microcystis holsatica*, which were found in 82 and 77 per cent., respectively, of the number of samples (92) that contained *Cyclotella Meneghiniana*.

Ecology. Both Sandbjerg Sø, Miang Dam, Flyndersø, Flødegaardens Dam, Hesteskodam, Frederiksborg Slotssø, Badstue-Dam and the pond in Fælledparken, København are typically eutrophic waters, lying in open land and nearly all of them with both inlets and outlets; several of them are highly polluted. The pond at Sønderborg, Badstue-Ødam and Vandingsdam stand between eutrophy and its mixotrophic phase whereas the overshadowed Hulsø is decidedly mixotrophic. The great Danish pH material allows us to say that the pH limits for *Cyclotella Meneghiniana* are probably not far beyond 7.4 and 9.2, most pH values lying above 8. Among the other environmental factors may be mentioned: consumption of $KMnO_4$ 40—57 mg/l, contents of CaO 27—90 mg/l, Fe 0.02—0.3 mg/l, NH_3-N 0.05—1.25 mg/l, NO_3-N 0—3 mg/l, and PO_4-P 0—1.5 mg/l, figures that are characteristic for this eutraphentous species.

Cyclotella stelligera Cleve et Grunow var. **subglabra** nov. var.

Fig. nostra 74.

Diagnosis. A forma typica hoc modo differt: pars centralis valvae incompte et saepe inconspicue punctata, non striata; pars marginalis lata, striis instructa. Cellulae minutissimae, 4—11 μ in diametro, $2^1/_2$—6 μ altae, distantia inter strias 0.6—1.1 μ.

Hab. In Badstue-Ødam, Hulsø et Furesø, Selandia; Sandbjerg Sø, Jutlandia meridionali, Dania, libere natans.

Systematics. The small *Cyclotella* species are difficult to determine, even under the best lenses (numerical aperture 1.40). The individuals pictured in Fig. 74 are drawn from material mounted in realgar. The individuals from Badstue-Ødam were only 5—8 μ in diameter, 2.5—4 μ high, and the distance between the *striae* was 0.6—0.7 μ. On May 21st, 1939 the individuals from Sandbjerg Sø were quite similar (4—7 μ in diameter, distance between the *striae* 0.56—0.75 μ); on September 4th, 1938, however, the individuals were somewhat larger: diameter 5—11 μ, height 3—6 μ, distance between *striae* 0.8—1.1 μ.

In structure the variety described differs from *Stephanodiscus Hantzschii* by the total lack of marginal spines and radial series of points from the centre to the margin of the valve. Apart from this the two forms are different in a biological respect as will appear from the following section.

Periodicity. Among the 4 localities mentioned Badstue-Ødam was examined fortnightly throughout the period June 1929—June 1930. By the end of July the variety appeared in very small quantities, but in August it reached an enormous maximum (at temp. 18—20° C.), which in a somewhat reduced state continued till the beginning of September. At the end of this month the species was comparatively rare, and it was seen for the last time on November 2nd (temp. 5.5° C.). It did not reappear until May 10th, 1930 (temp. 12° C.) and at the end of this month once more reached an enormous maximum at a temperature of 20.5° C. In June 1930 the variety was only common in the plankton.

In Sandbjerg Sø the variety was comparatively common on September 4th, 1938 (temp. 17° C.), but was not found on August 14th, 1938 when the temperature was 26.5° C. Both on May 21st, 1939 and on May 15th, 1940 the variety reached an enormous maximum.

In Hulsø the variety was rare in June 1928 and in Furesø it was also rare on August 21st, 1943.

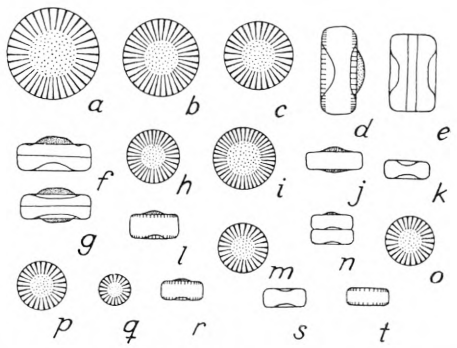


Fig. 74. *Cyclotella stelligera* Cleve et Grunow var. *subglabra* n. var.; *a*—*g* from Sandbjerg Sø, September 4th, 1938; *h*—*l* from Badstue-Ødam, August 17th, 1929; *m*—*t* from Sandbjerg Sø, May 21st, 1939. *a*, *b*, *c*, *h*, *i*, *m*, *o*, *p* and *q* vertical views, the other figures lateral views. 1070×.

From this very limited material one will be inclined to draw the following conclusions. *Cyclotella stelligera* var. *subglabra* is periodical, not occurring between December and April. It reaches 2 enormous maxima in the course of the year, both at temperatures of 18—20.5° C., one in May, the other in August (— September).

In comparison it may be stated that *Stephanodiscus Hantzschii* in Badstue-Ødam very normally reached a considerable maximum in October 1929 and an enormous maximum in April 1930. The latter declined during May, so that *Stephanodiscus Hantzschii* was rare on May 31st, at the very time when *Cyclotella stelligera* var. *subglabra* was abundant.

Sociology. The variety occurred in the following associations:

Badstue-Ødam.

July 26th, 1929: *Rhi lo*-association (variety very rare).
Aug. 10th, — : *Cyc st su*-association with *Frg cr* as subdominant (variety abundant).
— 17th, — : ditto.
— 23rd, — : *Frg cr*-association with *Ana af in te* and *Cyc st su* as subdominants (variety common).
Sep. 3rd, — : *Cyc st su*-association with *Ana af in te* as subdominant (variety very common).
— 5th, — : *Ana af in te*-association with *Os li ac* as subdominant (variety rather common).

Sep. 12th, — : *Crym ov*-association (variety rather common).
— 23rd, — : *Ank co mi - Mio ho*-association with *Ste Ha* as subdominant.
Nov. 2nd, — : *Chry ma - Crym ov*-association (variety very rare).
May 10th, 1930: *Ste Ha - Sye ac an - Ura vo*-association (variety rare).
— 21st, — : *Ura vo*-association (variety not infrequent).
— 31st, — : *Cyc st su*-association (variety abundant).
June 16th, — : *Crym ov*-association with *Ana af in te* and *Cyc st su* as subdominants (variety common).

Sandbjerg Sø.

Sep. 4th, 1938: *Cyc Me*-association with *Ste Ha* as subdominant (variety rather common).
May 21st, 1939: *Cyc st su*-association (variety abundant).
— 15th, 1940: ditto.

Hulsø.

June 14th, 1928: *Din so am*-association (variety rare).

Furesø.

Aug. 21st, 1943: *Mel gr an*-association (variety rare).

Cyclotella stelligera var. *subglabra* itself may form associations; otherwise it mostly occurs in diatom associations of *Melosira*, *Cyclotella*, *Stephanodiscus*, *Rhizosolenia*, *Fragilaria* and *Synedra*, to a less degree in chrysophycean associations of *Chrysococcus*, *Uroglena* and *Dinobryon*, myxophycean associations of *Microcystis* and *Anabaena*, cryptophycean associations of *Cryptomonas* and chlorophycean associations of *Ankistrodesmus*.

The most constant associates were *Scenedesmus armatus*, which occurred in 89 % of the number (18) of samples that contained *Cyclotella stelligera* var. *subglabra*; *Coelastrum microporum* + forma *astroidea*, *Asterionella formosa* and *Cyclotella Meneghiniana*, all of which occurred in 83 % of the samples and *Pediastrum duplex* and *Cryptomonas ovata*, which occurred in 78 %.

Ecology. All 4 localities mentioned above are eutrophic; Furesø is a large, moderately eutrophic lake, Sandbjerg Sø a small, extremely eutrophic lake, Badstue-Ødam a typically eutrophic pond approaching mixotrophy and Hulsø a small, eutrophic forest lake of the mixotrophic phase. The plankton quotients for Furesø and Hulsø appear from Table I, for Badstue-Ødam from Table III, and for Sandbjerg Sø they are given on p. 204. The compound quotients are: for Furesø $\frac{22}{5} = 4.4$, $\frac{42}{12} = 3.5$ and $\frac{28}{8} = 3.5$, Hulsø $\frac{25}{1} = 25$ and $\frac{35}{7} = 5$, Badstue-Ødam $\frac{20}{2} = 10$ and $\frac{38}{3} = 12.7$, Sandbjerg Sø $\frac{31}{0}$, $\frac{26}{1}$, $\frac{39}{1}$, $\frac{34}{1}$, $\frac{39}{1}$, $\frac{31}{1}$ and $\frac{23}{1}$.

A few data of the ecology of the variety are: pH 7.8—8.8, content of CaO 75.3—81.4 mg/l (113.1 in Sandbjerg Sø on August 19th, 1945), consumption of $KMnO_4$ 54—57 mg/l (in Furesø about 10—20 mg/l), contents of PO_4-P 0—0.01 mg/l, NH_3-N 0.08—0.15 mg/l, NO_3-N 0—0.3 mg/l and Fe 0.02 mg/l.

Cryptophyceae.

Cryptomonadales.

Cryptomonadaceae.

Cryptochrysis minor n. sp.

Fig. nostra 75.

Diagnosis. Cellulae parvae, a latere visae subobovatae, ventraliter plusminusve applanatae sunt; latus ventrale brevius quam latus dorsale est; cellulae in parte anteriore oblique truncatae, posteriore attenuatae et rotundatae sunt. Unus chromatophorus dorsalis aureus, pyrenoide in latere dorsali instructus. Sulcus ventralis granula in duobus seriebus ordinata habet. Gula abest. Duo flagella, dimidia longitudine cellulae, in partem apicalem sulci inserta sunt. Longitudo cellularum 8—9 μ, latitudo 3—5 μ.

Hab. In Peblinge Sø, Hafnia, Dania, libere natans.

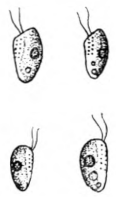


Fig. 75. *Cryptochrysis minor* n. sp. from Peblinge Sø in København, June 12th, 1930. 750×.

The species differs from *Cryptochrysis commutata* Pascher, which has been seen several times in Danish ponds, and from *C. polychrysis* Pascher by having only one chromatophore and by its small size.

Cryptochrysis minor swims in the same way as *Cryptomonas ovata* Ehrb. and like the latter is able to make very quick jumps. It was very common in Peblingesø on June 12th, 1930 at a temperature of 18.5° C. and pH 8.5. This shallow pond, which is situated in the middle of København, was rather poor in plankton, and the filtered plankton contained a great deal of detritus. On the said date the most numerous organism of the plankton—besides *Cryptochrysis minor*—was *Stephanodiscus Hantzschii* Grun.

Rhodomonas lacustris Pasch. et Ruttn.

Pascher's Süsswasserflora, Heft 2, 1913, p. 103, figs. 157—158.—*Fig. nostra* 76.

Cells obovate—cylindrical, twice as long as broad, not flattened, to some extent obliquely blunted in front, with flatter ventral than dorsal side. Edges of ventral furrow set with granules. Subapically inserted 2 nearly equally long flagella, the longer of which is a little shorter than the cell. One reddish-brown chromatophore with a distinct tinge of carmine; it possesses a deep, dorsal, longitudinal incision, which may give it the look of having 2 chromatophores. One non-axial pyrenoid halfway up the cell. Apically 1 big, pulsating vacuole; antapically the nucleus. Length of cells 14—15.5 μ, breadth 7—8 μ.

Occurrence: Esrom Sø and Furesø, NE-Seeland.

Systematics. It is with some hesitation that I identify the present individuals as *Rhodomonas lacustris* because the greatest breadth of the cells is not found so near the apex as in the type material and because the latter does not possess the dorsal incision of the chromatophore. Further the length is stated by RUTTNER & PASCHER to be only 10—13 μ (breadth 5—8 μ).

Periodicity. The species was seen only in Esrom Sø on September 8th, 1929 (temp. 16.5° C.) and in Furesø on September 1st, 1946 (temp. 17.5° C.).

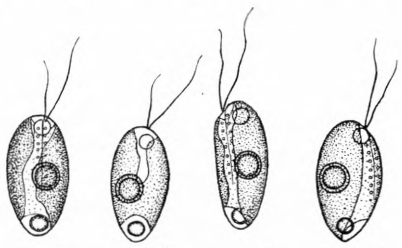


Fig. 76. *Rhodomonas lacustris* Pasch. et Ruttn. from Esrom Sø, September 8th, 1929. *a* ventral view, *b* dorsal view. 1100×.

Sociology. On September 8th, 1929 *Rhodomonas lacustris* was rare in the plankton of Esrom Sø, which consisted of a *Ce hi*-association, 10 *Ceratium* cells per ml, 37 species, the myxophycean quotient $\frac{6}{3}$, the chlorophycean quotient $\frac{7}{3}$, the diatom quotient $\frac{6}{5}$, the euglenine quotient $\frac{0}{13}$ and the compound quotient $\frac{19}{3} = 6.3$. On September 1st, 1946 it was also rare in the plankton of Furesø, which also consisted of a *Ce hi*-association, 15 *Ceratium* cells per ml, 54 species, the myxophycean quotient $\frac{15}{8}$, the chlorophycean quotient $\frac{10}{8}$, the diatom quotient $\frac{3}{5}$, the euglenine quotient $\frac{0}{25}$ and the compound quotient $\frac{28}{8} = 3.5$. In both cases the species thus occurred in *Ceratium hirundinella* associations.

Ecology. Both Furesø and Esrom Sø range among the largest Danish lakes; both are situated in tracts of moraine clay. It appears from BRØNSTED's and WESENBERG-LUND's investigations on Furesø (1912, pp. 440—42) and from KAJ BERG's investigations on Esrom Sø (1938, p. 30) that the oxygen graphs in late summer are "klinograd", typical of eutrophy. KAJ BERG has calculated $O_2 \frac{H}{E}$ for Esrom Sø, for three years getting 0.29 (September), 0.28 (August) and 0.25 (August). THIENEMANN (1928, p. 37) has calculated the same fraction for Furesø, getting the values 0.51 (July), 0.39 (August) and 0.50 (September), which shows us that both lakes are eutrophic and that Esrom Sø is more eutrophic than Furesø, which, incidentally, also appears from the values of the compound quotient given above.

According to BRØNSTED & WESENBERG-LUND (1912, p. 455—56) the calcium content of Furesø ranges between 54.5 and 65.4 mg CaO per litre, according to KROGH & LANGE (1931, p. 33) between 56.0 and 64.8 mg CaO per litre. In Esrom Sø the calcium content according to BRØNSTED & WESENBERG-LUND (1912, p. 475), KAJ BERG (1938, p. 28) and NYGAARD (1938, p. 684) varies between 45.9 and 58.8 mg CaO per litre.

In Furesø pH according to NYGAARD (1938, p. 684), BOISEN BENNIKE (1943, p. 21) and SIG. OLSEN (1944, p. 21) ranges between 7,5 and 8,6 (8,4 on September 1st, 1946 when *Rhodomonas lacustris* was found). In Esrom Sø pH according to KAJ BERG (1938, p. 28), NYGAARD (1938, p. 684) and BOISEN BENNIKE (1943, p. 21)

varies between 7.5 and 8.7. From 3 measurings in the summer half-year the last-mentioned author found that the colour of these two lakes, expressed in "Ohle-units," was 1 and 4 for Furesø and 3 for Esrom Sø.

Chroomonas acuta Utermöhl.

UTERMÖHL 1925, p. 399, fig. 34.—*Fig. nostra* 77.

Cells pyriform with an oblique and ventrally bent tail, provided with a lateral, intensely bluish-green, sometimes darkly olivaceous chromatophore with a distinct lateral pyrenoid in the vicinity. The 2 cilia, which are 5—8 μ long ($\frac{2}{3}$—$\frac{8}{9}$ of the cellular length) are inserted somewhat below the apex of the cell. Granulated furrow absent. Cells 8—10 μ long, 3—5 μ broad.

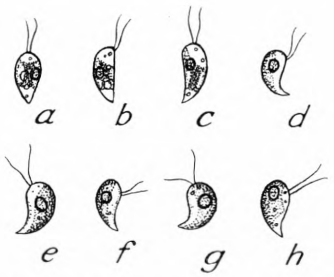


Fig. 77. *Chroomonas acuta* Utermöhl; *a*—*b* from pond in western Stavnsholt, June 26th, 1929; *c*—*h* from Birkerød Sø, July 22nd, 1929. 750×.

In Birkerød Sø, Bistrup Dam and a small pond in the western Stavnsholt, NE-Seeland.

The cells were very agile. When swimming they rotate about the longitudinal axis, so that the oblique tail seems to pendulate from one side to the other. The individuals are also able to rotate on the spot at an enormous rate.

Periodicity. Unlike UTERMÖHL's individuals from eastern Holstein, which were apparently oligo- to mesothermic, the Danish specimens occurred only during the summer months June, July and September. In Birkerød Sø the species appeared in small quantities on July 22nd, 1929 (temp. 23° C.). Also in the small pond of Stavnsholt only a few specimens were observed on June 26th, 1929 (temp. abt. 20° C.). In Bistrup Dam a few individuals were found on September 20th, 1929 (temp. 14° C.).

Sociology. *Chroomonas acuta* occurred in the following associations:

Birkerød Sø.

July 22nd, 1929: *Mio fl*-association with *Mio Bo* and *Os Ag* as subdominants (*Chroomonas* very rare). 27 species, myxophycean quotient $\frac{7}{2}$, chlorophycean quotient $\frac{12}{2}$, diatom quotient $\frac{1}{0}$, euglenine quotient $\frac{2}{19}$, compound quotient $\frac{22}{2} = 11$.

Bistrup Dam.

Sep. 20th, 1929: *Le ps - Eug pr*-association (*Chroomonas* very rare).

Small pond in western Stavnsholt.

June 26th, 1929: 90 % of the species were *Chlorococcales* (sample lost), *Chroomonas* very rare.

In other words the species occurred in associations characterised by blue-green algae (*Microcystis*), Euglenines (*Lepocinclis*, *Euglena*) and green algae (*Chlorococcales*). Constant associates cannot be given on account of the paucity of the material.

Ecology. Both Birkerød Sø and the pond of Stavnsholt are highly eutrophic waters situated in open land. In the former pH was 9.4, in the latter 9.8 on July 22nd, 1929. On August 12th, 1929 the water of Birkerød Sø contained 62.1 mg of CaO and 1.25 mg of PO_4-P per litre. Bistrup Dam is much more polluted than these two localities and must be called saprotrophic. On August 12th, 1929 this slightly alkaline pond contained 118.7 mg of CaO, 12 mg of NH_3-N, 0.25 mg of NO_3-N and 6 mg of PO_4-P per litre!

Chroomonas breviciliata n. sp.

Fig. nostra 78.

Diagnosis. Cellula pyriformis, cauda obliqua, chromatophoro laterali, valde aerogineo instructa. Pyrenoides invisibilis. Flagella bina, aequilonga, 5—7 μ longa, $\frac{1}{3}$—$\frac{1}{2}$ longitudinis cellulae, subapicaliter inserata. Sulcus granulatus deest. In antica parte cellulae vacuolum contractilium observatum. Cellulae 14—18 μ longae, 5—7 μ latae.

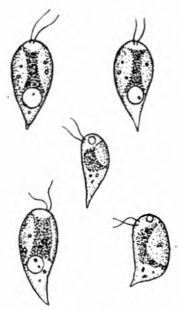


Fig. 78. *Chroomonas breviciliata* n.sp. from Sortedam II, July 10th, 1929. 750×.

Hab. In Sortedam II prope Hillerød, Dania, in coloniis *Sphaerocae volvocis*.

Systematics. This species bears some resemblance to *Chroomonas acuta*, from which it differs by its larger dimensions, shorter cilia and lack of a visible pyrenoid.

Periodicity and sociology. The species was found only on July 10th, 1929 (temp. 16° C.) in Sortedam II. *Chroomonas breviciliata* was rare in the *Ce hi*-association occurring then and showing 25 *Ceratium* cells per ml., 23 species, myxophycean quotient $\frac{0}{1}$, chlorophycean quotient $\frac{7}{1}$, diatom quotient $\frac{0}{0}$, euglenine quotient $\frac{6}{7}$, compound quotient $\frac{13}{1} = 13$.

Ecology. Sortedam II is a highly overshadowed, typically eutrophic pond of the mixotrophic phase. A few data of the ecology of the species are: pH 7.4, CaO 37.5 mg/l, NO_3-N 0.03 mg/l, PO_4-P 0.06 mg/l.

Chroomonas Nordstedtii Hansg. f. **minor** n. f.

Fig. nostra 79.

Diagnosis. Cellulae 7.5—9.5 μ longae, 3.5—5 μ latae, 1.9—2.4 plo longiores quam latiores, dorsaliter valde convexae, ventraliter rectae vel leviter tumidae, apicaliter saepe leviter excavatae, non vel paulum compressae, cum parte posteriore rotundata. Chromatophorus solitarius, pallide aerugineus; pyrenoides conspicuus,

dorsalis. Gula abest. Flagella bina, inaequalia, subapicaliter inserta, quorum longius paene eadem longitudine est ac cellula, brevius autem $\frac{3}{4}$ longitudinis cellulae.

Hab. In Rønhavegaard Dam, Alsia, Dania, libere natans.

Chroomonas Nordstedtii Hansg. is stated (PASCHER's Süsswasserflora, Heft 2, 1913, p. 104, Fig. 161) to be 9—16 μ long and 4—8 μ broad; otherwise there seems to be no substantial differences from the present specimens.

The species was observed in enormous quantities in Rønhavegaard Dam on March 12th and 19th, 1944 (temp. 4.5 and 6° C.); on March 8th (temp. 4° C.) and 22nd (temp. 7.5° C.), 1945 it was not infrequent. During the summer months of 1945 it was not observed. Most likely the species is a cold water form.

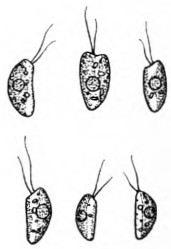


Fig. 79. *Chroomonas Nordstedtii* Hansg. f. *minor* n. f. from Rønhavegaard Dam, March 12th, 1944. 800×.

On March 12th, 1944 the plankton of Rønhavegaard Dam consisted of a *Chrom No mi*-association with *Chla Re* and *Ste Ha* as subdominants, on March 19th of a *Chrom No mi*-association with *Ste Ha* as subdominant. On March 8th and 22nd, 1945 the plankton communities were dominated by *Ste Ha* with *Eug mi* as subdominant.

Rønhavegaard Dam is a highly eutrophic pond, which is polluted *i. a.* by swimming birds. Such an enormous development of plankton is rarely observed in March; in 1944 its water had an intense and deep bluish-green colour originating from the large quantities of *Chroomonas* and *Chlamydomonas*, in 1945 it was intensely brownish-green from *Stephanodiscus Hantzschii*, *Euglena minima* and others. At these times pH was 8.2—9.6 at 3 p. m.

Dinophyceae.

Dinoflagellata.

Gymnodiniaceae.

Gymnodinium.

With a few exceptions (for instance *Gymn. tenuissimum*) the species of this genus can only be determined alive and after a careful and time-wasting observation. In this paper special attention is paid to the look and the course of the longitudinal furrow, which can only be seen by means of the immersion objective. The examination of the cold water forms is particularly difficult, but I managed to get a good image of the longitudinal furrow of *Gymn. tenuissimum* by carrying out the examination in a cold room though the lenses of the microscope often dimmed. In the figures of J. SCHILLER in Archiv für Protistenkunde, Bd. 56, 1926, p. 33 (figs. 29a—c) the

longitudinal furrow of this species stretches far onto epivalva; according to my experience its longitudinal furrow does not reach epivalva at all (see *fig. nostra* 94). In Dansk Planteplankton (NYGAARD 1945, t. 3, fig. 14) the chromatophores are too dark; they are generally ochraceous.

In the following I propose a classification of the *Gymnodinium* species basing on the build and the situation of the longitudinal furrow.

Survey of the Danish species of the genus Gymnodinium.

I. Gymnodinia rectisulcata. Longitudinal furrow straight, stretching some way onto epivalva.

A. Chromatophores blue-green; stigma lacking.

1. Hypovalva ob-bulbiform, chromatophores 4—7 μ in size, longitudinal furrow somewhat above middle crossed by a pointed, oblique process from epivalva ..... *Gymn. acidotum* n. sp. (Fig. 80 et 95)
2. Hypovalva nearly hemispherical, chromatophores 3—4 μ large, no process from epivalva at longitudinal furrow ... *Gymn. aeruginosum* Stein (Fig. 81)

B. Chromatophores ochraceous, reddish-brown or dark-brown.

1. Cells very much flattened, 6—9 μ thick, stigma of horseshoe form, carmine, both epi- and especially hypovalva mucronate, length 28—44 μ, breadth 22—35 μ ..... *Gymn. leopoliense* Wolosz. (Fig. 82)
2. Cells slightly compressed, 1—$1\frac{1}{2}$ times broader than thick; stigma lacking.
   α. Hypovalva coniform or bulbiform, chromatophores numerous, small, dark-brown, cells large (75 $\mu \times 47$ μ or larger) ..... *Gymn. fuscum* Stein (Fig. 83)
   β. Hypovalva broadly rounded, chromatophores ochraceous or reddish-brown.
      a. Epivalva much smaller than hypovalva, nucleus situated above middle of cell, cells 27.5—34 μ long, 22.5—29 μ broad ..... *Gymn. inversum* Nyg. (Fig.s 84, 98)
      b. Epivalva of the same size as epivalva, nucleus central, cells 39—50 μ long, 22.5—34 μ broad ..... *Gymn. inversum* var. *elongatum* n. var. (Fig.s 85, 99)

C. Chromatophores lacking. Both Hypo- and Epivalva coniform, the latter apically with double emargination, cells comparatively large (48 $\mu \times 33$ μ) *Gymn. helveticum* Pen. (Fig. 86)

II. Gymnodinia infractisulcata. Longitudinal furrow sharply bent where it is intersected by the transversal furrow, the former thus stretching some way onto epivalva. Length 32—45 μ, breadth 27—32 μ[1] ..... *Gymn. mirum* Uterm. (Fig. 87)

[1] In Dansk Planteplankton, 1945, p. 32, the measurements are misprinted.

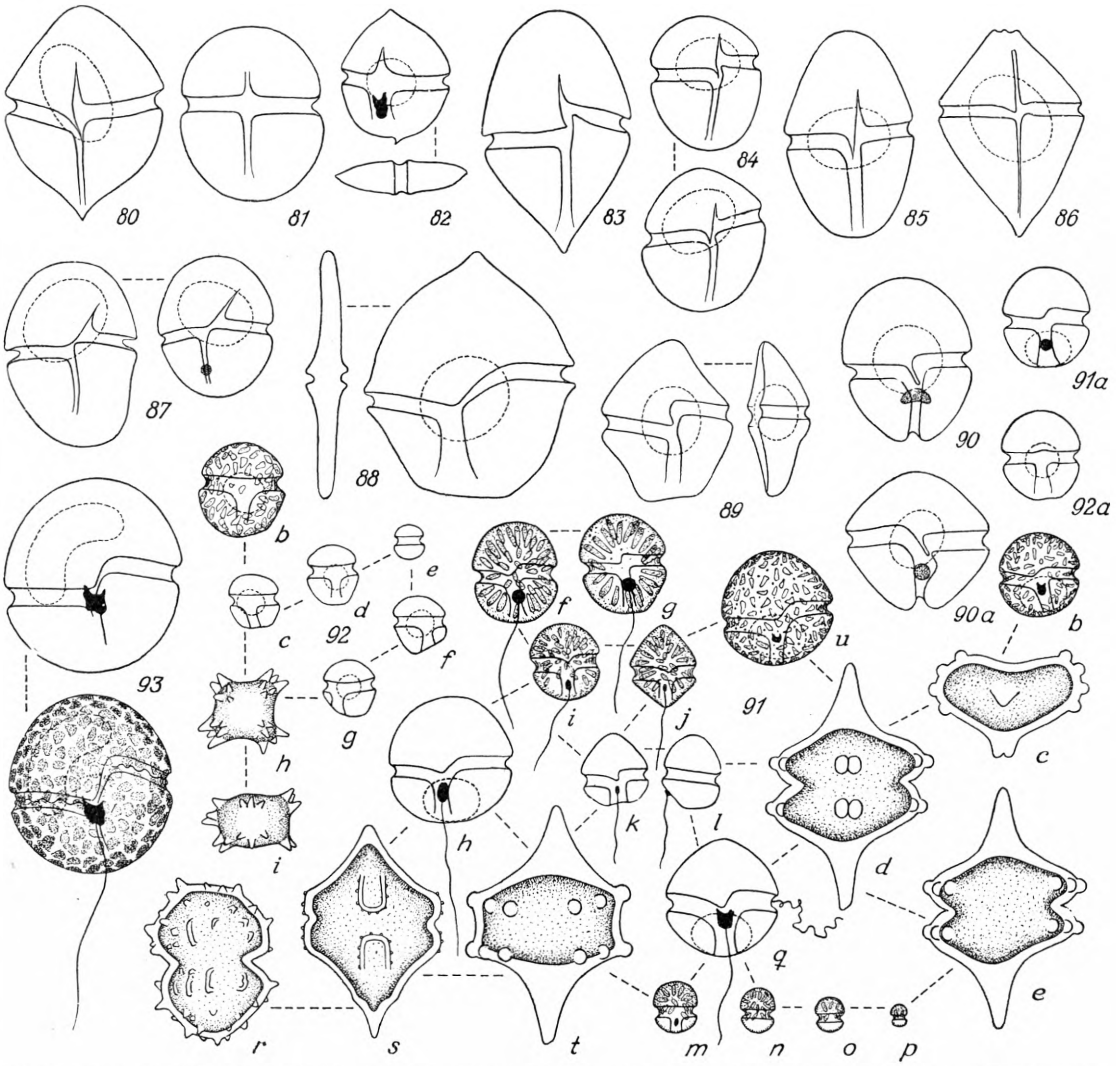


Fig. 80—93. Danish *Gymnodinium* species. 80: *G. acidotum* n. sp. from the pond at Hokkerup, September 14th, 1944, 800×. 81: *G. aeroginosum* Stein from Sortedam II, August 23rd, 1929, 560×. 82: *G. leopoliense* Wolosz. in ventral and lateral view from Andedam in Strødam, May 30th, 1930, 560×. 83: *G. fuscum* Stein from Lille Gribsø, August 22nd, 1929, 430×. 84: *G. inversum* Nyg. from Frederiksborg Slotssø, April 3rd, 1930, 560×. 85: *G. inversum* var. *elongatum* n. var. from Furesø, May 7th, 1931, 560×. 86: *G. helveticum* Penard (colourless) from Badstue-Ødam, April 25th, 1930, 560×. 87: *G. mirum* Uterm. from Lille Gribsø, July 5th and August 22nd, 1929, 560× and 430×. 88: *G. tenuissimum* Lautb. from Emdrup Sø at København, March 26th, 1946, 525×. 89: *G. hiemale* Wolosz. from Fønstrup Dam, November 24th, 1929, 560×. 90: *G. excavatum* Nyg. from Store Dam, August 17th, 1929, 560×. 90a: *G. excavatum* var. *dextrorsum* n. var. from Frederiksborg Slotssø, September 6th, 1929, 560×. 91: *G. paradoxum* Schill., *a* from Jægerbakke Dam, August 14th, 1929, 560×; *b*—*e* from Blankeborg I, *b* from June 10th, 1930, 560×, *c*, *d* and *e* cysts from August 17th, 1927, *c* vertical view, *d* and *e* dorsal and ventral view, 800×; *f*—*t* from Jægerbakke Dam, *f*—*g* from August 14th, 1929, 560×, *h*—t from September 18th, 1929, *h*—*q* 560×, *r*—*t* cysts 800×; *u* from Fønstrup Dam, November 24th, 1929. 92: *G. paradoxum* f. *astigmosa* Nyg., *a* from Jægerbakke Dam, February 17th, 1930, 560×, *b*—*i* from Vandingsdam, April 7th, 1930, 560×; *h* and *i* cysts, *h* vertical view, *i* lateral view. 93: *G. neglectum* Lindem. from pond at Søndre Landevej, Sønderborg, January 3rd, 1937, 800×.

III. Gymnodinia abruptisulcata. Longitudinal furrow does not reach onto epivalva.

A. Cells very much compressed, $2\frac{1}{2}$—5 times broader than thick, 10—11 μ thick, with an asymmetrical, subacute epivalva, a subtruncate or slightly emarginate hypovalva; stigma lacking. Typical cold water forms.

1. Cells in principle flat, 55—70 μ long, 45—60 μ broad, fields 5—6 μ broad *Gymn. tenuissimum* Lautb. (Fig. 88 et 94)
2. Cells in principle plano-convex, 30—38 μ long, 25—31 μ broad, fields 3.5—4.5 μ broad . . . . . *Gymn. hiemale* Wolosz. (Fig. 89)

B. Cells slightly compressed, 1—$1\frac{1}{2}$ times broader than thick.

1. Hypovalva antapically deeply emarginate, upper part of longitudinal furrow crossed by an oblique, finger-shaped process from epivalva.
   a. Transversal furrow sinistrorse . . . *Gymn. excavatum* Nyg. (Fig.s 90, 96)
   b. Transversal furrow dextrorse . . . . . *Gymn. excavatum* var. *dextrorsum* n. var. (Fig.s 90 a, 97)
2. Hypovalva antapically rounded or somewhat flattened.
   a. Nucleus broadly ellipsoidical, situated in hypovalva or centrally, comparatively distinct.
      α. With stigma; cysts in principle fusiform with equatorial constriction and 6 groups of big granules near the latter . . . . . *Gymn. paradoxum* Schill.[1] (Fig. 91)
      β. Without stigma; cysts flatly cubiform, with 3 obtuse, short spines at each of the 8 edges . . . *Gymn. paradoxum* f. *astigmosa* Nyg. (Fig. 92)
   b. Nucleus sausage-shaped, curved, situated in left part of epivalva (in ventral view), always indistinct when alive . . . . . *Gymn. neglectum* Lindem. (Fig. 93)

J. Schiller deals with the Dinoflagellates in an uncritical and sometimes vague way in Rabenhorst's Kryptogamenflora, Bd. 10, 3. Abt., 1932. The figures are not always accurate reproductions of the original drawings, and strange to say the original drawings are sometimes discarded for the benefit of more or less irrelevant drawings published later on. The work does not reach the standard of for instance Hustedt's treatment of the Diatoms and Krieger's treatment of the Desmids.

Gymn. lacustre Schiller (*loc. cit.*, p. 374, fig. 383) is incompletely described and depicted and should undoubtedly be rejected.

Gymn. rotundatum Schiller (non Klebs!) and *Gymn. obesum* Schiller (*loc. cit.*, pp. 407 and 391, figs. 427 a—i and 405 a—g) are both identical with *Gymn. mirum* Utermöhl (all three are found in Attersee!)

Gymn. undulatum Wolosz. (1925) is undoubtedly identical with *Gymn. hiemale* Wolosz. (1917).

[1] Identical with *Gymnodinium coronatum* Woloszynska? or var. *glabra* Woloszynska? (1917, p. 120, t. 11, figs. 10—19, t. 13, figs. I—L, N).

Gymn. hiemale Skvortzow (1927) is probably identical with *Gymn. rotundatum* Klebs. *Gymnodinium paradoxum* f. *astigmosa* is closely related to the latter species (KLEBS, 1912, pp. 392, 439, fig. 5).

SCHILLER may be right when saying that *Peridinium ornamentosum* Lindemann and *Peridinium* (*Gonyaulax*) *Jensenii* Nygaard are synonymous with *Peridinium africanum* Lemmermann.

As regards *Peridinium gatunense* Nyg. I am of the opinion expressed in my 1932 paper that it should only be considered a variety of *Peridinium cinctum* Ehrb. SCHILLER's original figures of this dinoflagellate (*loc. cit.* p. 156, figs. 155a—e) represent individuals that have nothing to do with *Peridinium cinctum* Ehrb. var. *gatunense* Nyg.

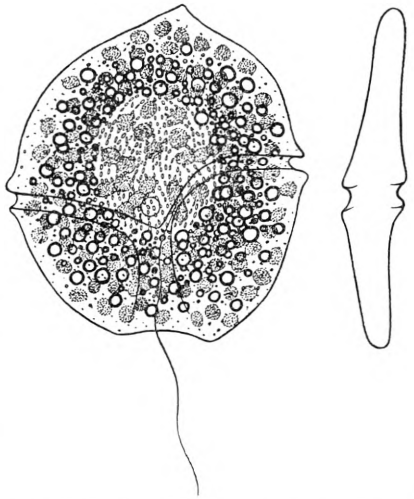


Fig. 94. *Gymnodinium tenuissimum* Lautb. from Emdrup Sø, March 26th, 1946. Front view and lateral view. 800×.

Most likely both *Glenodinium emarginatum* Klebs and *Peridinium* (*Glenodinium*) *imperfectum* Klebs, which were both found in the same pond at Buitenzorg (1912, pp. 394, 439 and 441, figs. 6 and 15) are identical with *Glenodinium geminum* Lindemann (or *Glenodinium guildfordense* Lindemann).

Gymnodinium acidotum n. sp.

Fig. nostra 95.

Diagnosis. Cellulae dorsiventraliter paulum applanatae, a fronte visae late pyriformes. Epivalva coniformis est atque apice rotundato instructa; hypovalva magnitudine simili, subbulbiformis, extremo abrupte acuminata est. Sulcus longitudinalis augustus, rectus, a polo antapicali hypovalvae partim in epivalvam attinens, ubi angulum acutum versus apicem cellulae directum format. Ab epivalva corpus acutum rectum vel leviter curvatum declive sulcum longitudinalem transgreditur. Membrana delicata, hyalina, sine structura visibili. Nucleus medius, ellipsoideus vel subcylindricus, apicibus rotundatis. Chromatophori satis magni (4—7 μ), discoidei, subangulati, valde aeruginei sunt. Stigma destitutum, sed corpuscula rubida 1—2 saepe prope sulcum transversalem occurrunt. Longitudo cellularum 33—37 μ, latitudo 24—30 μ.

Hab. In stagno parvo prope Søgaard, Jutlandia meridiana, Dania, libere natans.

This species differs from the previously described blue-green *Gymnodinia* by its bulbous hypovalva, the structure of its longitudinal furrow, its subconiform epivalva and its few big chromatophores.

Gymnodinium acidotum was comparatively rare on September 14th, 1944 in the pond that is situated near the beginning of the Hokkerup road from the Graasten-Søgaard road, and which is highly polluted by geese and ducks. PH was 8.5. In this

highly eutrophic pond the rich plankton consisted of an *Ank co mi - Eug*-association with *Chrym ov* and *Tra vo* as subdominants; among the other 37 organisms should be mentioned the characteristic *Trachelomonas granulata* Swir. Myxophycean quotient $\frac{1}{0}$, chlorophycean quotient $\frac{15}{0}$, diatom quotient $\frac{2}{1}$, euglenine quotient $\frac{17}{15}$, compound quotient $\frac{35}{0}$.

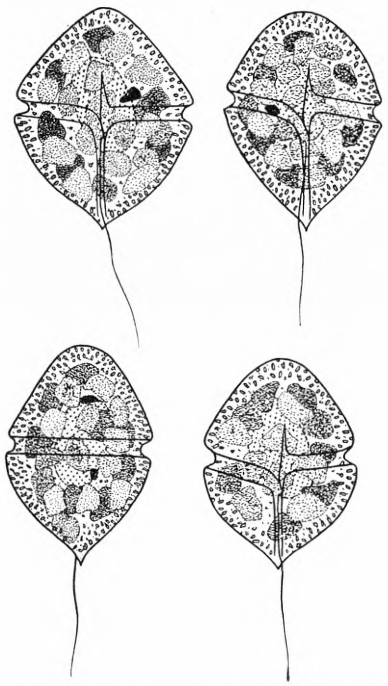


Fig. 95. *Gymnodinium acitodum* n. sp. from the pond near the beginning of the Hokkerup road from the Graasten-Søgaard road, September 14th, 1944. 800×.

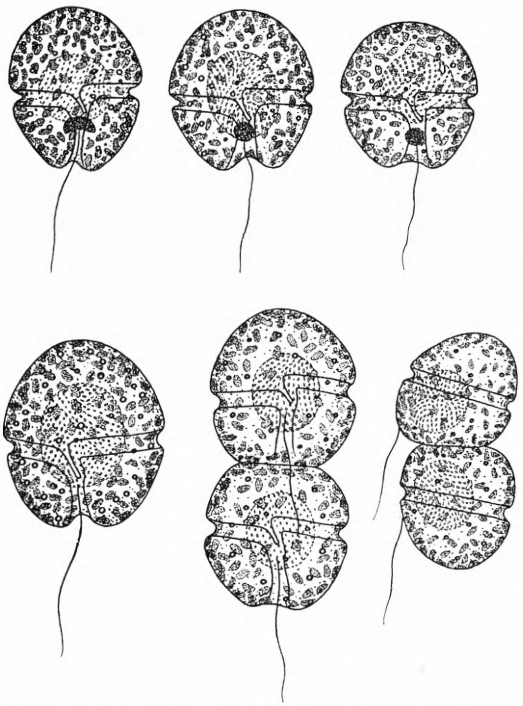


Fig. 96. *Gymnodinium excavatum* Nyg.; upper row of cells from Store Dam, July 6th, August 17th, 1929, and May 28th, 1930, 640×; lower row of cells from Sandbjerg Sø, September 4th, 1937, 800×.

Gymnodinium excavatum Nyg.

Dansk Plante-Plankton, 1945, p. 52, Fig. 20.—*Fig. nostra* 96.

Hab. In Brune Øje and Store Dam, NE-Seeland and Sandbjerg Sø in North Sleswick.

Systematics. This species is easily distinguished from all other previously described *Gymnodinium* species by its deeply emarginate antapical pole and the finger-shaped process at the intersection of the longitudinal and the latitudinal furrow. One individual was seen to creep out of its cell-wall, which remained as an extremely thin crumpled membrane without structure. In spite of intense searching I never managed in this species to find the plate structure that is characteristic of *Gymno-*

dinium. The division of the cell takes place in the free motile state (see Fig. 96) and without any tearing of the thin cell-wall.

In Archivum Balatonicum I, 1927, t. 6, fig. 3, G. Entz pictures a *Gymnodinium* species (in dorsal view), which he calls *Gymnodinium palustre*, but which is more probably identical with *Gymnodinium excavatum*.

Periodicity. In Brune Øje and Store Dam the species developed only during the warm season, May—October 1929, at temperatures between 9.5 and 23.5° C.; accordingly, it is periodic and meso- to polythermic. In June 1929 *Gymnodinium excavatum* was rare in the two ponds, but in August—September (temp. 14—19° C.) it reached its highest development; the great maximum occurred on August 17th: about 3100 individuals per ml in Brune Øje and about 2800 individuals per ml in Store Dam. During September its frequency decreased rapidly, and after the middle of October it disappeared completely from the plankton. It did not reappear in the plankton of these ponds until May 1930.

In Sandbjerg Sø, which unlike Brune Øje and Store Dam was not examined every 10. or 14. day throughout a whole year, the species, strange to tell, was not observed in the August samples, but in nearly all the September samples. On September 4th, 1937 it was rather common in the plankton; on September 15th and October 1st, 1938 and on September 3rd, 1939 the species was very rare in the plankton of Sandbjerg Sø.

Sociology. *Gymnodinium excavatum* occurred in the following associations:

Brune Øje.

June 19th, 1929: *Chry mi*-association (about 8000 cells per ml), *Gy ex* rare, about 75 per ml.

— 28th, — : *Din di*-association (about 200 colonies or about 1000 cells per ml), *Gy ex* rare, about 100 per ml.

July 6th, — : *Chry mi*-association (about 1500 cells per ml), *Gy ex* rare, about 100 per ml.

— 16th, — : *Crym ov*-association (about 2000 cells per ml), *Gy ex* rather common, about 500 per ml.

— 23rd, — : *Per pa*-association, *Gy ex* rather common.

— 26th, — : *Chry mi*-association (about 1800 cells per ml) with *Chla* (about 1200), *Per pa* (about 1200), *Sye ac* (about 1200) and *Tra vo* (about 1100) as subdominants, *Gy ex* rather common, about 500 per ml.

Aug. 10th, — : *Chla*-association (670 cells per ml) with *Crym ov* (550) as subdominant, *Gy ex* not infrequent, 360 per ml.

— 17th, — : *Gy ex*-association (about 3100 cells per ml) with *Per pa* and *Tra vo* as subdominants (about 2800 and 2500 per ml, respectively).

— 24th, — : *Chry mi* - *Tra vo*-association (1400 and 1350 cells per ml, respectively) with *Chla* and *Per pa* (1070 and 1020, resp.) as subdominants, *Gy ex* common, 920 per ml.

Sep. 3rd, 1929: *Chla - Gy ex*-association (both about 1600 cells per ml).
— 9th, — : *Gy ex*-association with *Chla* as subdominant, *Gy ex* common.
— 13th, — : *Chla*-association (about 900 cells per ml), *Gy ex* rare, about 100 per ml.
— 21st, — : *Per pa*-association with *Chla* as subdominant, *Gy ex* rare.
Oct. 11th, — : *Per pa*-association with *Syu Pe*, *Tra in* and *Per bi* as subdominants, *Gy ex* very rare.
May 21st, 1930: *Ura vo*-association with *Din so* and *Din di* as subdominants, *Gy ex* rare.
June 16th, — : *Sye ac an*-association with *Per pa* as subdominant, *Gy ex* rare.

Store Dam.

July 6th, 1929: *Gy ex*-association, *Gy ex* common.
Aug. 17th, — : *Oo cr mi*-association (about 3000 cells and colonies per ml) with *Gy ex* (about 2800 cells per ml) as subdominant.
Sep. 9th, — : *Oo cr mi*-association with *Gy ex* as subdominant.
— 21st, — : *Oo cr mi*-association, *Gy ex* not infrequent.
May 28th, 1930: *Gy ex - Sye ac an*-association, *Gy ex* common.
June 16th, — : *Tra vo*-association with *Gy ex* as subdominant, *Gy ex* rather common.

Sandbjerg Sø.

Sep. 4th, 1937: *Os li*-association with *Mia pu* as subdominant, *Gy ex* common.
— 15th, 1938: *Ste Ha*-association with *Mel gr* as subdominant, *Gy ex* very rare.
Oct. 1st, — : *Mel gr*-association with *Ste Ha* as subdominant, *Gy ex* very rare.
Sep. 3rd, 1939: *Ana sp tu - Ste Ha*-association with *Mel gr* as subdominant, *Gy ex* very rare.

In other words *Gymnodinium excavatum* principally occurs in chrysophycean associations (*Chrysococcus*, *Dinobryon* and *Uroglena*) and in diatomaceous associations (*Synedra*, *Stephanodiscus* and *Melosira*); besides it was found in myxophycean (*Oscillatoria*, *Anabaena*), chlorophycean (*Chlamydomonas*, *Oocystis*), dinophycean (*Peridinium*), cryptophycean (*Cryptomonas*) and euglenine (*Trachelomonas*) associations.

The most constant associates were *Trachelomonas volvocina*, which occurred in 100 % of the samples (26) containing *Gymnodinium excavatum*, and *Glenodinium edax* (88 %), *Cryptomonas ovata* (83 %) and *Peridinium palatinum*, *Chlamydomonas* sp. and *Trachelomonas intermedia* (all three 77 %).

Ecology. Store Dam and Brune Øje are very lime-rich ponds of the eutrophic type approaching the mixotrophic phase. They are connected by a short canal. Brune Øje is highly overshadowed by spruce and therefore cold in summer; it shows a higher degree of eutrophy than Store Dam. On August 17th, 1929 the myxophycean quotient was $\frac{1}{0}$, the chlorophycean quotient $\frac{4}{0}$, the diatom quotient $\frac{1}{2}$, the euglenine

quotient $\frac{2}{4}$ and the compound quotient $\frac{8}{0}$ by 21 species. Desmids were not observed at all in Brune Øje, but in May 1930 a few floating masses of algae occurred, consisting mainly of the saprobic *Oscillatoria chlorina*. In Store Dam the quotients (mentioned in the same order as above) were on June 6th, 1929: $\frac{1}{1}$, $\frac{4}{1}$, $\frac{0}{1}$, $\frac{2}{4}$ and $\frac{7}{1} = 7$, on August 17th $\frac{1}{5}$, $\frac{6}{5}$, $\frac{0}{1}$, $\frac{3}{7}$ and $\frac{10}{5} = 2$ and on June 16th, 1930 $\frac{0}{2}$, $\frac{6}{2}$, $\frac{2}{2}$, $\frac{5}{6}$ and $\frac{13}{2} = 6.5$; the values 7, 2 and 6.5 for the compound quotient thus indicate a marked eutrophy. Sandbjerg Sø, however, is much more contaminated; in this 5 m deep, slightly overshadowed and lime-rich[1] pond the compound quotient reached the following values: $\frac{31}{0}$, $\frac{26}{1}$, $\frac{39}{1}$, $\frac{34}{1}$, $\frac{39}{1}$, $\frac{31}{1}$ and $\frac{23}{1}$ (see also p. 204), thus ranging between 23 and 39.

Some of the ecological data of *Gymnodinium excavatum* are: pH 7.3—8.6, CaO 95.7—118.5 mg/l, consumption of $KMnO_4$ 45—65 mg/l, content of PO_4-P 0—0.04 mg/l, NH_3-N 0.1—0.2 mg/l, NO_3-N 0—0.25 mg/l, Fe 0.03—0.2 mg/l (as far as the iron is concerned the figures are based on June analyses alone).

var. **dextrorsum** n. var.

Fig. nostra 97.

Diagnosis. A typo fossa transversali perspicue dextrorsa differt. Chromatophori elongati, subirregulares. Longitudo cellularum 33—35 μ, latitudo 31—35 μ.

Hab. In Frederiksborg Slotssø prope Hillerød, Dania, libere natans.

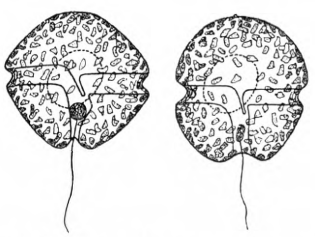


Fig. 97. *Gymnodinium excavatum* Nyg. var. *dextrorsum* n. var. from Frederiksborg Slotssø, September 6th and October 5th, 1929. 560×.

In Badstue-Dam *Gymnodinium excavatum* was not infrequent on May 16th, 1930, but it does not appear from my notes on the examination of the living plankton whether the main species or the variety was observed. However, Badstue-Dam and Frederiksborg Slotssø are connected with each other, and so it is likely that the organism found in Badstue-Dam is var. *dextrorsum*.

Periodicity. This characteristic variety with its dextrorsal transversal furrow seems to be eurythermic: it was observed during the period September—November at temperatures between 18.5° and 3.5° C.; in Frederiksborg Slotssø it was not observed during the rest of the year. It was always rare in the plankton, but on September 17th, 1929 (temp. 18.5° C.) more than 10 individuals were seen, and on September 23rd (temp. 14.5° C.) the frequency may have been about 30 individuals per ml (the countings of the rare species are too inexact for a precise statement of the frequency).

Sociology. The variety occurred in the following associations in Frederiksborg Slotssø:

[1] 113.1 mg CaO per litre on August 19th, 1945.

Sep. 6th, 1929: *Os Ag*-association (variety very rare).
— 17th, — : *Os Ag*-association (variety rare).
— 23rd, — : *Os Ag*-association (about 12.400 trichomes per ml), variety rare.
Oct. 5th, — : *Os Ag*-association (variety very rare).
Nov. 21st, — : *Sce arm*-association (variety very rare).

This means that the variety occurs in myxophycean associations (*Oscillatoria*) and a chlorophycean association (*Scenedesmus*).

The most constant associates were *Pteromonas angulosa*, *Dictyosphaerium pulchellum*, *Oocystis Marssonii*, *Pediastrum Boryanum*, *Scenedesmus armatus*, *Staurastrum tetracerum* var. *validum*, *Melosira granulata*, *Trachelomonas intermedia*, *Trach. volvocina*, *Coelosphaerium Nägelianum*, *Gomphosphaeria lacustris*, *Microcystis flos aquae*, *Micr. pulverea*, *Micr. viridis*, *Micr. aeruginosa* and its var. *major*, *Anabaena flos aquae* and *Oscillatoria Agardhii*, which occurred in 100 % of the number of samples (5) that contained *Gymnodinium excavatum* var. *dextrorsum*. The following species occurred only in 80 % (4) of the samples: *Chlamydomonas Reinhardii*, *Pandorina morum*, *Pediastrum duplex* var. *reticulatum*, *Scenedesmus falcatus*, *Tetraëdron limneticum* var. *simplex*, *Closterium gracile*, *Stephanodiscus dubius* and *Lyngbya limnetica*.

Ecology. Frederiksborg Slotssø is highly eutrophic (Table III gives the phytoplankton quotients, and the qualitative composition of the plankton on September 23rd, 1929 appears from Table IV). Suffice it to mention that the compound quotient was $\frac{24}{3} = 8$, $\frac{36}{4} = 9$ and $\frac{40}{4} = 10$ for 3 summer samples. Some of the ecological data of the variety are: pH 7.6—9.1, CaO 69.3—72.2 mg/l, consumption of $KMnO_4$ 40—42 mg/l, content of NO_3-N 0—0.35 mg/l, NH_3-N 0.05—1.25 mg/l, PO_4-P 0.25—1.5 mg/l; two analyses from January and June gave 0.15 and 0.01 mg/l of Fe.

Gymnodinium inversum Nygaard.

Berg and Nygaard 1929, p. 294, t. 5, figs. 28—36. Nygaard 1945, p. 29, t. 3, fig. 11. *Fig. nostra* 98.

Diagnosis. Cells ellipsoidical, dorsiventrally slightly compressed; both epi- and hypovalva broadly rounded; hypovalva considerably bigger than epivalva. Transversal furrow sinistrorse, longitudinal furrow reaching far down on hypovalva and continuing straightly a little way onto epivalva where it ends pointedly; at the intersection between longitudinal and transversal furrow a pointed process protrudes straightly towards the hypovalvar part of the longitudinal furrow. The cell-wall extremely thin. The nucleus broadly oval, mainly situated in epivalva. Chromatophores numerous, round—oblong or elongated and somewhat irregular, 2—4 μ long, brown. Stigma lacking. Length of cells 27—36 μ, breadth 22—29 μ, thickness 20—27 μ.

Distribution: In Frederiksborg Slotssø, Lyngby Sø and Furesø, NE-Seeland, Denmark, pelagic.

Systematics. My 1929 description of the species contains no information on the look of the longitudinal furrow, and so a more detailed diagnosis of the species has been given here. The species perhaps shows the closest relation to *Gymnodinium mirum* Utermöhl (1925, p. 408, Fig. 35 *a—o*; synonyms *Gymn. obesum* Schiller and *Gymn. rotundatum* Schiller non Klebs in Rabenhorst's Kryptogamenflora, X. Bd., 3. Abt., 1932, pp. 391 and 407, Fig.s 405 *a—g* and 427 *a—i*, both of which are found in Attersee together with *Gymn. mirum*!), the longitudinal furrow of which, however, shows a sharp bend where it is tranversed by the transversal furrow, the epivalva of which is of nearly the same size as hypovalva and the chromatophores of which are often olivaceous; besides this it has no pointed process from epivalva towards the hypovalvar part of the longitudinal furrow.

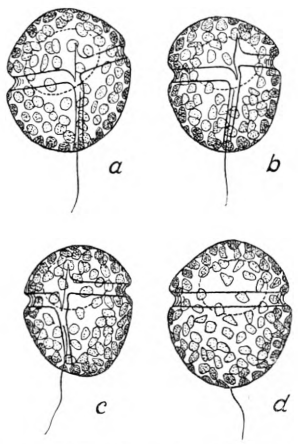


Fig. 98. *Gymnodinium inversum* Nyg.; *a—b* from Frederiksborg Slotssø, April 3rd, 1930; *c—d* from Furesø, May 7th, 1931. 560×.

Periodicity. In Frederiksborg Slotssø *Gymnodinium inversum* occurred only in the months of February, March and April, 1930 (temp. 1—12° C.). During the other 9 months of the year it was never observed in the plankton. Its highest development, during which it was not very conspicuous, was reached at the end of April (temp. 12° C.). In Furesø a dozen individuals were seen on May 7th, 1931, when the temperature was exceptionally low (5.5° C.). In Lyngby Sø the species was not infrequent on March 25th, 1946 (temp. 3.5° C.). In 1927 the species was not infrequent in Frederiksborg Slotssø on March 12th (temp. 5.5° C.), cp. Berg & Nygaard 1929, p. 295.

In other words this typically vernal form is oligo- to mesothermic, occurring at temperatures between 1 and 12° C.

Sociology. The species occurred in the following associations:

Frederiksborg Slotssø.

Feb. 17th, 1930: *Ste Ha*-association (the species very rare).
Mar. 1st, — : association dominated by minute green algae cells (about 120.000 individuals per ml, more than 90 % of which are *Trochiscia granulata* f. and the rest perhaps *Stichococcus*) with *Ste Ha* as subdominant (about 19,500 cells per ml); the species very rare).
— 15th, — : *Ste Ha*-association with *Mel it su* as subdominant (the species very rare).
Apr. 1st, — : *Trochiscia granulata* f.-association (about 24,000 cells per ml, 2.5—3.5 μ large) with *Ste Ha* as subdominant (about 13,000 cells per ml); the species rare (about 100 individuals per ml).

Apr. 3rd, 1930: *Ste Ha*-association (the species rare).
— 25th, — : *Ste Ha - Sce arm*-association (the species not infrequent).

Furesø.
May 7th, 1931: *Asi fo*-association (the species rare).

Lyngby Sø.
Mar. 25th, 1946: *Beggiatoa*(?)-association (the species not infrequent).

This means that *Gymnodinium inversum* was observed in diatom associations (*Stephanodiscus*, *Asterionella*) and in chlorophycean associations (*Trochiscia* and *Scenedesmus*).

The constant associates were *Chlamydomonas Reinhardii* and *Stephanodiscus Hantzschii*, which occurred in 100 % of the number of samples (8) that contained *Gymnodinium inversum*. *Ankistrodesmus falcatus* var. *acicularis* f. *longissima*, *Micractinium pusillum*, *Scenedesmus armatus*, *Melosira italica* subsp. *subarctica* and *Cryptomonas ovata* were found in 87.5 % and *Chlamydomonas bicocca*, *Asterionella formosa*, *Glenodinium aciculiferum*, *Glen. edax* and *Microcystis pulverea* var. *racemiformis* in 75 % of the samples.

Ecology. All 3 lakes are eutrophic. In Furesø the values of the compound quotient were found to be 3.5, 3.5 and 4.4, while Frederiksborg Slotssø showed the values 8, 9 and 10. Some ecological data of the species are: pH 7.8—9.4, CaO 66.8—71 mg/l (in Furesø the annual variation of calcium was 54.5—65.4 mg CaO per l according to Brønsted & Wesenberg-Lund, 1912), consumption of $KMnO_4$ 14—48 mg/l, NH_3-N 0.02—0.2 mg/l, NO_3-N 0.03—1.1 mg/l, PO_4-P 0.015—0.16 mg/l. Analyses of the iron content of Frederiksborg Slotssø in January and June gave 0.15 and 0.01 mg/l of Fe, respectively.

var. **elongatum** nov. var.

Fig. nostra 99.

Diagnosis. A typo hoc modo differt: epivalva subconica et hypovalva subsemisphaerica aequales sunt; cellulae multo elongatiores quam cellulae typi, e 5 mensionibus 1.4—1.7 plo longiores quam latiores. Nucleus late ellipsoideus, in media cellula. Chromatophori numerosi, rufo-brunnei, rotundati—ovales (3—4 μ) vel elongati et subirregulares (—5 μ longi, 1—2 μ lati). Longitudo cellularum 39—50 μ, latitudo 22.5—34 μ.

Hab. In Furesø et Emdrup Sø, Selandia, Dania, libere natans.

Systematics. This variety is easily distinguished by its long cells with the subconiform epivalva, by its straight longitudinal furrow and by its reddish-brown chromatophores. In Emdrup Sø there was a very distinct difference in colour between

the ochraceous chromatophores of *Gymnodinium tenuissimum* and the reddish-brown chromatophores of *Gymnodinium inversum* var. *elongatum*.

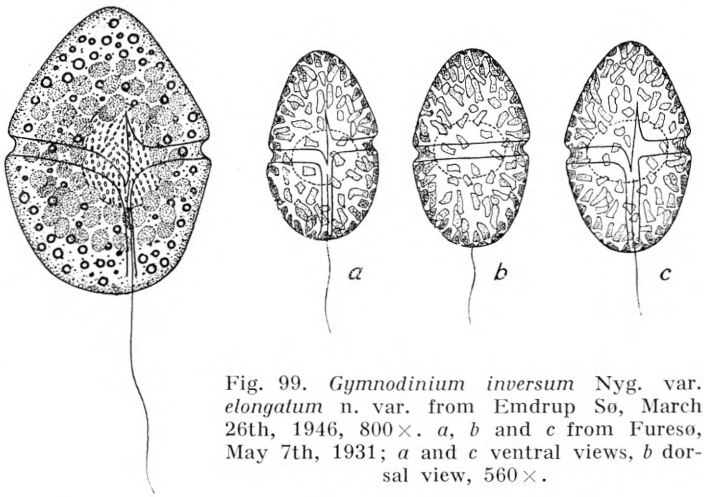


Fig. 99. *Gymnodinium inversum* Nyg. var. *elongatum* n. var. from Emdrup Sø, March 26th, 1946, 800×. *a*, *b* and *c* from Furesø, May 7th, 1931; *a* and *c* ventral views, *b* dorsal view, 560×.

Periodicity. The variety was only seen on May 7th, 1931 in Furesø at a temperature of 5.5° C. when it was very rare in the plankton, and on March 26th, 1946 in Emdrup Sø (temp. 5° C.) where it was very rare, too. The material is too small for a decision whether the variety is a cold water form.

Sociology. The variety occurred in the following 2 associations:

Furesø.

May 7th, 1931: *Asi fo*-association (variety very rare).

Emdrup Sø.

Mar. 26th, 1946: *Gle ac*-association with *Ste Ha* as subdominant (variety very rare).

The variety thus appeared in a diatom association (*Asterionella*) and a dinoflagellate association (*Glenodinium*).

Ecology. As will appear from Table I Furesø is a clear, alkaline, moderately eutrophic lake; Emdrup Sø is a small lake, somewhat polluted (by ducks and other swimming birds); on July 29th, 1941 the compound quotient was $\frac{6}{0}$ and on November 29th, 1946 (temp. 5.5° C., pH 7.9) $\frac{32}{2} = 16$, which indicates a high degree of eutrophy.

Euglenineae.

Euglenaceae.

Euglena phacoides n. sp.

Fig. nostra 100.

Diagnosis. Cellulae mediae, elongate fusiformes, compressae, e duodecim mensionibus cellularum in statu metabolico 2.1—3.7 plo longiores quam latiores, sic submetabolicae, ut cellulae paulo supra medium anulariter inflentur. Pars anterior cellulae gracilis, interdum leviter curvata, apice oblique truncato-rotundata; pars posterior longe attenuata et acutissima. Periplastus delicatus, distincte et spiraliter

striatus, 6—9 striis pro 10 μ. Chromatophori numerosi, discoidei, parietales, sine pyrenoidibus. Granula paramylacea multa, parva, bacilliformes vel longe ellipsoidea, supra medium cellulae. Nucleus centralis vel paulum infra mediam cellulam situs, atque late ellipsoideus est. Flagellum circiter $\frac{1}{2}$ longitudinis cellulae, in gula lagenaeformi insertum. Stigma ovale in parte anteriore apud gulam situm est. Longitudo

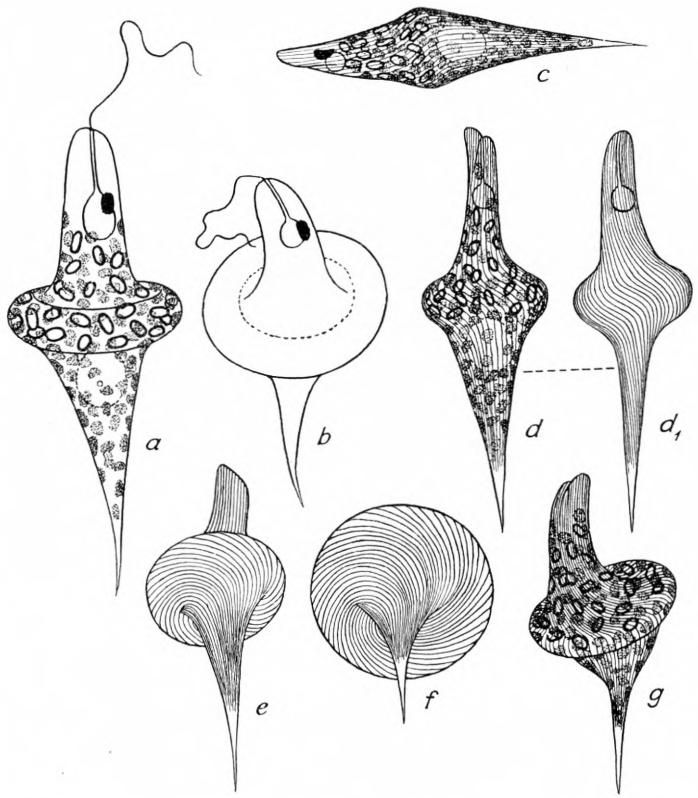


Fig. 100. *Euglena phacoides* n. sp.; *a*—*f* from Bistrup Dam, *a*—*b* from July 11th, 1929 (the striation is not delineated), *c* from September 20th, 1929, *d*, d_1, *e* and *f* from November 16th, 1929; *g* from Sortedam II, April 10th, 1930. *d* front view, d_1 lateral view, *f* oblique basal view. *a*—*b* 840×, *c* 560×, *d*—*g* 800×.

cellularum 56—78(95) μ, latitudo 16—28 μ; anulus 8—9 μ crassus, ad 30 μ in diametro.

Hab. In Bistrup Dam, Sortedam II, Lynge Vandingsdam et palude Eriophori prope Sorø, Selandia, Dania, libere natans.

Systematics. The species looks like *Euglena proxima* and *Euglena acus*, but differs from both of these terete species in being distinctly compressed; this is easily seen when the swimming individual slowly rotates round its own longitudinal axis. Unlike *Euglena proxima* the individuals of *Euglena phacoides* are unable to assume a spherical shape. *Euglena phacoides* is easily distinguished by the fact that in the meta-

bolic state it forms a pronounced or even enormous ring-shaped thickening a little above or in the middle of the cell; in this state it is able to approach its anterior part to the point of its posterior part. *Euglena acus*, however, is very disinclined to show metaboly; it is only very slowly and with difficulty that it grows shorter and much thicker, but roughly speaking it retains its fusiform shape. Swimming individuals of *Euglena phacoides* from Eriophorum moor measured up to 95 μ in length.

Periodicity. *Euglena phacoides* was found in 8 months of the year, April—November, at temperatures between 5° and 19° C. In December, January, February and March no samples were taken in Bistrup Dam, which showed the most frequent occurrence of the species, and so it cannot be safely established whether the species is eurythermic, which seems very probable: in Bistrup Dam it was common in the plankton on November 16th, 1929 (temp. 5° C.; 60 individuals per ml); on October 24th, 1929 its frequency was 8 individuals per ml, and in the summer samples it was very rare. In Sortedam II it was observed only on April 10th, 1930 and in Lynge Vandingsdam on June 30th and August 6th, 1947; all the 3 samples showed very small quantities. In the *Eriophorum* moor S. of Sorø *Euglena phacoides* was not found in the samples from July, August, September and October 1947, but it appeared on November 15th (temp. 2.5° C.), December 13th (temp. 3° C.) and January 10th, 1948 (temp. 1° C.); it was very rare on these three occasions. On February 21st (temp. 2° C., ice 8 cm thick) the species was rare; it disappeared in the *Eriophorum* moor before March 20th (temp. 7.5° C.) and was no more present in the April sample. On the basis of the sparse material it is perhaps legitimate to conclude that *Euglena phacoides* seems to reach its maximum development during the cold season.

Sociology. The species was found in the following associations:

Bistrup Dam: all associations were dominated by Bacteria and "Chlorobacteria" in enormous quantities; the following organisms are given as the most frequent non-bacterial species of the samples though their frequencies are but smal fractions of those of the Bacteria.

July 11th, 1929: *Ank fa se br* and *Le ps* (the species very rare).
Sep. 9th, — : the species very rare.
— 20th, — : *Eug pr* and *Le ps* (the species very rare).
Oct. 24th, — : *Phu pl* (6 individuals per ml) and *Le ps* (the species not infrequent).
Nov. 16th, — : *Euglena phacoides* and *Phu os* (the species common).
Apr. 12th, 1930: *Chla ol* (the species not infrequent).
May 1st, — : *Phu os* and *Le ps* (the species very rare).

In Table IV we find the qualitative composition of the associations from October 24th and November 16th, 1929.

Sortedam II.

Apr. 10th, 1930: *Crym ov*-association with *Chla ac* as subdominant (the species very rare).

Lynge Vandingsdam.

June 30th, 1947: *Tra vo*-association with *Chla ci* as subdominant (the species very rare).

Aug. 6th, — : *Eug ob*-association (23,300 individuals per ml) with Bacteria and and *Se ca* as subdominants (the species very rare).

The qualitative composition of the two last-mentioned associations appears from Table IV.

Eriophorum moor.

Nov. 15th, 1947: *Sce arm*-association with *Gy ne* as subdominant (the species rare).

Dec. 13th, 1947: *Gle Lo - Per Wi*-association (the species very rare).

Jan. 10th, 1948: *Gle Lo*-association (the species very rare).

Feb. 21st, 1948: *Chry ma - Ma te* - association with *Gle Lo* as subdominant (the species rare).

In other words *Euglena phacoides* occurs in associations characterized by Bacteria and "Chlorobacteria" together with green algae, *Chlorococcales* (*Ankistrodesmus* and *Scenedesmus*), Flagellates (*Cryptomonas*), Dinoflagellates (*Glenodinium* and *Peridinium*) and Euglenines (*Euglena*, *Phacus* and *Lepocinclis*).

The most constant associates cannot be given because no single species occurred in as much as 75 % of the number of samples (14) that contained *Euglena phacoides*; in 75 % of the samples, however, large quantities of Bacteria were present.

Ecology. Bistrup Dam was a distinctly saprotrophic pond, Sortedam II a polluted eutrophic pond of the mixotrophic phase and Lynge Vandingsdam an enormously polluted eutrophic pond approaching saprotrophy. Table III gives the phytoplankton quotients of these three ponds. Suffice it to mention here that in Bistrup Dam the compound quotients for October 24th, and November 16th, 1929 were $\frac{9}{0}$ and $\frac{8}{0}$, respectively, the euglenine quotients for the same dates $\frac{8}{1} = 8$ and $\frac{8}{0}$, respectively. In Lynge Vandingsdam the compound quotients for June 30th and August 6th, 1947 were $\frac{31}{1} = 31$ and $\frac{29}{0}$, respectively, and the euglenine quotients for the same dates $\frac{18}{12} = 1.5$ and $\frac{21}{7} = 3$, respectively. The *Eriophorum* moor is an almost overgrown fen, the narrow peripheral water edge of which during the summer months contains a marked Desmid plankton (up to 33 Desmids per sample!); the water, the pH of which during the investigation varied between 6.4 and 6.9, is polluted by cattle grassing near its margin. Each of the three samples mentioned above from the *Eriophorum*-moor contained so much as 9 or 10 euglenines.

Accordingly, it must be legitimate to consider *Euglena phacoides* a mesosaprobic-polysaprobic organism. A few data of the ecology of the species are: pH 6.4—9.0, CaO about 40—118.7 mg/l (Aug. 12th, 1929, Bistrup Dam), consumption of $KMnO_4$ 84 mg/l (April 26th, 1930, Sortedam II), content of NH_3-N 0.55—20 mg/l, NO_3-N 0.06 mg/l and PO_4-P 0.015—4 mg/l.

Lepocinclis fusiformis Lemm. var. **amphirhynchus** nov. var.

Fig. nostra 101.

Diagnosis. Cellulae citriformes, polis valde productis, $1\frac{1}{4}$—$1\frac{1}{2}$ plo longiores quam latiores, apicaliter productae et truncatae, antapicaliter abrupte et obtuse acutatae sunt. Stigma compositum, ovale, prope partem apicalem. Flagellum 1—$1\frac{1}{2}$ longitudinis cellulae. Chromatophori multi et disciformes. Granula paramylacea grandia, lateralia et anularia. Pellicula sine colore, spiraliter striata, 9—10 striis pro 10 μ, secunda quaeque interdum praecipue conspicua; directio striarum a vertice visa contra itionem horologii. Longitudo cellularum 30—35 μ, latitudo 22.5—26 μ.

Hab. In Sortedam II prope Hillerød, Dania, libere natans.

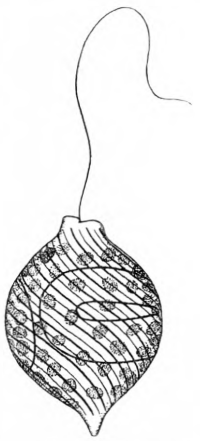


Fig. 101. *Lepocinclis fusiformis* Lemm. var. *amphirhynchus* n. var. from Sortedam II, September 12th, 1929. 800×.

Systematics. The variety differs from the main species by its highly protruding poles (see W. Conrad 1934, p. 225, fig. 30). Habitually it shows some likeness to *Lepocinclis sphagnophila* Lemm. (Pascher's Süsswasserflora, Heft 2, 1913, p. 134, fig. 229), which, however, according to the figure is twice as long as broad, according to the two measurements given nearly 3 times longer than broad! According to Conrad (*loc. cit.* p. 244) this species is dubious. I have not chosen to call the new variety var. *sphagnophila* (Lemm.) mihi because the identity of Lemmermann's and my specimens is improbable.

Periodicity. A total of 7—8 specimens of the described variety were observed in Sortedam II and only in the month of September: on September 3rd, 5th and 12th, 1929; during the remaining 11 months it was not observed. Being observed only at temperatures between 16 and 18.5° C. it thus seems to be polythermic.

Sociology. The variety was found in the following association containing 12 euglenines:

Crym ov-association with *Ste Ha*, *Gy aer* and *Eug ac* as subdominants (the variety very rare).

Ecology. Sortedam II is a highly overshadowed pond, cold in summer, eutrophic of the mixotrophic phase, sometimes completely covered with *Lemna*; see Table III. The following are a few data of the ecology of the variety in question: pH 7.1—7.15, CaO 39.1 mg/l, consumption of $KMnO_4$ 104 mg/l, contents of PO_4-P 0.015 mg/l, NH_3-N 0.2 mg/l and NO_3-N 0 mg/l.

Phacus anomalus Fritsch et Rich var. **pullus gallinae** nov. var.

Fig. nostra 102.

Diagnosis. Cellulae parvae, paulum compressae, a fronte visae concinne ellipticae, e 11 mensionibus 1.2—1.6 plo longiores quam latiores, cum fossa 3—4 μ lata,

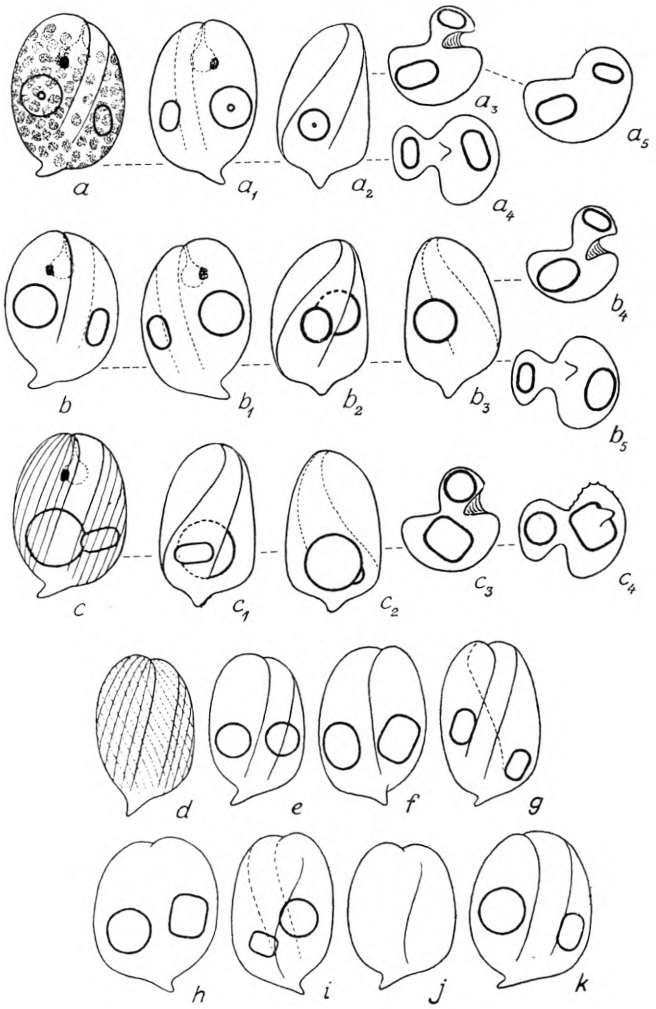


Fig. 102. *Phacus anomalus* Fritsch et Rich var. *pullus-gallinae* n. var. from Lynge Vandingsdam, June 30th, 1947. *a*, *b*, *c*, *d*, *e*, *g*, *j* and *k* ventral views, a_1, b_1, *f*, *h* and *i* dorsal views, a_2, b_2, b_3, c_1 and c_2 lateral views, a_3, b_4 and c_3 vertical views, a_4, b_5 and c_4 basal views, a_5 vertical view by deep focussing. 800×.

ventrali, decliviter longitudinali, fere partem posteriorem cellulae attingenti. Pars posterior cum cauda breviter coniformi, obtusa, obliqua et leviter curvata. A vertice visa cellula ex partibus duabus valde inaequalibus constare videtur, quarum altera major semicircularis, altera minor capiti avis similis. Cellula a latere visa dorsaliter

subrecta, ventraliter valde convexa; pars minor ("ala") obliqua, cuneata apparet, ab apice cellulae ad partem posteriorem attingens. Granula paramylacea bina disciformia vel brevissime cylindracea angulis valde rotundatis, interdum cum foramine medio; alterum, quod in "ala" cellulae situm est, minus est quam alterum in "corpore" cellulae. Pellicula interdum decleviter et tenuiter striata, 8 striis pro 10 μ.

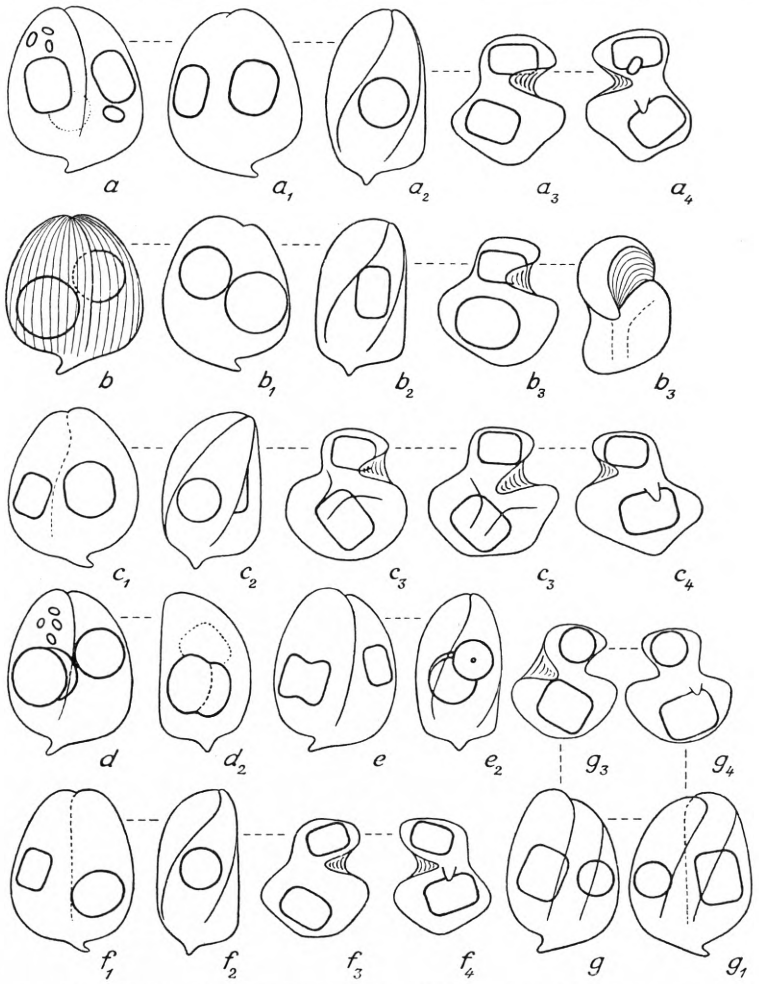


Fig. 103. *Phacus anomalus* Fritsch et Rich from Griqualand West, sample 844. *a*, *b*, *d*, *e* and *g* ventral views, a_1, b_1, c_1, f_1 and g_1 dorsal views, a_2, b_2, c_2, d_2, e_2 and f_2 lateral views, a_3, b_3, c_3, f_3 and g_3 vertical views, a_4, c_4, f_4 and g_4 basal views. 800×.

Chromatophori numerosi, parvi, disciformes. Stigma ovale vel rotundum in parte anteriore apud gulam lagenae-formem. Longitudo cellularum sine cauda 21.5—26 μ, latitudo 16—20.5 μ, crassitudo "corporis" 14—15 μ, crassitudo "alae" 7—10 μ; longitudo caudae circiter 2—3 μ.

Hab. In Lynge Vandingsdam, Selandia prope Sorø, Dania, libere natans.

Systematics. I am highly indebted to Professor F. E. FRITSCH, London, for the reception of type material of *Phacus anomalus* Fritsch et Rich. *Fig. nostra* 103 shows some drawings of individuals in various positions.

FRITSCH and RICH (1929, p. 73, fig. 24 *H—N*) give the following measurements: long. cell. sine spin. 24—27 μ, lat. 26—27 μ (fig. 24 *I* is only about 20 μ broad), crass. corp. 17—22 μ, crass. alae 11—12 μ. They further illustrate the typical *Phacus anomalus* cell in fig. 24 *I*; it is egg-shaped in front view.

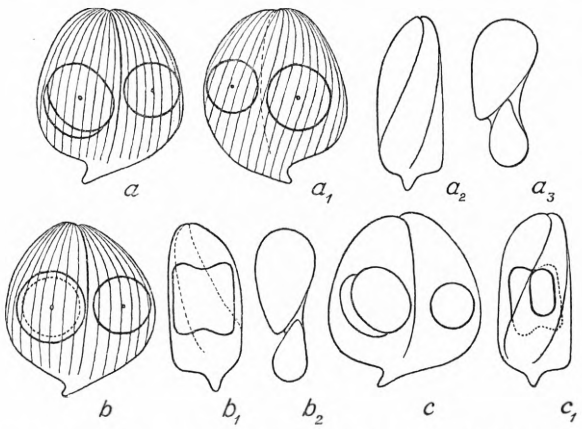


Fig. 104. *Phacus curvicauda* Swirenko emend. Nygaard from Blankeborg I, August 17th, 1927. *a*, *b* and *c* ventral views, a_1 dorsal view, a_2, b_1 and c_1 lateral views, a_3 and b_2 vertical views. 800×.

My measurings of the type material for 8 individuals gave the following dimensions: long. cell. sine cauda 23.5—27 μ, lat. 19—22 μ, crass. corp. 14—21 μ, crass. alae 10—12 μ, in other words a good correspondence with the measurings of FRITSCH and RICH, though I never found cells that are as broad as long. In the 8 individuals measured the ratio of axes was 1.1—1.4, averaging 1.25. There were 8 striae pro 10 μ.

Var. *pullus gallinae* differs from the main species by its elliptical shape of cells in front view. According to 11 measurings the ratio of axes is 1.2—1.6, 1.4 in mean, which shows that the cells of the variety are comparatively longer than those of the main species. In vertical (or basal) view the corpus of the variety is hemispherical, that of the main species often somewhat angular though it may be hemispherical.

Phacus curvicauda Swirenko (see A. POCHMANN 1942, p. 155, figs. 48—51) is not easily distinguished from *Phacus anomalus*. Apparently SWIRENKO pictures it only in front view, in which position it is completely like *Phacus anomalus*. The individuals figured by POCHMANN in Fig. 50 are hardly identical with those of Fig. 49, the difference between the vertical views being too great.

Fig. nostra 104 shows some individuals which I have called *Phacus curvicauda* Swirenko emend. Nygaard and I will here try to give this species a clearer definition. The individuals from Blankeborg I were broadly egg-shaped in front view, and the paramylon grain of corpus was cylindrical or clepsydriform. A very conspicuous fact, however, is that corpus is thinner, so that the cells are much more flattened than in *Phacus anomalus* and its var. *pullus gallinae*. Long. cell. sine cauda 26—28 μ, lat. 24—26 μ, crass. corp. 10—12 μ, crass. alae 7—9.5 μ, long. caudae 2.5—4 μ, 6—8 striis pro 10 μ.

The specimen figured in "Dansk Plante-Plankton", fig. 90 (*sub nomine Phacus alata* var. *latviensis*), which originates from Blankeborg I on June 2nd, 1927, in all

respects corresponds to the individuals from Blankeborg I on August 17th, 1927, August 18th, 1928 and June 10th, 1930.

Sociology. The species was found only in the following 2 associations:

June 30th, 1947: *Tra vo*-association with *Chla ci* and Bacteria as subdominants (the species rare).

Aug. 6th, — : *Eug ob*-association (23.300 individuals per ml) with *Se ca* and Bacteria as subdominants (the species very rare).

The qualitative composition of these two associations appears from Table IV. In other words *Phacus anomalus* var. *pullus gallinae* was found in associations dominated by Euglenines (*Euglena*, *Trachelomonas*).

Ecology. The material does not allow any conclusions on the vegetation period or the maximum of the species. Lynge Vandingsdam is a very shallow, highly contaminated watering pond on the transition stage between eutrophy and saprotrophy. At 10 a. m. on August 6th, 1947 the temperature was 19.5° C. and pH 9.0; the compound quotient was $\frac{29}{0}$ and the euglenine quotient no less than $\frac{21}{7} = 3$, which shows quite an extraordinary richness in Euglenines. On June 30th the compound quotient was $\frac{31}{1} = 31$ and the euglenine quotient $\frac{18}{12} = 1.5$.

Phacus Manginii Lefèvre var. **inflatus** nov. var.

Fig. nostra 105.

Diagnosis. A typo cellulis majoribus cum margine ventrali inflato et cum axe longitudinali dorsiventraliter et leviter curvato differt; carina minus projecta quam in typo. Longitudo cellularum cum cauda 50—52 μ, sine cauda 36—38 μ, latitudo 29—30 μ, crassitudo 10—14 μ, cauda circiter 14 μ longa, 5—7 striae pro 10 μ.

Hab. In Sortedam II prope Hillerød, Dania, libere natans.

Systematics. The dorsal keel is not so protruding as in the main species (Pochmann 1942, p. 149, figs. 40 *a*—*i*), but it is running longitudinally over the whole of the convex, dorsal surface. In front view the cells are very regularly egg-shaped. The big round and the smaller ellipsoidical and antapical paramylon granule are

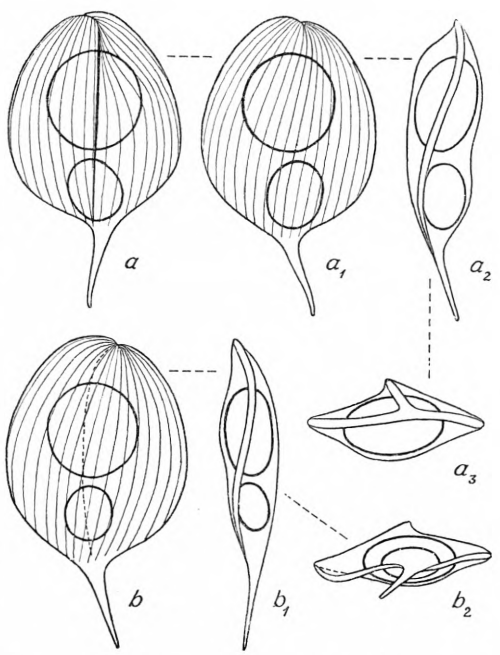


Fig. 105. *Phacus Manginii* Lef. var. *inflatus* n. var. from Sortedam II, July 1st, 1929; *a* dorsal view, a_1 and *b* ventral views, a_2 and b_1 lateral views, a_3 vertical view, b_2 basal view. 800×.

situated in the longitudinal axis of the cell; in lateral view both of them turn out to be compressed. On the ventral side of the cell there are two inflations, one off each paramylon granule.

Periodicity. The variety was observed in Sortedam II in June, July and September and at the beginning of October at temperatures between 11.25 and 21° C. It was always rare; the most individuals were seen in the sample from September 5th, 1929 (temp. 16° C.).

Sociology. *Phacus Manginii* var. *inflatus* occurred in the following associations:

June 8th, 1929: *Ce hi*-association with *Cl Kü* and *Ana fl* as subdominants (the variety very rare); see Table IV.
July 1st, — : *Ce hi*-association with *Ma ca* as subdominant (the variety very rare); see Table IV.
— 10th, — : *Ce hi*-association with *Ma ca* and *Tra ve* as subdominants (the variety very rare).
Sep. 5th, — : *Crym ov*-association with *Phu su*, *Gy aer* and *Ste Ha* as subdominants (the variety rare).
— 23rd, — : *Crym ov*-association (the variety very rare); see Table IV.
Oct. 7th, — : ditto.
June 16th, 1930: *Dic pu*-association with *Dic Eh* as subdominant (the variety very rare).

In other words the variety occurred in dinophycean (*Ceratium*), cryptophycean (*Cryptomonas*) and chlorophycean (*Dictyosphaerium*) associations.

The constant associates were *Scenedesmus armatus*, which occurred in 100 % of the number of samples (7) that contained *Phacus Manginii* var. *inflatus*; *Trachelomonas hispida* and *Trach. volvocina* (both 86 %). (*Ankistrodesmus falcatus*, *Dictyosphaerium pulchellum*, *Scenedesmus arcuatus*, *Oocystis Marssonii*, *Cyclotella Meneghiniana* and *Gymnodinium aeruginosum* in only 71 % of the samples, the last-mentioned perhaps in more because not all samples were examined alive).

Ecology. Sortedam II is a highly overshadowed, shallow, eutrophic pond of the mixotrophic phase, sheltered from winds and contaminated by ducks and other swimming birds. On July 17th, 1929 the whole surface of the pond was covered by *Lemna*. The following data can be given concerning the ecology of *Phacus Manginii* var. *inflatus*: pH 7.1—7.4, CaO 34—39.1 mg/l, consumption of $KMnO_4$ 75—93 mg/l, contents of PO_4-P 0.005—0.095 mg/l, NH_3-N 0.15—0.2 mg/l, NO_3-N 0—0.03 mg/l, Fe 0.1 mg/l.

Phacus suecicus Lem. var. **inermis** nov. var.

Fig. nostra 106.

Diagnosis. Cellulae ellipsoideae, raro subtrapeziformes, valde applanatae, e 11 mensionibus 1—1.5 (vulgo 1.2) plo longiores quam latiores (excl. cauda). Pars

anterior leviter excavata cum verruca parva, conica, centrali, per quam flagellum exit. Cauda obliquior, non vel leviter curvata. Stigma grande, subangulatum. Pellicula glabra, vel in utroque latere cellulae circiter 13—16 striis longitudinalibus tenuissimis instructa est. Inter strias interdum series granulorum tenuissimorum (circiter

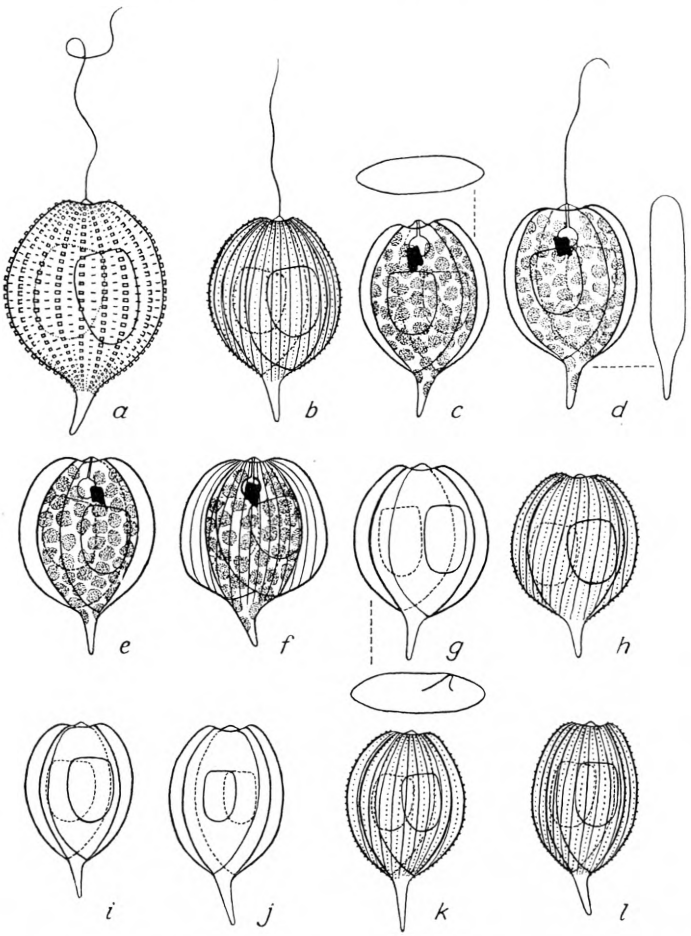


Fig. 106. *Phacus suecicus* Lemm.; *a* from Sortedam II, August 23rd, 1929, 800×. *b*—*l* var. *inermis* n. var. from Bøllemosen, September 5th, 1946. *b*, *h*, *k* and *l* are striated and punctuated individuals (eyespot, chromatophores, reservoir and nucleus are omitted). *c*, *d*, *e*, *g*, *i* and *j* represent smooth individuals (eyespot, chromatophores, reservoir and nucleus are omitted in *g*, *i* and *j* in order to demonstrate the look of the paramylon grains). *f* is a striated individual. *c* shows an individual in vertical and front view, *d* in front and lateral view, *g* in front and basal view. The lower lying paramylon grain is stippled in all the figures. 800×.

30 granula pro serie). In media cellula circiter 9 granula pro 10 μ, ad fines serierum granula minores et constipatiores. Granulis paramylaceis binis, grandibus, inverse stapediformibus. Flagello cellulae longitudine aequilongo. Chloroplastis multis, parvis, rotundis vel angulatis. Nucleus grandis, sphaericus, basalis est. Longitudo cellu-

larum 23—26.5 μ, latitudo 17—24 μ, crassitudo 6—7.5 μ; cauda 6.5—9 μ longa; 6—7 striae pro 10 μ in media cellula.

Hab. In Bøllemosen, Selandia, et Flødegaardens Dam, Fionia, Dania, libere natans.

The variety differs from the main species by its smooth or delicately striated cells; if granules are present, they are always very much reduced. Besides the dimensions of the variety are smaller than those of the main species.

Strange to say A. POCHMANN, who in his monography (1942) has subjected the *Phacus* species to a close study, did not observe the stirrup-shaped paramylon granules in *Phacus suecicus*. All *Phacus suecicus* observed by me in Danish localities had paramylon granules of this shape (cp. NYGAARD 1945, t. 2, fig. 35, drawn from living material); as mentioned the same is true of var. *inermis*. In my opinion, however, it would be as illegitimate to set up a new species on the basis of these characteristic paramylon granules as to retain a "species" like *Phacus multiannulatus* Pochmann (loc. cit., p. 206, Fig. 118).

Phacus suecicus var. *inermis* was observed on September 5th, 1946 in Bøllemosen where it was infrequent in a *Dic pu*-association with *Ma ca* as subdominant; beside these two characteristic indicatory species *Dinobryon pediforme* was rather common in the plankton. In Flødegaardens Dam the variety was seen on August 3rd, 1939, where it was very rare in a *Dic pu*-association with *Ste Ha* as subdominant.

Bøllemosen is probably oligotrophic of the dystrophic phase: at the said time the water was very brown, and pH was 4.9. Flødegaardens Dam is a contaminated, highly eutrophic pond; on August 3rd, 1939 the compound quotient was $\frac{35}{4} = 8.75$.

In an ecological respect the described variety thus holds a somewhat exceptional position among the *Phacus* species, the great majority of which are found in eutrophic (and mixotrophic ponds.)

Trachelomonas chlamydophora n. sp.

Fig. nostra 107.

Diagnosis. Cellulae magnae, saepe obovatae apice subtruncato, raro ellipsoideae, rarissime cordiformes, quaeque cellula tegimento gelatinoso, 4.5—5 μ crasso circumdata. Theca ochracea, saepe punctulata, 4—5 punctulis pro 5 μ, raro scaberula vel tenuissime et disperse spinulosa, in primis ad fines. Apex collo brevissimo, 1—1.5 μ alto et 4 μ lato instructus est. Pellicula protoplasti tenuiter et spiraliter striata, 16—17 striis pro 10 μ. Nucleus magnus, rotundus, in parte posteriore cellulae situs est. Chromatophori multi, subrotundi; granula paramylacea numerosa, ellipsoidea vel breviter bacilliformia; stigma rubrum satis magnum in parte anteriore cellulae apud vacuolum; flagellum circiter $1\frac{1}{2}$ longitudinis cellulae. Longitudo cellularum sine mucilagine 39—42 μ, latitudo 30—35 μ.

Hab. In palude Eriophori prope Sorø, Dania, libere natans.

Systematics. At first I considered the individuals in question to be identical with *Trachelomonas hispida* Stein var. *punctata* Lemm. (DEFLANDRE 1926, p. 651, figs. 209—211, 215—217); especially DEFLANDRE's fig. 211 is very similar in outline. DEFLANDRE, however, gives the measurements 26—32 $\mu \times 19$—23 μ for the variety

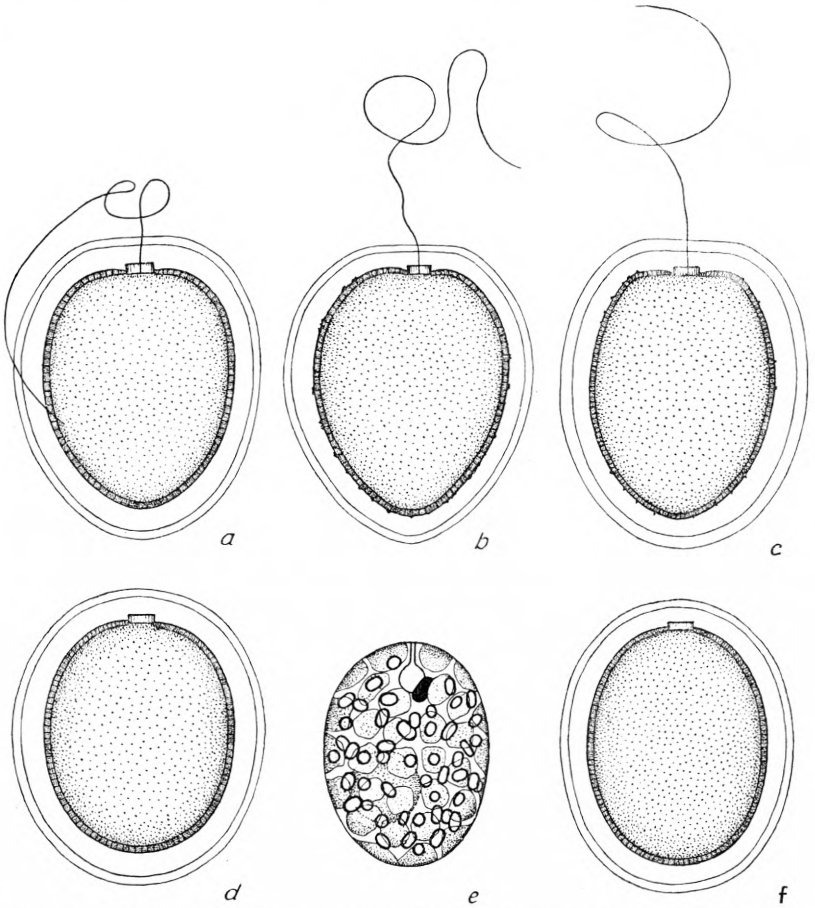


Fig. 107. *Trachelomonas chlamydophora* n. sp. from the Eriophorum moor; *a*—*e* from August 6th, 1947, *f* from July 9th, 1947. *e* the naked protoplast. 800×.

mentioned; further it has no collum, and the gelatinous envelope is lacking. Consequently, the two forms cannot be identical.

Within the genus *Trachelomonas* only a single species was hitherto known to possess a thick gelatinous envelope outside the cell, viz. *Trachelomonas mucosa* Swirenko (DEFLANDRE 1926, p. 72, t. 2, fig. 154). This species exhibits the same dimensions as *Trachelomonas chlamydophora*, but its cells are ellipsoidical and provided with a rather long collum, which measures 3×4.5 μ; further its flagellum is 2—3 times as long as the cell.

The dimensions of *Trachelomonas mucosa* Swir. var. *brevicollis* Skvortz. are only 28—35 $\mu \times 16$—25 μ.

In material fixed in formalin the gelatinous envelope of *Trachelomonas chlamydophora* is not visible.

Periodicity. The species was very rare on July 9th, 1947, but common on August 6th and September 6th at temperatures of 19.5—19° C. On October 4th (temp. 13° C.) the species had become rare again, and it was not observed in the samples from November, December, January, February, March and April. So *Trachelomonas chlamydophora* seems to be periodical and meso- to polythermic, obtaining a considerable maximum in August—September at temperatures about 19° C.

Sociology. The species was found in the following associations:

July 9th, 1947: *Sta Be*-association with *Dic pu* as subdominant (the species very rare).
Aug. 6th, — : *Tra ch*-association (the species common).
Sep. 6th, — : *Tra ch*-association (the species common).
Oct. 4th, — : *Tra*-association (the species rare); see p. 78.

The species thus occurred in associations dominated by the desmid *Staurastrum*, the Chrysophycea *Synura* and the euglenine *Trachelomonas*.

Ecology. The *Eriophorum* moor is mentioned on p. 166. Its water is brownish and slightly acid (pH was 6.5—6.8 at the times when *Trachelomonas chlamydophora* occurred) and somewhat contaminated by cattle grazing near the margin.

Uncoloured flagellates.

Bicoecaceae.

Bicoeca turrigera n. sp.

Fig. nostra 107 *bis.*

Diagnosis. Loricae parvae, e 13 mensionibus 1.3—1.7-plo longiores quam latiores, ampullaceae et teretes, postremus conicae sunt; pars antica cylindracea vel subconica apice truncato cum ora incrassata, sub medio plusminusve inflata est, atque conus basalis semper verruca parva et conica instructus; loricae vulgo incoloratae, interdum pallide ochraceae, transverse anulatae sunt, pars antica cum 8—10 anulis pro 5 μ, conus basalis cum 5 raro 6 anulis pro 5 μ; margo loricae a fronte visae dense et tenuiter dentatus. Protoplastus multo minor quam lorica, sine colore, vulgo sphaericus, raro obovatus, pedicello contractili lateraliter inserto protoplasto circiter $2\frac{1}{2}$-plo longiore basi loricae affixus, oram loricae attingens; nucleo plusminusve centrali. Flagellum unum cellula ad 4-plo longius, lateraliter insertum. Longitudo

loricae 15.5—20 μ (vulgo 16—17.5 μ), latitudo 9—15.5 μ (vulgo 10.5—11.5 μ), latitudo orae 7—11.5 μ (vulgo 7.5—8.5 μ); diameter protoplasti 4—8 μ (vulgo 5—6 μ).

Hab. In Fønstrup Dam prope Hillerød, Dania, libere natans.

Systematics. This new species is easily distinguished from *Bicoeca planctonica* Kisselew (Huber-Pestalozzi 1941, p. 284, fig. 353) and *Bicoeca* (*Bicocoeca*) *multiannulata* Skuja (1948, p. 298, t. 34, figs. 6—11) by the shape of the house and the protoplast.

The protoplast is able to retire lightning-swift from the edge of the house to its basis.

Periodicity. Fønstrup Dam was explored every fortnight during a whole year, but the species was only observed in August and September 1929 by temperatures of 13—16.5° C. It always occurred in small quantities except on September 7th (temp. 13° C.), where it was rather common. Allready on September 22nd it had disappeared. Accordingly the organism must be considered meso- to polythermic.

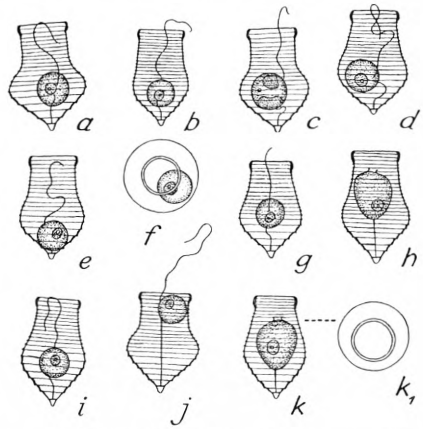


Fig. 107 bis. *Bicoeca turrigera* n. sp. from Fønstrup Dam, September 7th, 1929. *e*, *i* and *j* are drawn after living material, the other figures after material fixed in formalin. *f* and k_1 vertical views, the others front views. 800×.

Sociology. *Bicoeca turrigera* was found in associations of different flagellates as i. e. *Cryptomonas*, *Synura*, *Euglena*, *Lepocinclis*, *Phacus*, and especially *Trachelomonas volvocina*. The plankton was always exceedingly poor in individuals in August and September, only on September 7th, it was distinctly dominated by one organism, and just *Bicoeca turrigera*.

Ecology. Fønstrup Dam (see Nygaard 1938, p. 528, t. 4, figs. 15—16) is a neutral-alkaline forest pond, rich in submerged vegetation, but poor in plankton, ammonia, nitrate and phosphate. Here is a little contribution to the ecology of the species: pH 7.0—7.2, content of CaO 63.3—68.6 mg/l, consumption of $KMnO_4$ 90 mg/l, contents of PO_4-P 0.05—0.06 mg/l, NH_3-N 0.15—0.3 mg/l, NO_3-N 0 mg/l.

Myxophyceae.

Chroococcales.

Chroococcaceae.

Microcystis.

In 1941 Einar Teiling gave an account of the difference between the 3 widely distributed species *Microcystis aeruginosa* Kg. emend. C. Wesenberg-Lund, *Microcystis flos aquae* Kirchner emend. C. Wesenberg-Lund and *Microcystis viridis* Lemm. Wesen-

BERG-LUND was the first to clearly apprehend the difference between *Microcystis aeruginosa* and *Microcystis flos aquae* in the consistency of the gelatinous envelope. However, TEILING paid no regard to the size of the cells, and the key in his 1942 paper (p. 63—64) is determined only for *Microcystis* species with cells larger than 5 μ.

TEILING's definition of the 3 species, which appears distinctly from his instructive Fig.s 1—7, Fig.s 8—9 and Fig. 12, is very practical and no doubt represents a significant progress within the systematics of *Microcystis*. In order to examine whether TEILING's characteristics of species within this difficult genus are hereditary constants or only modifications I made, on July 4th, 1945, 6 clones of *Microcystis flos aquae* (from Mølledammen, Sønderborg) in 6 different culture fluids, *i. a.* in ultra-filtered Mølledam water of various dilutions. On July 20th there was no development of *Microcystis* in any of the glasses, and on August 26th the clones were discarded because no *Microcystis* would develop. The failure of these pure culture experiments is no doubt caused by the fact that there was no constant, slight stirring of the water, for instance by means of a slow up- and downward moving of a plate in the culture fluid throughout the experiment.

In order to demonstrate how the said 3 *Microcystis* species are defined in this paper a small survey is given here:

A. Mucilage sharply delimited, with highly refractive margin; colonies composed of lobulate, rounded partial colonies.
   1. Cells 3—4.5 μ ..... *Microcystis aeruginosa*
   2. Cells 5—7 μ ..... *Microcystis aeruginosa* var. *major* Wittr.

B. Mucilage without visible or with indistinct delimination; colonies of nebulous shape.
   1. Cells 3—4.5 μ ..... *Microcystis flos aquae*
   2. Cells 5—7 μ ..... *Microcystis flos aquae* var. *major* nov. var.

C. Margin of mucilage distinct, but not highly refractive, set with small, rounded bulges; partial colonies somewhat angular, with cells arranged in $\pm$ distinct series or planes;
   Cells 5—7 μ ..... *Microcystis viridis*

Microcystis chroococcoidea West var. **minor** nov. var.

Fig. nostra 108.

Diagnosis. Coloniae parvae, subrotundae, e 6—15 cellulis compositae, sine mucilagine conspicua. Cellulae rotundae, satis dense conglomeratae, olivaceae, subhomogenae, sine vacuolis. Diam. cellularum 2.5—3 μ, diam. coloniarum 7—11.5 μ.

Hab. In Mølledammen in Sønderborg, Dania, libere natans.

The main species differs from this characteristic variety by its larger cells (4—7 μ) and colonies (14—33 μ); besides it occurred in quite another *milieu*, an antarctic

salt lake (W. & G. S. West 1911, p. 296, t. 26, figs. 107—114). F. E. Fritsch & E. Stephens further reports the main species from South Africa (1921, p. 60: diam. of cells 4 μ).

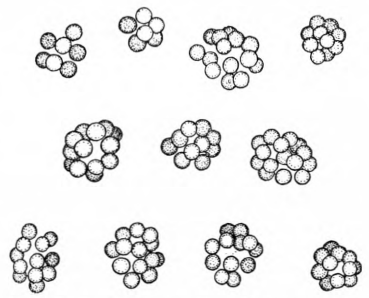


Fig. 108. *Microcystis chroococcoidea* West var. *minor* n. var.; 11 colonies from Mølledammen in Sønderborg, August 26th, 1944. 800×.

The variety was found in enormous quantities in the plankton from Sønderborg Mølledam on August 26th, 1944. This pond is highly eutrophicated by various swimming birds (ducks, swans etc.), which are often fed by the inhabitants of the town. On the said date the plankton was dominated by *Microcystis chroococcoidea* var. *minor* and *Oscillatoria limnetica* var. *acicularis* n. var. f. *brevis* n. f.; the sample contained 24 species, and the myxophycean quotient was $\frac{7}{1}$, the chlorophycean quotient $\frac{8}{1}$, the diatom quotient $\frac{0}{1}$, the euglenine quotient $\frac{3}{14}$ and the compound quotient $\frac{18}{1} = 18$, which indicates a high degree of eutrophy.

Microcystis flos aquae Kirch. em. W.-L. var. **major** nov. var.

A typo cellulis majoribus differt; diameter cellularum 5—7 μ.

Hab. In Nors Sø, Birkerød Sø, Hulsø et Frederiksborg Slotssø, Dania, libere natans.

Here and under the following *Microcystis* species the only intention is to define the variety or species and not to give a detailed account of its distribution, periodicity, sociology or ecology since this would require a renewed trial of the whole of my great plankton material from Danish lakes and ponds.

Microcystis holsatica Lemm.

E. Lemmermann 1910, p. 77.—*Fig. nostra* 109.

Hab. Nors Sø, Furesø, Hostrup Sø, Mossø, Tissø, Sorø Sø, Salten Langsø, Nordborg Sø, Huno Sø, Sandbjerg Sø, Tranekjær Sø, Frederiksborg Slotssø, Badstue-Ødam, Vandingsdam, Spejldam, Hulsø, Teglgaard Sø, Sortedam II, Badstue-Dam, Longet Sø at Nyborg, Flødegaardens Dam, Blankeborg I & II, Jægerbakke Dam and Pond at Ragebøl, pelagic.

For several years I considered *Microcystis holsatica* to be identical with the closely related species *Microcystis pulverea* Mig. var. *incerta* (Lemm.) Crow. As the cells of the Danish colonies are 1 μ in diameter and the colonies are irregularly shaped and may be clathrate, it will be correct provisionally to identify them as *Microcystis holsatica* though they have an invisible—exceptionally indistinctly visible—margin of the mucilage.

According to diagnosis and picture (LEMMERMANN 1901, p. 93, t. 4, fig. 8) *Microcystis pulverea* var. *incerta* has spherical-ellipsoidal colonies with a distinct, later on "zerfliessende Gallerthülle", and the cells are stated to be 1—2 μ in diameter. In 1930 Prof. C. H. OSTENFELD presented me with an exsiccate of the plankton from Vombsjön in Schonen, containing *Microcystis incerta* Lemm. (determ. E. LEMMERMANN); reiterated examinations of soaked material from this exsiccate, however, gave no adequate picture of the species. According to LEMMERMANN (1910, pp. 76—77)

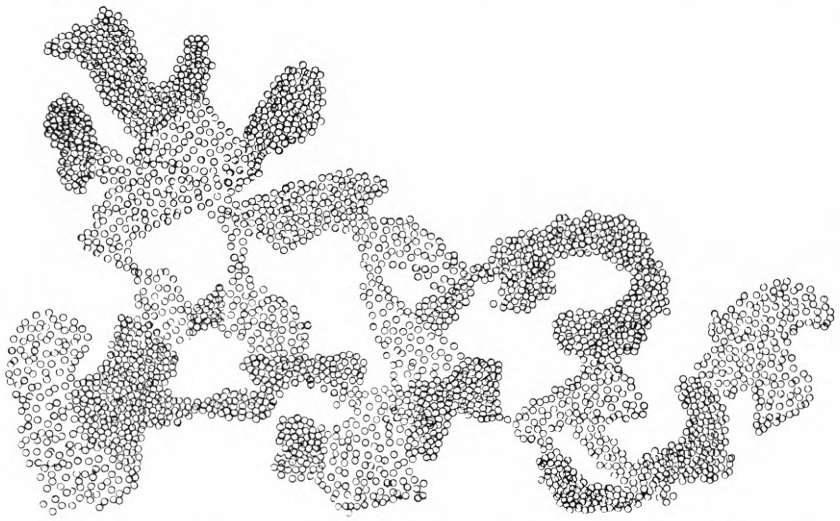


Fig. 109. *Microcystis holsatica* Lemm., a large, clathrate colony from Jægerbakke Dam, September 18th, 1929. 800×.

Microcystis incerta is widely distributed in the lakes of Brandenburg, whereas *Microcystis holsatica* seems to be comparatively rare.

Only in the sample from Sandbjerg Sø, September 3rd, 1939, I did see a *Microcystis* species that corresponded fairly well to *Microcystis incerta*, the colonies being mostly roundish, rarely oblong and a little irregular; however, the cells measured 1 μ in diameter, and the margin of the colonial mucilage was invisible.

Future investigations will no doubt prove the two species to be identical.

Also CROW (1923, p. 65) maintains that "the margin of the colonial mucilage is clearly defined". We are much in need of a thorough revision of the genus *Microcystis*, mainly based on pure or unialgal cultures, cultivated under different ecological conditions.

Such culture experiments and on the whole all culture experiments with plankton organisms should not be confined to such artificial substrata as agar and gelatine, but the conditions of growth should be made as natural as posible. Unless they are 'specialists' the organisms should be cultivated in a suspension of earth saturated in a cold state and sterilized not by boiling but by filtration through bacterium-proof asbestos filters as recommended by FRANZ MOEWUS for experiments on germination

of zygotes. Moreover the culture fluid should be constantly stirred, for instance by moving a plate slowly up- and downwards in the fluid or—what is no doubt much easier—by letting all the cultures rotate slowly on a turn-plate.

Microcystis minutissima W. West.

1912, p. 41.—*Fig. nostra* 110.

I have often been in doubt whether *Microcystis minutissima* or *Aphanothece clathrata* West var. *brevis* Bachmann (1923, p. 165, t. 3, figs. 1—2) were before me because every kind of transition occurred between colonies in which the cells are distinctly crowded in clusters (Hunø Sø), thus being totally identical with W. West's specimens, and colonies the cells of which are more diffuse (Jægerbakke Dam, Blankeborg I, Furesø, Tissø). Even in the last-mentioned ponds and lakes colonies may be found in which the cells are crowded in some places.

The Danish colonies always had an invisible margin of the mucilage, and the cells measured 1.1—2 μ in length and 0.9—1 μ in breadth. Only in Furesø colonies were observed to be slightly clathrate (not at all like the original drawing quoted from Bachmann); but according to Naumann (1925, p. 47) this character seems to be a modification depending on the low intensity in the movement of the water, and so these colonies, too, have been termed *Microcystis minutissima*.

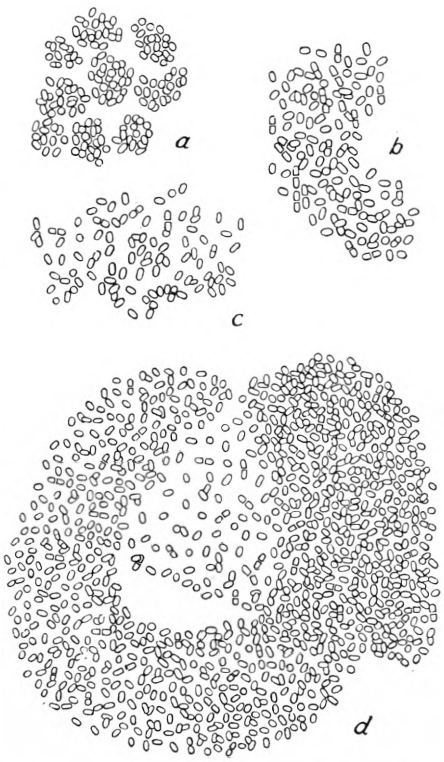


Fig. 110. *Microcystis minutissima* West; *a* from Hunø Sø, Møen, September 17th, 1937; *b* from Blankeborg I, August 18th, 1928; *c* from Jægerbakke Dam, July 17th, 1929; *d* from Furesø, August 21st, 1943. 800×.

Distribution. Seeland: Jægerbakke Dam, Frederiksborg Slotssø, Hulsø, Furesø, Tissø; Møen: Hunø Sø; Funen: Blankeborg I; North Jutland: Nors Sø, Hampen Sø, Salten Langsø; North Sleswick: Hostrup Sø.

Microcystis pulverea Migula.

Migula in Kryptogamenflora von Deutschland, Deutsch-Österreich und der Schweiz, Bd. II, 1907, p. 36.—*Fig. nostra* 111.

Colonies irregularly shaped, with rounded edges, very rarely sausage-shaped, without or with very indistinctly visible margin of mucilage, several (up to 8) united

in mucilage which normally also has an invisible margin; exceptionally, the latter is visible and irregularly lobulate, but is never highly refractive as in *Microcystis aeruginosa*. Cells very densely situated, 2—2.5 μ in diameter, rarely 3 μ, without air vacuoles; partial colonies 15—62 μ in size.

Hab. In Blankeborg II, Jægerbakke Dam, Flødegaardens Dam, Lille Gribsø, Hostrup Sø and Nors Sø, pelagic.

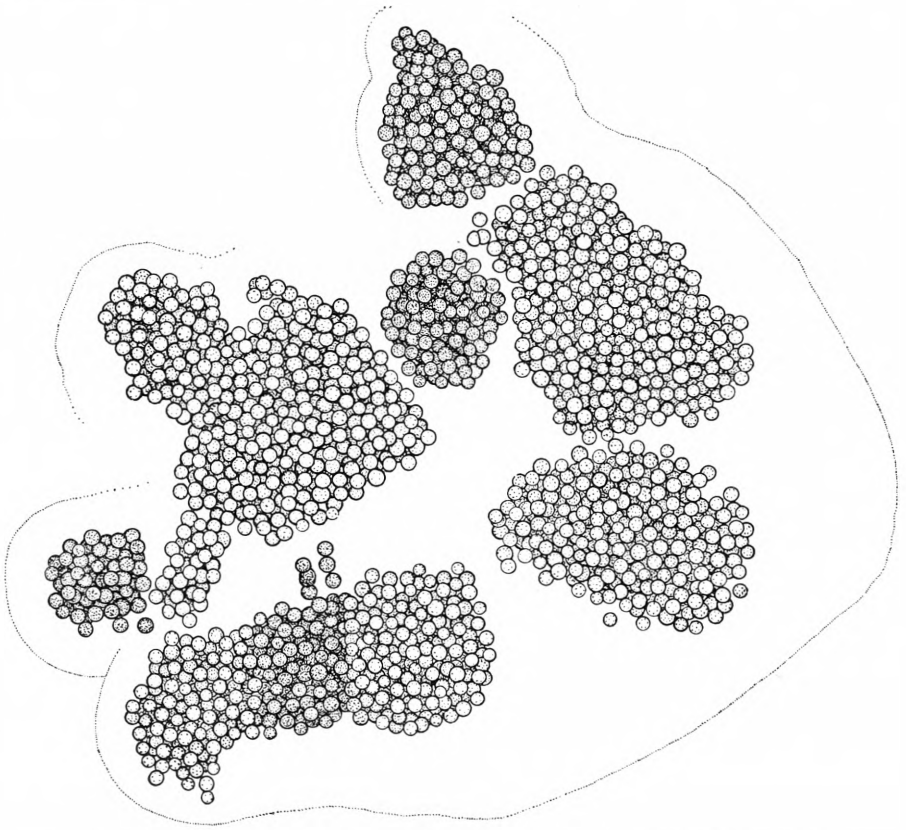


Fig. 111. *Microcystis pulverea* Mig. from Hostrup Sø, June 23rd, 1925. 800×.

According to the original diagnosis *Microcystis pulverea* has a visible margin of the mucilage; my experience shows that pelagic *Microcystis* colonies with cells of 2—2.5 μ generally have no visible margin of the mucilage, but in potassium acetate slides it may be comparatively distinct when the immersion objective is used. However, *Microcystis parasitica* Kg., which is stated to have an indistinct margin of the mucilage, is hardly before us since this species is said normally to be attached to water-plants.

var. **racemiformis** nov. var.

Fig. nostra 112.

Diagnosis. Coloniae parvae, subracemiformes, subrotundatae vel irregulares, lobulatae, interdum ex coloniis minimis compositae. Mucilago cum margine perspicuo raro indistincto vel destituto. Cellulae rotundae, aeruginosae, tenuiter granulatae, dense conglomeratae, sine vacuolis, 1.5—2 μ in diametro. Dimensio coloniarum 8.5—27 μ.

Hab. In Frederiksborg Slotssø, Lille Gribsø, Sortedam II, Gadevang Mose, Vandingsdam, Jægerbakke Dam et Flødegaardens Dam, Dania, libere natans.

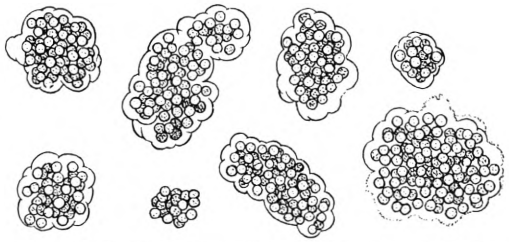


Fig. 112. *Microcystis pulverea* Mig. var. *racemiformis* n. var. from Vandingsdam, August, 10th 1929. 800×.

This variety differs from the main species by its small lobulate colonies with distinct margin of the mucilage and by its smaller, densely clustered cells. From the very closely related species *Microcystis exigua* Zalessky (1926, p. 34, t. 10, fig. 4) it differs by the small bulges of the surface of its mucilage, every bulge appearing to belong to its cell.

The diagnosis given above refers to the colonies from Vandingsdam where the variety was periodical and reached a great maximum in August—September.

In Frederiksborg Slotssø the colonies were mostly larger than in Vandingsdam, the mucilaginous envelope as a rule was indistinct, also in colonies smaller than 20 μ, but might be visible as a line near one side of the colony. Generally the colonies had a regular oval shape and frequently measured 40—50 μ in length and about 25 μ in breadth. The older colonies had no visible edge of the mucilage and were irregular of shape, in rare cases even clathrate and 60—65 μ long and 20—45 μ broad. These types of colonies were found all the year round in Frederiksborg Slotssø and also in Jægerbakke Dam.

Also the large amounts of colonies found in Hesteskodam on September 10th, 1929 only exceptionally had a finely bulged edge of the mucilage. Here the colonies were small and round (14—15 $\mu \times$ 13—14 μ) or oval (25 $\mu \times$ 21 μ), rarely longish (102 $\mu \times$ 30 μ).

In spite of the fact, therefore, that the edge of the mucilage is often indistinct I refer these colonies to *Microcystis pulverea* var. *racemiformis* because the cells measured 1.75—2 μ in diameter and were always densely clustered.

Microcystic robusta Nyg.

Ostenfeld and Nygaard 1925, p. 8, figs. 1—4; Nygaard 1926, p. 204, t. 2, figs. 17—18; t. 3, figs. 22—23.—*Fig. nostra* 113a.

Both the Central American and the Malayan material contained both colonies with distinctly refractive margin of mucilage and rounded, lobulate partial colonies

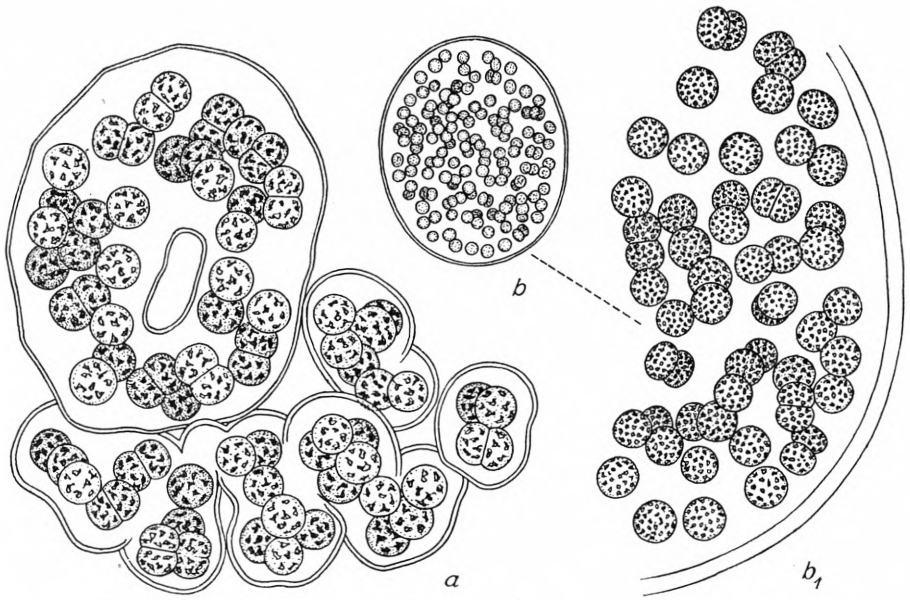


Fig. 113. *Microcystis robusta* Nyg.; *a* from Furesø, August 21st, 1943, 800×; ? *b* from Mørksø, July 6th, 1938. 260× and 800×.

and colonies without visible surface of the mucilage. The size of the cells in the original material from Guatemala was 6—9 μ, from Panama 5—8 μ and from Key Islands 5—8.5 μ.

In this country the species was safely established in Furesø only where I found it in a plankton sample from August 21st, 1943, sent to me by E. Fjerdingstad. The association was dominated by *Melosira granulata* var. *angustissima*; its qualitative composition appears from Table II. The cells had a diameter of 6.5—8.5 μ; the very few colonies observed were small and had lobulate, rounded partial colonies with clearly defined, highly refractive margin of the mucilage. It is questionable whether *fig. nostra* 113b from the plankton of Mørksø is also a *Microcystis robusta*; the colony was ellipsoidical, 114 μ × 92 μ, the cells 6—7.5 μ in diameter, but the material is too sparse for a closer identification.

If researches of the future show that TEILING's criterions of species are hereditarily determined, *Microcystis robusta* must presumably be distinguished as

Microcystis aeruginosa var. *robusta* and
Microcystis flos aquae var. *robusta*.

Dactylococcopsis scenedesmoides n. sp.

Fig. nostra 113 *bis.*

Diagnosis. Cellulae curvate baculiformes, $5\frac{1}{2}$—7-plo longiores quam latiores, in medio plusminusve infractae et dorsaliter subinflatae, apicibus paulo vel distincte tenuioribus et interdum leviter recurvatis et subcapitatis, in coloniis seriatis et quadrivel bicellularibus consociatae. Membrana cellulae tenuissima, cytioplasma pallide aeruginosum, dense et tenuiter granulosum. Longitudo cellularum 12.5—21.5 μ, latitudo 2—3.5 μ.

Hab. In Jægerbakke Dam in Hillerød, Dania, libere natans.

Systematics. This new species differs from all previously described *Dactylococcopsis*-species by the *Scenedesmus*-like arrangements of the cells. Fig. nostra 113 bis shows, however, that the colonies of *Dactylococcopsis scenedesmoides* are by far not so compactly builded as the colonies of the green alga *Scenedesmus*. The pressure of the coverglasses on the permanent slides containing *Dactylococcopsis scenedesmoides* is sufficient to loosen the cells of the colonies.

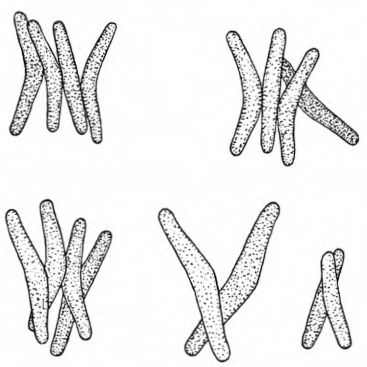


Fig. 113 bis. *Dactylococcopsis scenedesmoides* n. sp. from Jægerbakke Dam, October and November 1929. 1070×.

Periodicity. Jægerbakke Dam was explored regularly every fortnight during a whole year, from June 1929 to June 1930. *Dactylococcopsis scenedesmoides* occurred in all samples from the period of October to January (temperature 12—1° C) and in a single sample from May (temperature 23.25° C.) as will appear from the following section. No maximum was observed, the quantities of the organism always being very small. The species thus was eurythermic. It is possibly perennial; the fact that it was not observed in the periods of June to September and February to April may be explained by its marked scarceness.

Sociology. *Dactylococcopsis scenedesmoides* was found in the following associations:

Oct. 3rd, 1929: *Mio ho*-association (the species very rare).
— 14th, — : ditto.
— 23rd, — : *Mio ho*-association with *Os li* and *Sce arm* as subdominants (the species very rare).
Nov. 2nd, — : *Sce arm*-association with *Mio ho* as subdominant (the species very rare).
— 16th, — : *Mio ho*-association with *Ank fa se br* and *Sce arm* as subdominants (the species very rare).
— 30th, — : *Ank fa se br*-association with *Crym ov*, *Mio ho* and *Sce arm* as subdominants (the species very rare).
Dec. 16th, — : *Ank fa se br* - *Ki mi*-association with *Ank fa spa* and *Mio ho* as subdominants (the species very rare).
Jan. 15th, 1930: *Ki mi*-association with *Ank fa se br* and *Chla ka* as subdominants (the species very rare).
— 31st, — : ditto.
May 31st, — : *Mio ho*-association (the species very rare).

Dactylococcopsis scenedesmoides thus occurred in associations dominated by blue-green algae (*Microcystis*) and green algae (*Scenedesmus*, *Ankistrodesmus*, *Kirchneriella*).

The most constant associates were *Ankistrodesmus convolutus* var. *minutus*, *Ankistrodesmus falcatus* var. *setiformis* f. *brevis* and var. *spiralis*, *Microcystis holsatica*, *Oscillatoria limnetica* and var. *acicularis*, *Scenedesmus armatus*, *Scenedesmus falcatus* f. *tortuosa*, *Selenastrum Westii*, all of which were found in 100 % of the number of samples (10) containing *Dactylococcopsis scenedesmoides*. *Ankistrodesmus falcatus* and var. *spirilliformis*, *Chlamydomonas kakosmos*, *Microcystis minutissima*, *Scenedesmus quadricauda* and *Tetraëdron caudatum* var. *longispinum* occurred in 90 %, *Anabaena tenericaulis* and *Chlamydomonas retroversa* in 80 % of the samples.

Ecology. Jægerbakke Dam is a partly overshadowed, highly eutrophic pond, sheltered by winds; it is peculiar in being poor in calcium. The undermentioned dates all refer to the period of October to January; pH was 9.8 on May 31st, 1930. The species was found by pH 6.9—7.7, content of CaO 7.3—9.7 mg/l, consumption of $KMnO_4$ 28—32 mg/l, contents of PO_4-P 0—0.008 mg/l, NH_3-N 0.08—0.75 mg/l, NO_3-N 0—0.01 mg/l; on january 31st the content of Fe was 0.45 mg/l.

Hormogoneales.

Oscillatoriaceae.

Oscillatoria Borneti Zukal f. **tenuis** Skuja.

H. Skuja 1929, p. 18, t. 1, fig. 16.

The specimens, which corresponded closely to the diagnosis, had a thickened hood (calyptra) on the endcell as shown in Pascher's Süsswasserflora, Heft 12, Cyanophyceae, Fig. 434. Skuja states the thickness of f. *tenuis* to be 5.5—7 μ while the main species measures 12—16 μ. The present individuals were about 8 μ thick.

This presumably tychoplanktic and easily recognizable organism is possibly a summer form in Northern Europe. Skuja found it in two localities in Estonia in July. In this country it occurred in very small quantities in Kalgaard Sø on June 23rd, 1929 (but not in May 1929) and rather sparsely in Præstesø on June 24th—28th, 1930 (temp. 20—21° C.).

On June 23rd, 1929 the plankton of Kalgaard Sø consisted of an *Ura am*-association. On June 28th, 1930 the plankton of Præstesø consisted of an *Ana fl*-association; among the Desmids of this lake *Staurastrum arctiscon* is noteworthy. The phytoplankton quotients appear from Table I and the composition of the associations from Table II.

Both lakes, which contain vegetations of *Lobelia Dortmanna*, are clear and chiefly neutral (Kalgaard Sø pH 6.9 and Præstesø pH 7.0—7.1 on the dates mentioned); in July 1940, however, Boisen Bennike (1943, p. 34) found pH to be > 9.0, a colour of 10 "Ohle-units" and a $KMnO_4$ consumption of 37 mg/l in Præstesø. In Kalgaard Sø it was impossible on June 23rd, 1929 to find the slightest trace of phosphate, ammonia and nitrate!

Oscillatoria limnetica Lemm. var. **acicularis** nov. var.

Fig. nostra 114.

Diagnosis. Trichomata solitaria, recta vel leviter curvata, ad dissepimenta non constricta, pallide aeruginosa, 1—1.5 μ lata. Dissepimenta saepe difficulter visibilia. Cytioplasma cellularum homogenea, longitudo cellularum 8—12 μ. Cellula terminalis longe acuminata, spinacea, recta, sine calyptra.

Hab. In Badstue-Ødam et Jægerbakke Dam prope Hillerød, et Hostrup Sø in Jutlandia, Dania, libere natans.

Systematics. The variety differs from *Oscillatoria limnetica* by its non-constricted, slightly narrower trichomes with spine-like end-cells. In the fixed material from Badstue-Ødam the dissepiments were invisible; the cell lengths of 8—12 μ were measured in living material. Not even the use of the best immersion objectives made it possible to see any constriction whatever, neither in living nor in fixed material.

During the great *Oscillatoria limnetica* maximum in Sandbjerg Sø on September 4th, 1937 trichomes were found that apparently had pointed end-cells. However, a close examination of both living and fixed material showed that this rough and rather abrupt pointing is due to degeneration of the end-cell. Such a phenomenon was never observed in trichomes of *Oscillatoria limnetica* var. *acicularis* (and, incidentally, not in the trichomes of *Oscillatoria limnetica* from Badstue-Ødam and Jægerbakke Dam).

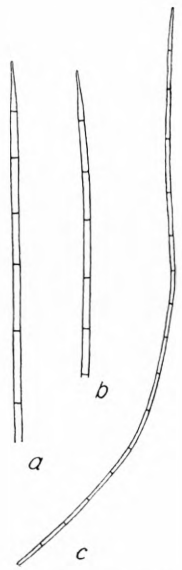


Fig. 114. *Oscillatoria limnetica* Lemm. var. *acicularis* n. var. from Badstue-Ødam, September 5th, 1929. *a*—*b* 800×, *c* 560×.

It appears from Tables II and IV in which Danish ponds and lakes *Oscillatoria limnetica* and its var. *acicularis* are found. The main species is found in 11 localities, the variety in 4; with one exception (Sønderborg Mølledam, see below) these 4 localities contain both the main species and the variety.

Accordingly, only the main species was found in Sandbjerg Sø (see NYGAARD 1945, t. I, fig. 14); its trichomes were 2 μ thick and the cells 3.5—12 μ (generally 5—7 μ) long. In Badstue-Ødam and Jægerbakke Dam, where both the main species and the variety occurred together, the trichomes of the main species were 1.5 μ thick and its cells 4—10 μ long. According to LEMMERMANN (1910, p. 112, Fig. 5 on p. 91) the thickness of the cells is 1.5 μ and their length 4—12 μ.

In his vague description of thin *Oscillatoria* species G. PLAYFAIR (1914, pp. 129—132, t. 6) has pictured and described Australian forms that are similar to *Oscillatoria limnetica* and its var. *acicularis*. His *Oscillatoria splendida* Grev. var. *limnetica* (Lemm.) Playfair is not, as supposed by him, identical with *Oscillatoria limnetica* Lemm. and *Lyngbya limnetica* Lemm. on account of the lack of constriction, the smooth tapering of the trichomes towards apices and the two granules at each dissepiment. PLAYFAIR'S var. *limnetica* (Lemm.), var. *amylacea* and presumably f. *clarescens* Playf. (all of *Oscillatoria splendida*) should be considered synonymous with *Oscillatoria splendida* Grev. PLAYFAIR'S *Oscillatoria splendida* forma (1914, p. 132, t. 6, figs. 8 *a*—*d*) are identical with a *Chamaesiphon* species, no doubt *Chamaesiphon incrustans* Grun. f. *longissima* Wille.

Periodicity. As will appear from the sociological survey *Oscillatoria limnetica* var. *acicularis* is perennial. In Jægerbakke Dam it reached a high maximum in August 1929 (temp. 17—22.5° C.); but also in June and July the variety was common whereas it was rare during the other months of the year; during the ice period it was not observed at all.

In Badstue-Ødam the considerable maximum was reached at the beginning of September 1929 (temp. 18—18.5° C.). Already before the middle of this month it disappeared though quite a few individuals were observed on November 30th,

December 16th and January 15th, 1930. The variety, which apparently find better conditions in Jægerbakke Dam, did not reappear until June 16th, 1930 (temp. 24° C.) when it was common.

In Hostrup Sø the variety was common on July 5th, 1927.

In other words *Oscillatoria limnetica* var. *acicularis* is a eurythermic plankton form (amplitude of temperature 1—28.5° C.) with a distinct maximum in August or September (temp. 17—22.5° C.).

Sociology. The variety occurred in the following associations:

Jægerbakke Dam.

June 12th, 1929: *Mio mi*-association with *Ana Vi da*, *Mio ho* and *Ra pe* as subdominants (the variety rather common); see Table IV.

— 18th, — : *Mio mi*-association with *Ana te*, *Ana Vi da*, *Mio ho* and *Sce arm* as subdominants (the variety rather common).

— 27th, — : *Mio mi*-association with *Ana Vi da* as subdominant (the variety rather common).

July 4th, — : *Mio mi*-association with *Ana Vi da* as subdominant (the variety rather common).

— 11th, — : *Ana Vi da*-association with *Mio mi* as subdominant (the variety rather common).

— 17th, — : *Ana Vi da - Sce arm*-association with *Mio mi*, *Mio ho* and *Os li ac* as subdominants (the variety common).

— 27th, — : *Ana Vi da*-association with *Mio ho* as subdominant (the variety rather common).

Aug. 10th, — : *Ana Vi da - Mio ho - Os li ac - Sce arm*-association (the variety very common).

— 21st, — : *Ana Vi da - Mio ho - Os li ac*-association with *Mio mi* and *Sce arm* as subdominants (the variety very common).

Sep. 2nd, — : *Ana Vi da*-association with *Mio ho* as subdominant (the variety rare).

— 13th, — : *Ana Vi da - Mio ho*-association (the variety very rare).

— 17th, — : *Mio ho*-association with *Sce arm* as subdominant (the variety very rare); see Table IV.

Oct. 3rd, 14th, 23rd, 1929: *Mio ho*-association with *Sce arm* as subdominant (the variety very rare).

Nov. 2nd, 1929: *Sce arm*-association with *Mio ho* as subdominant (the variety rare).

— 16th, — : *Mio ho*-association with *Sce arm* and *Ank fa se br* as subdominants (the variety rare).

— 30th, — : *Ank fa se br*-association with *Crym ov*, *Mio ho* and *Sce arm* as subdominants (the variety very rare).

Dec. 16th, — : *Ank fa se br - Ki mi*-association (the variety very rare).

Jan. 15th, 1930: *Ki mi*-association with *Ank fa se br* and *Chla ka* as subdominants (the variety very rare).
— 31st — : ditto.
Mar. 15th, — : *Ki mi*-association (the variety very rare).
Apr. 10th, — : *Din se pr*-association (the variety very rare).
— 22nd, — : *Din se pr*-association with *Ge mi* as subdominant (the variety very rare).
May 1st, — : *Ge mi*-association (the variety very rare).
— 10th, — : ditto.
— 21st, — : *Mio ho*-association with *Sce arm* as subdominant (the variety rare).
— 31st, — : ditto.
June 16th, — : *Mio ho*-association with *Ana si* and *Sce arm* as subdominants (the variety rare).

Badstue-Ødam.

Aug. 10th, 1929: *Cyc st su*-association with *Frg cr* as subdominant (the variety not infrequent).
— 17th, — : ditto.
— 23rd, — : *Frg cr*-association with *Ana af in te* and *Cyc st su* as subdominants (the variety not infrequent); see Table IV.
Sep. 3rd, — : *Cyc st su*-association with *Ana af in te* and *Os li ac* as subdominants (the variety common).
— 5th, — : *Ana af in te*-association with *Os li ac* a subdominant (the variety common).
— 12th, — : *Crym ov*-association with *Ank co mi*, *Cyc st su* and *Sce arm* as subdominants (the variety rare).
Nov. 30th, — : *Chry ma - Crym ov*-association (the variety very rare).
Dec. 16th, — : ditto.
Jan. 15th, 1930: *Chry ma*-association (the variety very rare).
June 16th, — : *Crym ov*-association with *Ana af in te* and *Cyc st su* as subdominants (the variety common).

Hostrup Sø.

June 23rd, 1925: *Api fl*-association (the variety very rare); see Table II.
July 5th, 1927: *Coo Nä*-association with *Api fl* and *Os li ac* as subdominants (the variety common); see Table II.

It appears from this that *Oscillatoria limnetica* var. *acicularis* mainly occurs in myxophycean (*Microcystis*, *Anabaena*, *Oscillatoria*, *Aphanizomenon*, *Coelosphaerium*) and chlorophycean associations (*Scenedesmus*, *Ankistrodesmus*, *Kirchneriella* and *Geminella*), but also in chrysophycean (*Dinobryon*, *Chrysococcus*), diatomaceous (*Cyclotella*, *Fragilaria*) and cryptophycean associations (*Cryptomonas*).

The most constant associates were *Scenedesmus armatus*, which occurred in 100 % of the samples (40) that contained *Oscillatoria limnetica* var. *acicularis*; *Micro-*

cystis holsatica (95 %), *Oscillatoria limnetica* (92.5 %), *Scenedesmus falcatus* (80 %) and *Ankistrodesmus falcatus* var. *spirilliformis* (77.5 %).

Ecology. Jægerbakke Dam is a highly eutrophic, lightly overshadowed, small pond, conspicuous by its lime-deficiency (7.3—11.2 mg CaO per litre); there are no in- or outlets. The eutrophic pond Badstue-Ødam, which is somewhat overshadowed but has both in- and outlets, approaches the mixotrophic phase: throughout the year its consumption of $KMnO_4$ may vary slightly about the accepted border value of 50 mg per litre. Hostrup Sø is a moderately eutrophic, comparatively large lake of the mixotrophic phase, lime-deficient (12 mg CaO per litre were observed); see further Tables I and III.

Some few data of the ecology of *Oscillatoria limnetica* var. *acicularis*: pH 6.6—9.8, CaO 7.3—80 mg/l, consumption of $KMnO_4$ 27—57 mg/l, contents of PO_4-P 0—0.035 mg/l, NH_3-N 0—0.75 mg/l, NO_3-N 0—3 mg/l, Fe 0.02—0.45 mg/l.

f. **brevis** n. f.

Fig. nostra 115.

Diagnosis. Trichomata solitaria, irregulariter curvata, raro subrecta vel sigmoidea, sine mucilagine visibile, 20—75 μ longa, circiter 1 μ lata, apicibus binis inaequaliter acutatis, quorum alter acutus, alter acuminatus; cytioplasma incompte granulosum.

Hab. In Mølledammen in Sønderborg, Dania, libere natans.

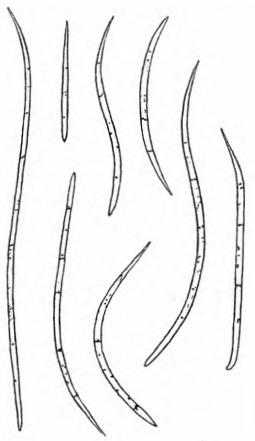


Fig. 115. *Oscillatoria limnetica* Lemm. var. *acicularis* n. var. f. *brevis* n. f. from Mølledammen in Sønderborg, August 26th, 1944. 800×.

It is with some hesitation that I refer this organism to the form cycle of *Oscillatoria limnetica* var. *acicularis*. The contents are somewhat granular and heterogeneous and in spite of a careful examination under the immersion objective it was impossible to decide whether dissepiments were actually present or only seemed to be so in consequence of the position of some granules. The trichomes are very characteristic, one end being tapering and spine-like (as in *Oscillatoria limnetica* var. *acicularis*), the other being abruptly pointed.

On the admixture of iodine dissolved in potassium iodide the trichomes stained with a palish brown like *Merismopedia tenuissima*, *Oscillatoria Agardhii* and *Anabaena flos aquae*; *Microcystis chroococcoidea* var. *minor* (see p. 178), however, stained with an intense reddish-brown colour. So there is hardly any doubt that the organism is in fact a blue-green alga.

Within the *Dactylococcopsis* genus species are known to be just as thin and long, for instance the spirally twisted *Dact. irregularis* G. M. Smith (1921, p. 6, figs. 26—28),

but these long and thin species do not show the same characteristic difference of the ends as the present trichomes. If the latter do not really possess dissepiments, they may be called *Dactylococcopsis inaequalis* n. sp.

The form occurred in enormous quantities in Mølledammen, Sønderborg on August 26th, 1944. The plankton association, the quotients of which are given on p. 179, was dominated by *Oscillatoria limnetica* var. *acicularis* f. *brevis* and *Microcystis chroococcoidea* var. *minor*.

Sønderborg Mølledam is a highly eutrophic pond, contaminated by swimming birds, which are often fed; on August 26th, 1944 the compound quotient was $\frac{18}{1} = 18$. In the summer months there is often a considerable water-bloom, pH then being > 9.

Nostocaceae.

Synonyms within the **Anabaena** genus.

Anabaena contorta Bachmann is a young stage of *Anabaena flos aquae* Breb. *Anabaena limnetica* G. M. Smith is a synonym for *Anabaena planctonica* Brunnth.

"*Anabaena planctonica* Brunnth." as pictured by G. M. Smith with a spherical spore is a synonym for *Anabaena Scheremetievi* Elenk. var. *recta* Elenk. f. *rotundospora* Elenk.

Anabaena Scheremetievi Elenk. is a doubtful species, for according to the description it includes forms of variuos thicknesses. Var. *recta* Elenk. f. *rotundospora* Elenk. and var. *incurvata* Elenk. may be retained being conspicuous by their spherical spores remote from the heterocysts; whether they are "8.5—9 μ vel 11—12 μ (rarius 13 μ) latis" does not appear from the specific descriptions. For the same reason it is difficult to establish the possible identity of var. *recta* Elenk. f. *ovalispora* Elenk. with *Anabaena planctonica* Brunnth. I also consider var. *incurvata* Elenk. f. *ovalispora* Schkorb. a little doubtful as the thickness of the trichomes is said to range between 6 and 12 μ and the breadth of the heterocysts between 7.5 and 13 μ! This form possibly includes elements of *Anabaena spiroides*. Var. *Ukraïnica* Schkorb. is possibly identical with var. *incurvata* Elenk.

Anabaena cylindrica Lemm. var. *marchica* Lemm. is presumably identical with *Anabaena subcylindrica* Borge.

E. Fjerdingstad (1945, p. 14, text-figure 1) speaks of 3 forms of *Anabaena planctonica* Brunnth., but they must undoubtedly fall under the variational range of the main species because the spherical spores are young, immature spores unless they have had a homogeneous content or a thick wall; this does not appear from text-figure 1.

Anabaena affinis Lemm. var. **intermedia** Griffiths. f. **tenuis** n. f.

Fig. nostra 116.

Diagnosis. Trichomata solitaria et recta, cellulis vegetativis aerugineis, cum vacuolis, sphaericis vel paulo brevioribus quam latioribus, $6\frac{1}{2}$—9 μ latis. Heterocystis similibus, 8.5—12 μ latis. Sporis semper ab heterocystis remotis, singulis vel binis, initio subsphaericis, postea ellipsoideis et postremo breve cylindricis apicibus hemisphaericis, 1.3—1.8 plo longioribus quam latiores, 22—26 μ longis, 12.5—18 μ latis. Episporio levi, sine colore.

Hab. In Badstue-Ødam, Selandia, Dania, libere natans.

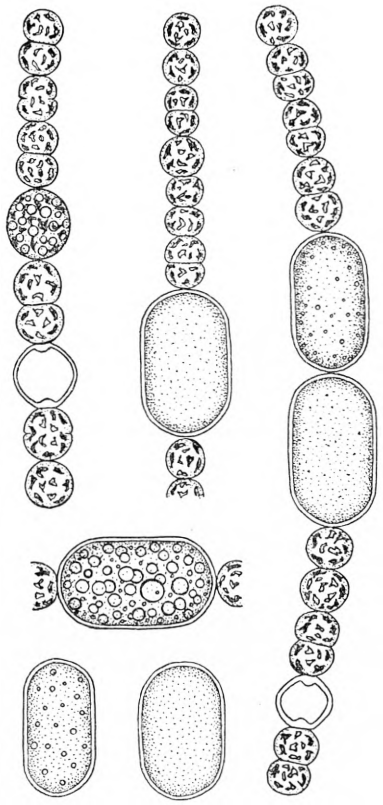


Fig. 116. *Anabaena affinis* Lemm. var. *intermedia* Griff. f. *tenuis* n. f. from Badstue-Ødam, September 5th, 1929. 800×.

Systematics. This variety differs from the main species by its broader spores. In the Kryptogamenflora der Mark Brandenburg, 3. vol., p. 183 Lemmermann gives the length of the spores of the main species as 20—26 μ (i. e. the same as the present variety) whereas the breadth is only 9.5—12 μ. In other words the spores of the main species may be more than twice as long as broad, but according to 12 measurements the present spores were only 1.3—1.8 (mostly 1.5) times longer than broad (see Fig. 116). Fig. 374 (after G. M. Smith) in Pascher's Süsswasserflora, Heft 12, is no typical *Anabaena affinis* because the spore is only about 1.3 times longer than broad.

It appears from the diagnosis that there is no complete agreement with Griffith's description (1925, t. 1, fig. 8) of the English specimens, the Danish specimens from the Badstue-Ødam being 6.5—9 μ, the English specimens 8—10 μ thick. The small difference in the size of the heterocysts is hardly of systematic value. This is confirmed, and in full, by Lotte Canabæus' close studies on the varying size of the heterocysts at different concentrations of sodium chloride, conditions of light and oxygen tensions (1929, pp. 9, 20 and 21). Canabæus emphasizes (*loc. cit.*, p. 36) the vegetative cells as the most invariable element of an *Anabaena* species. Even if there may be an exceptional variation of the shape, the thickness of the cells is apparently one of the best systematic characters. It will therefore be more correct to classify the individuals from the Badstue-Ødam as *Anabaena affinis* Lemm. var. *intermedia* Griffiths f. *tenuis* mihi.

In the Furesø, on August 7th, 1932, an *Anabaena* species was observed that is no doubt identical with *Anabaena affinis* var. *intermedia* (see Fig. 117). The vegetative cells measured 7.5—8.5 μ in breadth, were spherical or a little shorter than broad; the heterocysts 9—10 μ in diameter; the spores, sometimes occurring in series of 2, were always found remote from the heterocysts and measured 21.5—27 μ in length, 15—16 μ in breadth; a few measurements showed the ratio between length and breadth to be 1.4—1.7. The fact that the spores were not cylindrical with hemispherical ends but ellipsoidical, may be due to their not being quite mature.

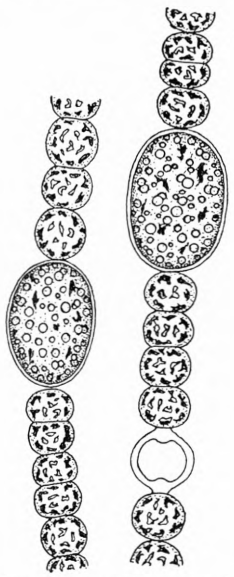


Fig. 117. *Anabaena affinis* Lemm. var. *intermedia* Griff. from Furesø, August 7th, 1932. 800 ×.

Periodicity. In the Badstue-Ødam *Anabaena affinis* var. *intermedia* f. *tenuis* was observed in small quantities on June 6th, 1929 at the beginning of the examination. Both in July and the former half of August the sterile trichomes occurred sparsely, but at the end of August and the beginning of September (temp. 18—18.5° C.) it had a great maximum and even formed water bloom during the first days of September, at which time it was fertile. Already on September 12th there were only a few spores left in the plankton, and during this month every trace of it disappeared. In 1930 the first, sterile trichomes appeared already on April 10th (temp. 10° C.), but it was not until the end of the investigation on June 16th (temp. 24° C.) that it became common and showed a beginning fertility. This early beginning of the formation of spores is possibly connected with the unusually hot and sunny early summer of 1930.

Strange to say no traces of this form were observed in the Badstue-Ødam on September 5th, 1941.

In the Furesø *Anabaena affinis* var. *intermedia* was comparatively rare, but showed a beginning fertility on August 7th, 1932 (temp. 20° C.).

Accordingly, *Anabaena affinis* var. *intermedia* f. *tenuis* must be characterized as meso- to polythermic with its period of vegetation in April-September (range of temperature 8.5—24° C.) and with the maximum development and formation of spores normally occurring in August-September at temperatures between 18 and 20° C. and pH values of 8.2—8.5.

Sociology. In the Badstue-Ødam the form was found in the following successive associations, the brackets stating its estimated frequency in the associations.

June 6th, 1929: *Mel gr an - Sye ac an*-association (*Anabaena* very rare).
July 26th, — : *Rhi lo*-association (*Anabaena* very rare).
Aug. 10th, 17th, and 23rd, 1929: *Cyc st su - Frg cr*-association with *Sce arc ca* as subdominant (*Anabaena* gradually rather common).
Sep. 3rd, 1929: *Cyc st su*-association (*Anabaena* common).

Sept. 5th, 1929: *Ana af in te*-association with *Os ac*, *Os li* and *Sce arm* as subdominants.
— 12th, — : *Crym ov*-association (*Anabaena* very rare).
— 23rd, — : *Ank co mi - Mio ho*-association (*Anabaena* very rare).
Apr. 10th, 1930: *Ste Ha - Sye ac an*-association (*Anabaena* very rare).
— 25th, — : *Din so - Sye ac an*-association with *Ma pe ec* as subdominant (*Anabaena* very rare).
May 1st, — : *Ura vo*-association with *Ste Ha* and *Sye ac an* as subdominants (*Anabaena* very rare).
— 21st, — : *Ura vo*-association with *Ma pe ec* as subdominant (*Anabaena* rare).
— 31st, — : *Cyc st su*-association (*Anabaena* rather rare).
June 16th, — : *Crym ov*-association with the following subdominants: *Ana af in te*, *Cyc st su*, *Os li ac* and *Os li*.

As will be seen the form—apart from the association formed by itself in September—is found in diatom-associations composed of *Melosira*, *Synedra*, *Rhizosolenia*, *Cyclotella* and *Fragilaria* and in flagellate-associations with *Uroglena*, *Dinobryon* and *Cryptomonas* as dominants.

The most constant associates were *Asterionella formosa* and *Cyclotella Meneghiniana*, which occurred in 93 % (13) of the number of samples (14) that contained *Anabaena affinis* var. *intermedia* f. *tenuis*. *Microcystis holsatica*, *Scenedesmus armatus* and *Pediastrum duplex* var. *clathratum* occurred in 86 % of the samples, while *Anabaena incrassata*, *Dinobryon sociale*, *Cryptomonas ovata*, *Ankistrodesmus falcatus* (with forms), *Fragilaria crotonensis* and *Trachelomonas intermedia* were found in 78 % of the samples.

In the Furesø the plankton on August 7th, 1932 was dominated by *Anabaena flos aquae* (fertile), *Asterionella formosa* and *Ceratium hirundinella*.

Ecology. Both the Badstue-Ødam and the Furesø are permanently alkaline, eutrophic waters, the former, however, approaching the stage of mixotrophy (the consumption of $KMnO_4$ ranges between 40 and 57 mg per litre). Both of them have inlets and outlets. The Badstue-Ødam is a somewhat overshadowed, shallow pond whereas the Furesø is one of our largest lakes with clear water (consumption of $KMnO_4$ 7.5—14 mg per litre).

Anabaena affinis var. *intermedia* f. *tenuis* has been found at pH values of 7.6—8.8, at a consumption of $KMnO_4$ of 44—57 mg/l and at the following contents of CaO 75.3—82.2 mg/l, NH_3-N 0.05—0.1 mg/l, NO_3-N 0—0.35 mg/l, PO_4-P 0—0.02 mg/l and Fe 0.02 mg/l.

Anabaena heterospora n. sp.

Fig. nostra 118.

Diagnosis. Trichomata solitaria, recta vel leviter curvata, pallide aeruginosa, 75—450 μ, plerumque 200—250 μ longa. Cellulae sphaericae vel subsphaericae, cum

vacuolis, 4—6.5 μ longae, 5—6 μ latae. Heterocystae prope orculaeformes vel subsphaericae, 5.5—8 μ, saepe 6—7 μ latae. Sporae plerumque ab heterocystis remotes; in duobus modis formatis: aut cellulae in circuitu crescantes magnae sphaericae erunt, postea longe ellipsoideae et fortasse postremo cylindricae apicibus semisphaericis instructae; aut cellulae in longitudine crescantes cylindricae erunt, postea post aliquod incrementum crassitudinis cylindricae apicibus semisphaericis instructae. Sporis maturis singulis vel binis, 3.25—4 plo longioribus quam latiores, 26—33 μ longis, 8—9 μ latis. Episporio levi, sine colore, tenui, apicibus leviter incrassatis instructo.

Hab. In Blankeborg II et III, Fionia, Dania, libere natans.

Systematics. As far as I know none of the *Anabaena* species described till now have spores of a double origin. In spite of the difference in the development the spores obviously end by growing uniform. This is possibly only a semblance of a likeness, for the study of the preserved material seems to indicate that the phase developing through the spherical stage is possibly the result of a copulation (see Fig. 118) whereas the phase developing through the cylindrical stage is possibly simpler.

The species shows some likeness to *Anabaena affinis* Lemm., the heterocysts of which, however, are 7.5—10 μ broad, and the spores of which are at first spherical, later on elliptic, and finally nearly cylindrical with rounded apices, 9.5—12 μ broad, 17—26 μ long. As will be seen the cylindrical stage of development is lacking in the individuals of LEMMERMANN; their spores are also much shorter and broader than those of the present specimens.

The species should also be compared with *Anabaena solitaria* Klebahn (1895, p. 270, t. 4, fig. 25), the trichomes of which, however, are 8 μ thick and the heterocysts somewhat larger than in *Anabaena heterospora*; the dimensions of the spores are very similar to those of *Anabaena heterospora*, but Klebahn does not mention anything about the double origin of the spores.

The spherical or ovate, immature spores may be 12 μ broad. The cylindrical spores with granulated contents (not quite mature) measure 6—11 μ in thickness, 19.5—35 μ in length; according to 9 measurements they are $2\frac{1}{3}$—4 times longer than broad.

Periodicity. In Blankeborg II the species was found in a fertile state on July 17th—20th, 1928 (the examination of this pond was started on the former of these dates). At this time, when the temperature was 22—17.5° C., there were but few individuals left from a supposed maximum in June-July. During the month of August the species disappeared completely. In 1929 it reappeared on May 12th (temp. 16° C.) and grew more and more common until the maximum occurred on June 17th (temp. 19.25° C.) when the trichomes slowly began to form spores. This must have been completed before July 1st, for after this time the species was observed no more in this year. In 1930 the species did not appear until May 24th (temp. 19° C.), and at the end of the investigation on June 10th (temp. 21.5° C.) it was common but sterile.

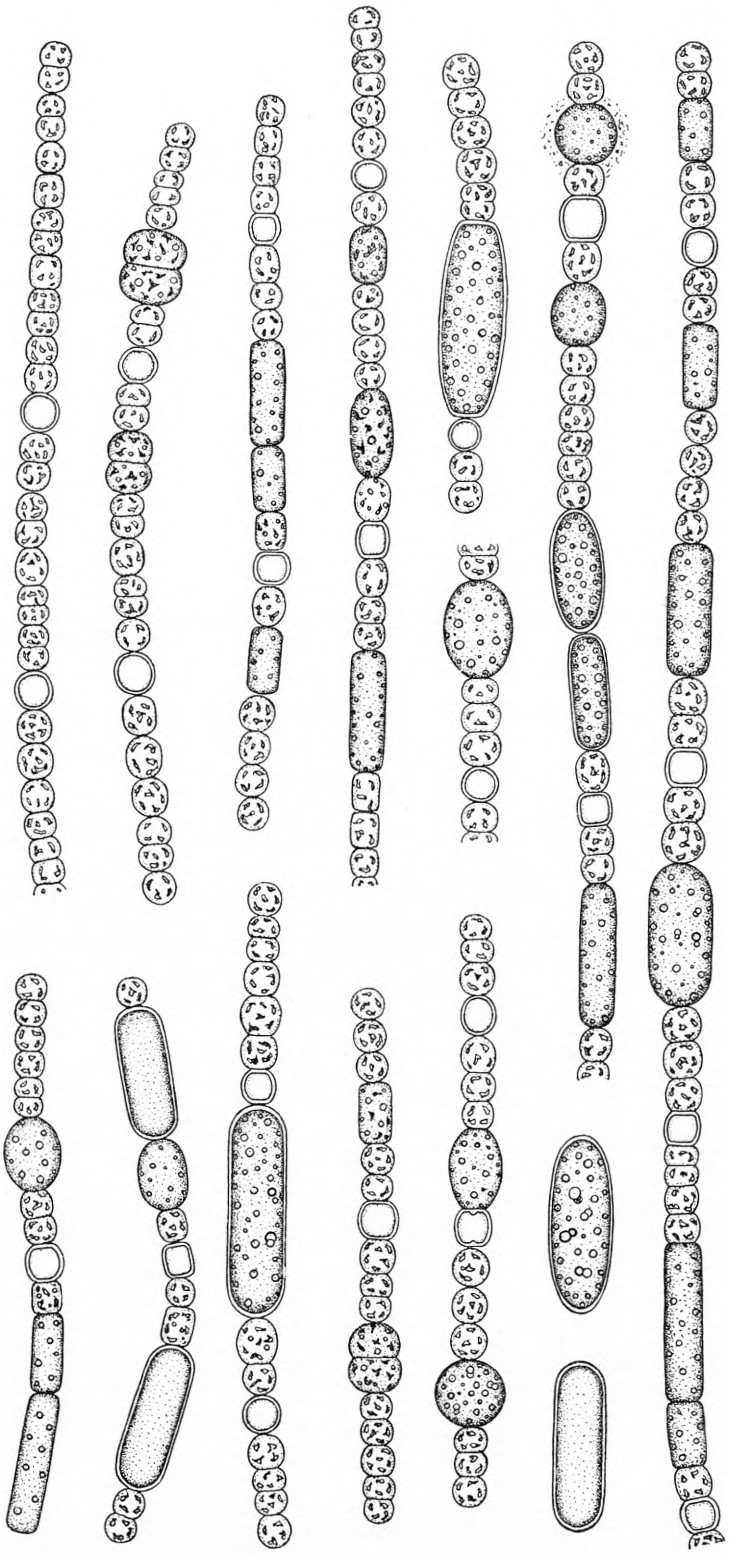


Fig. 118. *Anabaena heterospora* n. sp. from Blankeborg II and III. 800×.

In Blankeborg III the cold year of 1929 was obviously most unfavourable to the development of the species, but it was found in 1930 when it appeared already on April 19th (temp. 8.5° C.) and reached a great maximum on May 23rd (temp. 19.5° C.). The formation of spores did not begin until about June 10th (temp. 20.5° C.) when the species occurred sparsely in the plankton.

Anabaena heterospora must thus be considered a typical warm water form, more accurately meso- to polythermic with a period of vegetation from April to August (8.5—21.5° C.), sometimes only in May and June. It was never observed during the rest of the year. Its maximum, at the end of which the formation of spores takes place, occurs at temperatures of 19—20° C., from the end of May till well into July.

Sociology. The species was found in Blankeborg II in the following successive associations:

July 17th—20th, 1928: *Na be*-association with *Ste Ha* and *Chla ci* as subdominants (*Anabaena* rare).
— 25th, 1928: *Chla*(?)-association with *Na be* as subdominant (*Anabaena* very rare).
Aug. 2nd, — : *Chla*(?)-association with *Ste Ha* as subdominant (*Anabaena* very rare).
— 13th, — : *Ste Ha*-association with *Per pa* as subdominant (*Anabaena* very rare).
— 28th, — : *Ste Ha*-association (*Anabaena* very rare).
May 12th, 1929: *Se ca - Ste Ha*-association (*Anabaena* very rare).
— 21st, — : *Chla Re mi*-association with *Os li* as subdominant (*Anabaena* very rare).
June 2nd, — : *Os li*-association (*Anabaena* not infrequent).
— 17th, — : *Ana he - Cru qu*-association (*Anabaena* common).
May 24th, 1930: *Ste Ha*-association with *Chla Re mi* and *Crym ov* as subdominants (*Anabaena* rare).
June 10th, — : *Ste Ha*-association with *Se ca* as subdominant (*Anabaena* rather common).

It appears from this that *Anabaena heterospora* mainly occurs in green algae-associations, composed of *Nannokloster*, *Chlamydomonas*, *Selenastrum* and *Crucigenia* and in diatom-associations dominated by *Stephanodiscus*.

The constant associates were *Stephanodiscus Hantzschii* and *Peridinium palatinum*, which occurred in 100 % of the number of samples (12) that contained *Anabaena heterospora*; *Scenedesmus armatus* occurred in 92 % of the samples.

Ecology. Both Blankeborg II and Blankeborg III are mixotrophic turf pits (consumption of $KMnO_4$ 70—88 mg/l) situated in fennish ground, the former somewhat overshadowed and contaminated, the latter in open country. They have neither

inlets nor outlets; their calcium content in the winter of 1930 was no less than 153.5 and 134 mg of CaO per litre, respectively. They are therefore always alkaline: pH 7.6—8.5 (for No. II in 1928—29) and pH 7.7—8.1 (for No. III in 1928—29). In 1928 and 1929 pH was 8.1—8.5 at the time at which *Anabaena heterospora* occurred in Blankeborg II.

Anabaena sigmoidea n. sp.

Fig. nostra 119.

Diagnosis. Trichomata solitaria, irregulariter spiralia, subsigmoidea, circularia vel semicircularia, sine mucilagine visibili; spirae 20—37 μ latae sunt. Cellulae vege-

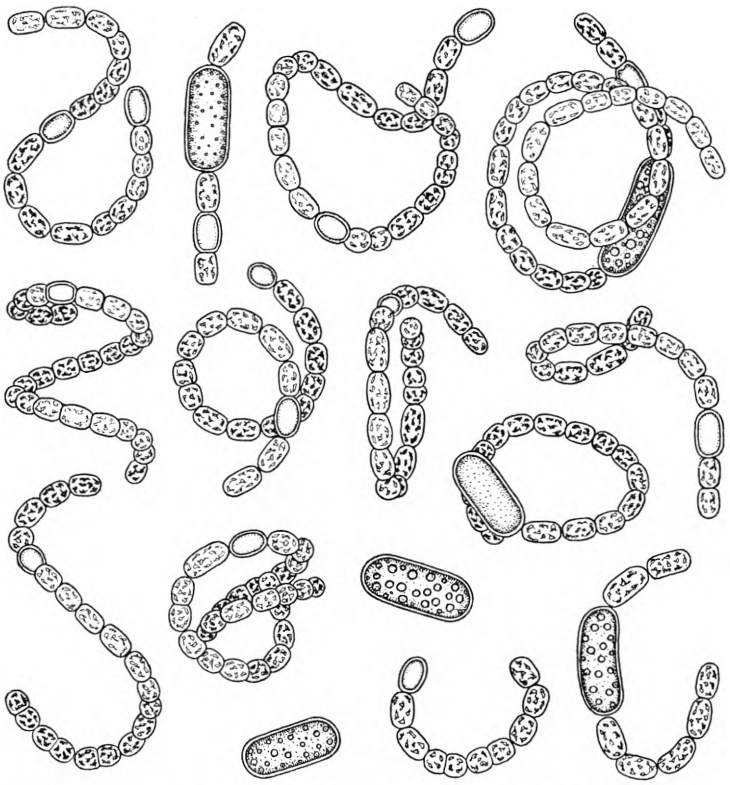


Fig. 119. *Anabaena sigmoidea* n. sp. from Jægerbakke Dam, July 18th, 1929. 800×.

tativae cylindricae angulis rotundatis vel apicibus semisphaericis, vel longe ellipsoideae vel dolioliformes, cum vacuolis, 1—$2\frac{1}{3}$ plo longiores quam latiores, 4—8 μ longae, 3—4 μ latae. Heterocystae ellipsoideae vel cylindicae apicibus semisphaericis, raro orculaeformes, 5.5—7.5 μ longae, 4—5 μ latae. Sporae semper ab heterocystis remotes, solitariae, rectae vel leviter curvatae, cylindricae apicibus semisphaericis, e

6 mensionibus 2.1—2.9 plo longiores quam latiores, 16—21.5 μ longae, 7.5—8.5 μ latae, episporio levi, sine colore.

Hab. In Jægerbakke Dam prope Hillerød, Dania, libere natans.

Systematics. The species is much like *Anabaena circinalis* Hansgirg (1892, p. 68, fig. 23; Lemmermann 1910, p. 187, figs. 6—7 on p. 159; Geitler 1925, p. 324; Hansgirg's *A. circinalis* is not even given as synonym in Geitler's investigation on the Cyanophyceae in Rabenhorst's Kryptogamenflora, Bd. 14, 1932). Hansgirg's specimens, however, have spores that are 4—5 times longer than broad (24—30 $\mu \times 6$ μ) and have a brownish wall.

We only get an adequate impression of the trichomes of an *Anabaena* species if we examine them before the coverslip is placed upon the suspension of plankton on the slide. It turned out that among the many trichomes of *Anabaena sigmoidea* examined only one was in fact spirally twisted (see Fig. 119 left); the very most of them were irregularly twisted spiral fragments.

Periodicity. The species was periodical: it was only observed within the period May—October at temperatures between 11 and 28.5° C., thus being meso- to polythermic. The species reached its highest development on June 16th, 1930 (temp. 28° C.) when it was common in the plankton of Jægerbakke Dam; it was not infrequent on May 31st (temp. 23.25° C.). In the summer months of 1929 it was present in very small quantities; only in certain samples from June, July and August (temp. 20.5—28.5° C.) the trichomes were so numerous, that they could be given the relative frequency degree of "rare". The species also requires much heat to enter into the fertile stage: formation of spores was observed only on July 11th—18th, 1929 (temp. 22.5—28.5° C.) and on June 16th, 1930 (temp. 28° C.).

In other words this periodical species is distinctly a high summer form with its maximum in June—July.

Sociology. The species was found in the following associations:

June 12th, 1929: *Mio mi*-association with *Ana Vi da*, *Mio ho* and *Ra pe* as subdominants (the species very rare); see Table IV.
— 18th, — : *Mio mi*-association with *Ana te*, *Ana Vi da*, *Mio ho* and *Sce arm* as subdominants (the species very rare).
— 27th, — : *Mio mi*-association with *Ana Vi da* as subdominant (the species rare).
July 11th, — : *Ana Vi da*-association with *Mio mi* as subdominant (the species rare).
— 17th, — : *Ana Vi da - Sce arm*-association with *Mio mi*, *Mio ho* and *Os li ac* as subdominants (the species rare).
— 27th, — : *Ana Vi da*-association with *Mio ho* as subdominant (the species very rare).
Aug. 10th, — : *Ana Vi da - Mio ho - Os li ac-Sce arm*-association (the species rare).

Aug. 21st, 1929: *Ana Vi da - Mio ho - Os li ac*-association with *Mio mi* and *Sce arm* as subdominants (the species very rare).
Sep. 2nd, — : *Ana Vi da*-association with *Mio ho* as subdominant (the species very rare).
Oct. 3rd, — : *Mio ho*-association with *Sce arm* as subdominant (the species very rare).
May 16th, 1930: *Ank fa spa - Mio ho - Sce arm*-association (the species very rare); see Table IV.
— 21st, — : *Mio ho*-association (the species very rare).
— 31st, — : *Mio ho*-association with *Sce arm* as subdominant (the species not infrequent).
June 16th, — : *Mio ho*-association with *Ana si* and *Sce arm* as subdominants (the species common).

Anabaena sigmoidea thus occurred in associations mainly dominated by blue-green algae (*Microcystis*, *Anabaena* and *Oscillatoria*), but also certain green algae (*Scenedesmus*, *Ankistrodesmus* and *Radiococcus*) were a distinct feature of these myxophycean associations.

The most constant associates were *Microcystis holsatica*, *Scenedesmus armatus* and *Scenedesmus falcatus*, which occurred in 100 % of the samples (14) containing *Anabaena sigmoidea*. Species like *Microcystis minutissima*, *Oscillatoria limnetica* and its var. *acicularis*, *Ankistrodesmus falcatus* var. *spirilliformis* occurred in 93 % of the samples while *Anabaena tenericaulis*, *Anabaena Viguieri* var. *danica*, *Chlamydomonas kakosmos* and *Chlamydomonas retroversa* were found in 86 % of the samples.

Ecology. Jægerbakke Dam is a wind-sheltered, highly eutrophicated, small and shallow pond, conspicuous by its deficiency in lime. As will appear from Table III the compound quotient for June 12th, 1929 was $\frac{30}{7} = 4.3$ and for May 16th, 1930 $\frac{35}{2} = 17.5$. Some data of the ecology of *Anabaena sigmoidea* are: pH 7—9.8, CaO 7.8—10.9 mg/l, consumption of $KMnO_4$ 35—49 mg/l, PO_4-P 0—0.005 mg/l, NH_3-N 0.05—0.1 mg/l, NO_3-N 0 mg/l and Fe 0.02 mg/l.

Anabaena spiroides Klebahn var. **tumida** Nyg.

Dansk Planteplankton 1945, p. 52, t. I, fig. 11.—*Fig. nostra* 120.

Trichomes single, free floating, spirally twisted, without directly visible gelatinous envelope, windings 33—53 μ broad, 10—20 (—35) μ high; vegetative cells spherical or subspherical, mostly somewhat shorter than broad, 6.5—9 μ (mostly 7—8 μ) broad, 4—9.5 μ long, with pseudo-vacuoles; the heterocysts spherical, 8—10 μ broad; spores always remote from the heterocysts, often in series of 2—4, at first ovate, later on somewhat asymmetrical (nearly straight at the inner side), 10—13.5 μ broad, 18—23 μ long, 1.7—2.1 times longer than broad, with smooth, colourless outer layer.

In Sandbjerg Sø, Sundeved, Lille Søgaard Sø, North Sleswick and Flynder Sø, North Jutland, pelagic.

Systematics. This variety is closely related to var. *contracta* Klebahn (1895, p. 265, t. 4, figs. 14—15), the windings of which, however, are only 20—25 μ broad,

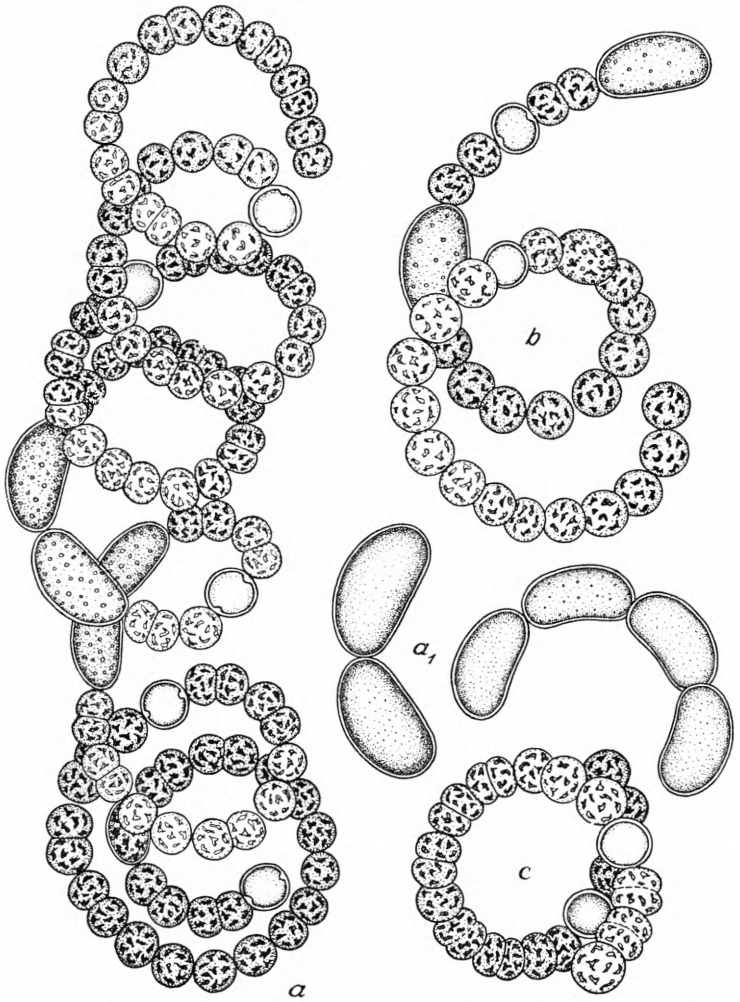


Fig. 120. *Anabaena spiroides* Klebahn var. *tumida* Nyg.; *a*—a_1 from Sandbjerg Sø (*a* from September 10th, 1937, a_1 mature spores from October 1st, 1938); *b* from Flyndersø, July 6th, 1938; *c* from Lille Søgaard Sø, July 25th, 1926. 800×.

and the immature spores of which are spherical and no less than 14 μ broad. It does not appear from the literature whether or not the spores of var. *contracta* may occur in series.

Periodicity. In September 1937 this variety was so common, that it formed water-bloom. During the period between August 14th and October 1st, 1938 (temp.

26.5—14.5° C. and pH 8.8—8.3) it was at first comparatively rare in the plankton of Sandbjerg Sø; gradually, however, it grew frequent, especially at the beginning of October when both this and *Anabaena Scheremetievi* Elenk. var. *recta* Elenk. f. *rotundospora* Elenk. were actively forming spores. In August 1939 it occurred in large quantities (August 6th, temp. 22° C.) and has no doubt been forming water-bloom in calm weather. In September (temp. 21.6° C., pH 8.4) the variety was even more abundant in the plankton. Also in August 1944 it was common. Thus the late summer (at temperatures between 22 and 15° C.) seems to be the most favourable time for the development of *Anabaena spiroides* var. *tumida*.

In Lille Søgaard Sø var. *tumida* was found to be common in the plankton on July 25th, 1926, but rare on August 27th of the same year (pH 8.3). In the large lake of Flynder Sø the variety was found on July 6th, 1938 (temp. 18° C., pH 9.0).

Sociology. In Sandbjerg Sø (see p. 159) the form was found in the following associations:

Sep. 4th, 1937: *Os li*-association with *Mia pu* and *Gy ex* as subdominants (*Anabaena* rather rare).
— 10th, — : ditto.
Aug. 14th, 1938: *Pa mo*-association with a spherical green alga as subdominant (*Anabaena* rare).
Sep. 4th, — : *Cyc Me*-association with *Ste Ha* as subdominant (*Anabaena* rare).
— 15th, — : *Ste Ha*-association with *Mel gr* as subdominant (*Anabaena* comparatively rare).
Oct. 1st, — : *Mel gr*-association with *Ste Ha* as subdominant (*Anabaena* common).
Aug. 6th, 1939: *Mel gr*-association with *Ana sp tu* and *Cyc Me* as subdominants (*Anabaena* common).
Sep. 3rd, — : *Ana sp tu - Ste Ha*-association with *Mel gr* as subdominant (*Anabaena* very common).
Aug. 26th, 1944: *Sce ec*-association (*Anabaena* common).

In Lille Søgaard Sø *Anabaena spiroides* var. *tumida* was found in the following associations:

July 25th, 1926: *Ana pl te*-association with *Api fl Kl* and *Mel gr* + *an* as subdominants (*Anabaena* common).
Aug. 27th, — : *Ana fl - Api fl Kl*-association with *Mel gr* + *an* as subdominants (*Anabaena* very rare).

In Flynder Sø the variety was comparatively rare on July 6th, 1938 when the lake contained a typical *Api fl*-association.

In other words *Anabaena spiroides* var. *tumida* principally occurs in blue-green algae-associations with *Oscillatoria*, *Anabaena* and *Aphanizomenon* as dominants and

in diatom-associations, dominated by *Cyclotella*, *Stephanodiscus* and *Melosira*, more rarely in green algae-associations (*Pandorina* and *Scenedesmus*).

The most constant associate was *Coelastrum microporum*, which was found in 90 % of the number of samples (10) that contained *Anabaena spiroides* var. *tumida*. *Cyclotella Meneghiniana*, *Dictyosphaerium pulchellum*, *Melosira granulata* and its var. *muzzanensis* occurred in 80 % of the samples.

Ecology. Sandbjerg Sø is a highly eutrophic lakelet, which in August 1945 contained 113 mg of CaO per litre. Lille Søgaard Sø is also eutrophic. Flynder Sø is a comparatively large, eutrophicated moor lake, the calculated calcium content of which is stated by Boisen Bennike to be 40 mg of "CaO" per litre for July 1940 (1943, p. 20). By way of illustrating the trophic degree of 2 of these lakes I give the different quotients for their *Nannoplankton*.

Lakes	Sandbjerg Sø							Flynder Sø
Dates of sample-collecting.	10–IX 1937	14–VIII 1938	4–IX 1938	15–IX 1938	1–X 1938	6–VIII 1939	3–IX 1939	6–VII 1938
Total number of species ..	41	31	50	42	49	38	36	34
myxophycean quotient	$\frac{6}{0}$	$\frac{7}{1}$	$\frac{9}{1}$	$\frac{4}{1}$	$\frac{5}{1}$	$\frac{8}{1}$	$\frac{5}{1}$	$\frac{7}{4}$
diatom quotient	$\frac{3}{1}$	$\frac{3}{0}$	$\frac{7}{3}$	$\frac{5}{1}$	$\frac{5}{0}$	$\frac{6}{1}$	$\frac{4}{1}$	$\frac{8}{4}$
chlorophycean quotient ...	$\frac{14}{0}$	$\frac{13}{1}$	$\frac{15}{1}$	$\frac{21}{1}$	$\frac{17}{1}$	$\frac{14}{1}$	$\frac{9}{1}$	$\frac{8}{4}$
euglenine quotient	$\frac{8}{20}$	$\frac{3}{20}$	$\frac{8}{24}$	$\frac{4}{25}$	$\frac{12}{22}$	$\frac{3}{22}$	$\frac{5}{14}$	$\frac{0}{15}$
compound quotient	$\frac{31}{0}$	$\frac{26}{1} = 26$	$\frac{39}{1} = 39$	$\frac{34}{1} = 34$	$\frac{39}{1} = 39$	$\frac{31}{1} = 31$	$\frac{23}{1} = 23$	$\frac{23}{4} = 5.75$

Besides conveying an impression of the fluctuations of the different quotients in September of 3 successive years the quotients of Sandbjerg Sø show much higher values than those of Flynder Sø. The small body of water of Sandbjerg Sø is contaminated from the neighbouring habitations to a much higher degree than Flynder Sø, which is situated in a thinly populated moor district.

The few data that can be given of the ecology of the species are pH 8.3—9.0 and CaO (40—)113 mg/l.

Anabaena spiroides Klebahn var. **minima** Nyg.

Dansk Planteplankton, 1945, p. 52, t. I, fig. 12.—*Fig. nostra* 121.

Trichomes single, pelagic, densely and often irregularly spirally twisted, with up to 25 windings per trichome. Cells spherical, 4—5 μ broad, containing pseudovacuoles. The heterocysts spherical, 5.5—6 μ broad. Spores broadly ovate, single or 2 in series, always remote from the heterocysts, 11—12.5 μ long, 8—10.5 μ broad, 1.2—1.4 times as long as broad.

f. *compacta* Nyg. (Fig. 121 *b*, *c*, c_1, c_2, and c_3). Spirals 11—16 μ broad, 4—12 μ high.

In Sandbjerg Sø at Alssund and Emdrup Sø at Copenhagen.

f. *remota* Nyg. (Fig. 121 *a*—a_1). Spirals 17—27 μ broad, 9—21 μ high.

In Lille Søgaard Sø at Aabenraa, North Sleswick.

In Sandbjerg Sø f. *compacta* was found on August 14th, 1938 (very rare) and August 6th, 1939 (not infrequent). In Emdrup Sø f. *compacta* was very abundant in the plankton on July 29th, 1941. In Lille Søgaard Sø f. *remota* was rather common on July 25th, 1926, but was lacking on August 27th of the same year.

In contrast to var. *tumida* *Anabaena spiroides* var. *minima* seems to be a distinct high summer form: it was found only in July and August at temperatures between 22 and 26.5° C.

Sociology. In Sandbjerg Sø *Anabaena spiroides* var. *minima* f. *compacta* was found in the following associations:

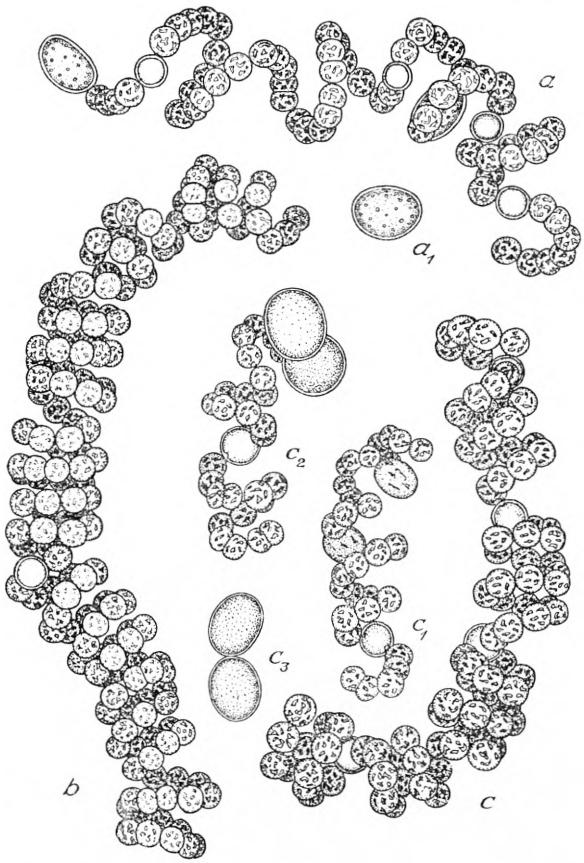


Fig. 121. *Anabaena spiroides* Klebahn var. *minima* Nyg.; *a*—a_1 f. *remota* Nyg. from Lille Søgaard Sø, July 25th, 1926; *b*, *c*, c_1, c_2 and c_3 f. *compacta* Nyg., *b* from Emdrup Sø, July 29th, 1941, *c*, c_1, c_2 and c_3 from Sandbjerg Sø, August 6th, 1939, c_2 and c_3 showing mature spores. 800×.

Aug. 14th, 1938: *Pa mo*-association with a spherical green alga as subdominant.
— 6th, 1939: *Mel gr*-association with *Ana sp tu* and *Cyc Me* as subdominants.

In Emdrup Sø it dominated on

July 29th, 1941: *Ana sp mi*-association with *Pho le* as subdominant.

In Lille Søgaard Sø *Anabaena spiroides* var. *minima* f. *remota* was rather common on

July 25th, 1926: *Ana pl te*-association with *Api fl Kl* and *Mel gr* + *an* as subdominants.

In other words *Anabaena spiroides* var. *minima* was observed in blue-green algae-associations with *Anabaena* and *Aphanizomenon*, a diatom-association with *Melosira* and a green algae-association with *Pandorina* as dominants.

Survey of the spirally twisted *Anabaena* species.

Name	Breadth of windings	Height of windings	Breadth of cells	Shape of cells	Diameter of heterocysts	Position of spores	Length and breadth of spores
A. spiroides Kleb.	45—54 μ	40—50 μ	6.5—8 μ	nearly spherical or somewhat shorter than broad	7 μ	adjoining the heterocysts (?)	
var. crassa Lemm.	45—70 μ	17—55 μ	11—14 μ	spherical or somewhat shorter than broad	10—17 μ	remote from the heterocysts	27—42 μ long, 15—25 μ broad
var. latizona Nyg.	75—120 μ (generally 90—100 μ)	20—50 μ	11—14 μ	spherical or somewhat shorter than broad	12—14 μ	remote from the heterocysts	24—30 μ long, 17—20 μ broad
var. tumida Nyg.	33—50 μ	10—20 μ	6.5—9 μ (7—8 μ)	spherical or somewhat shorter than broad	8—10 μ	remote from the heterocysts	18—23 μ long, 10—13.5 μ broad
var. Talyschensis Wor.	50—59 μ	16.5-19 μ	8—9 μ	only 2—3 μ long	8 μ	?	?
var. contracta Kleb.	20—25 μ	10—15 μ	7—8 μ	nearly spherical	7 μ	remote from the heterocysts	?
var. minima Nyg.	11—27 μ	4—21 μ	4—5 μ	spherical	6 μ	remote from the heterocysts	11—12.5 μ long, 8—10.5 μ broad
var. spiroides (Wor.) mihi	9—12 μ	20—30 μ	6 μ	nearly spherical	?	remote from the heterocysts	14—17.3 μ long, 8—9.4 μ broad
var. africana mihi	30-37.5 μ	15—22 μ	5—6 μ	spherical or somewhat shorter than broad	6—7 μ	remote from the heterocysts	16—16.5 μ long, 10—11 μ broad
A. reniformis Lemm.	16—17 μ	?	4 μ	longish (7—8 μ)	nearly spherical (about 4 μ in diameter)	?	?
A. Utermöhli (Ut.) Geitl.	17—30 μ	27—40 μ	4—4.5 μ	longish (4—6.5 μ)	4.7—5.7 μ × 4—4.5 μ	adjoining the heterocysts	19—20 μ long, 7—8 μ broad

The most constant associates were *Anabaena spiroides* var. *tumida*, *Trachelomonas intermedia*, *Pediastrum Boryanum* and *Scenedesmus armatus*, which were found in 75 % of the number of samples (4) that contained *Anabaena spiroides* var. *minima*.

Ecology. Sandbjerg Sø, Lille Søgaard Sø and Emdrup Sø are highly eutrophic lakelets (cp. the survey of the phytoplankton quotients for Sandbjerg Sø on p. 204). On Aug. 14th, 1938 pH was 8.8 in Sandbjerg Sø; on Aug. 19th, 1945 the lake contained 113 mg CaO per litre.

In my opinion *Anabaena flos aquae* Breb. var. *intermedia* Woronich f. *spiroides*, as described by the Russian author from a lake in the Caucasus, is a variety of *Anabaena spiroides*, and I propose to term it:

Anabaena spiroides Kleb. var. *spiroides* (Woronich) mihi.

The specimens from the Transvaal described by me (Nygaard 1932, p. 121, Fig. 6) under the name of *A. flos aquae* Breb. var. *intermedia* Woronich f. *spiroides* Woronich correspond well to the Caucasian ones except in the size of the spiral windings which is different. In the Caucasian specimens the breadth of the windings were 9—12 μ and their height 20—30 μ, but those of the individuals from South Africa are 30—37.5 μ in width and 15—22 μ in height. These specimens from the Transvaal I therefore propose to call

Anabaena spiroides Kleb. var. *africana* mihi.

The schematic survey above will show the differences between the described varieties of *Anabaena spiroides* Klebahn and closely related species.

Anabaena tenericaulis n. sp.

Fig. nostra 122.

Diagnosis. Trichomata solitaria, recta vel minute flexuosa, sine tegumentis gelatineis visibilibus, 90—220 μ, plerumque 100—200 μ longa, ad apices leviter attenuata, cellulis vegetativis longe cylindraceis, pallide aerugineis, cum vacuolis, saepe 2—3 plo longioribus quam latioribus, $3\frac{1}{2}$—8 μ longis, 2—$2\frac{1}{2}$ μ (raro 3 μ) latis. Cellula terminalis rotundata. Heterocystae cum tegumentis laxis, cylindricae apicibus rotundatis vel ellipsoideae, raro subsexangulatae, 4—7 μ longae, 2—3 μ latae sunt. Sporis solitariis, cylindraceis apicibus rotundatis, semper ab heterocystis remotis, $2\frac{1}{2}$—$3\frac{1}{2}$ plo longioribus quam latiores, $13\frac{1}{2}$—23 μ longis, 5—$6\frac{3}{4}$ μ latis, episporio levi et sine colore.

Hab. In Jægerbakke Dam, Selandia, Dania, libere natans.

Systematics. This euplanktic species is closely related to *Anabaena Jonssonii* Boye Petersen 1923, (p. 299, Fig. 11), *Anabaena minutissima* Lemm. and *Anabaena delicatula* Lemm. (Lemmermann 1910, p. 182 and 183). In these species both the vegetative cells and the heterocysts have another shape than in *Anabaena tenericaulis*,

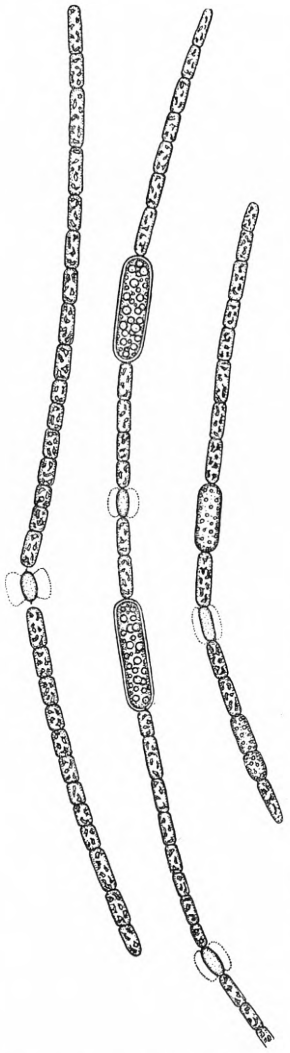


Fig. 122. *Anabaena tenericaulis* n. sp. from Jægerbakke Dam, May 16th, 1930. 800 ×.

which is conspicuous by its long, cylindrical cells. A closer comparison will show that there are also other points of difference.

Anabaena tenericaulis is by the present author placed as an *Anabaena* because of the lacking colourless endcells of the trichome; moreover it never occurs in bundles (compare also *Aphanizomenon gracile* Lemm. in which the spores are more elongated). The cylindrical spores, the slightly attenuated trichomes, and the long-elliptical heterocysts, however, give reason to assume that near relations consist between the genera *Anabaena* and *Aphanizomenon*.

Fig. 122 right shows a spore which is possibly composed of 2 cells; this has been noticed several times. As, however, 2 mature spores have never been observed to occur in series, it is possible that the spores are formed by a fusion of 2 adjoining cells, in other words that a sexual propagation takes place (cp. p. 197 and Nygaard 1932, p. 121).

Periodicity. The species is perennial and eurythermic, having been found at all temperatures between 0 and 28° C. It reached its highest development in May—June, especially on June 12th—18th (by temperatures of 23.75—25.25° C. and a pH value of 9.4) when it was very common in the plankton. Both in July and August it was extremely rare; throughout the autumn and the winter and at the beginning of the spring it occurred sparsely in Jægerbakke Dam (strange to say it was just as common in the middle of February under 8—9 cm of ice as in May!). The formation of spores began in May and terminated during June, this occurring at temperatures between 18 and 28° C. As a characteristic feature in the biology of the species may be mentioned that between October and April heterocysts were lacking in the trichomes (again with the exception of the sample from the middle of February when nearly all trichomes had heterocysts!). It was not until the beginning of May that some of the trichomes were carrying heterocysts, and in June, at any rate, all trichomes contained heterocysts. In August there were trichomes both with and without heterocysts.

Sociology. The species occurred in the following associations in Jægerbakke Dam:

June 12th, 1929: *Mio mi*-association with *Ana Vi da*, *Mio ho* and *Ra pe* as subdominants (*A. tenericaulis* common).

June 18th, 1929: *Mio mi*-association with *Ana Vi da*, *Mio ho* and *Sce arm* as subdominants (*A. tenericaulis* very common).
— 27th, — : *Mio mi*-association with *Ana Vi da* as subdominant (*A. tenericaulis* not infrequent).
July 4th, — : *Mio mi*-association with *Ana Vi da* as subdominant (*A. tenericaulis* rare).
— 11th, — : *Ana Vi da*-association with *Mio mi* as subdominant (*A. tenericaulis* rare).
— 17th, — : *Ana Vi da - Sce arm*-association with *Mio mi*, *Mio ho* and *Os li ac* as subdominants (*A. tenericaulis* very rare).
— 27th, — : *Ana Vi da*-association with *Mio ho* and *Sce arm* as subdominants (*A. tenericaulis* very rare).
Aug. 10th, — : *Ana Vi da - Mio ho - Os li ac - Sce arm*-association (*A. tenericaulis* very rare).
Oct. 3rd, — : *Mio ho*-association with *Sce arm* as subdominant (*A. tenericaulis* very rare).
— 23rd, — : *Mio ho*-association with *Sce arm* and *Os li* as subdominants (*A. tenericaulis* very rare).
Nov. 2nd, — : *Sce arm*-association with *Mio ho* as subdominant (*A. tenericaulis* very rare).
— 16th, — : *Mio ho*-association with *Ank fa se br* and *Sce arm* as subdominants (*A. tenericaulis* very rare).
— 30th, — : *Ank fa se br*-association with *Crym ov*, *Mio ho* and *Sce arm* as subdominants (*A. tenericaulis* very rare).
Jan. 15th, 1930: *Ki mi*-association with *Ank fa se br* and *Chla ka* as subdominants (*A. tenericaulis* very rare).
— 31st, — : *Ki mi*-association with *Ank fa se br* and *Chla ka* as subdominants (*A. tenericaulis* rare).
Feb. 17th, — : *Ki mi*-association with *Chla ka* as subdominant (*A. tenericaulis* not infrequent).
Mar. 1st, — : *Din cy al - Ki mi*-association (*A. tenericaulis* very rare).
— 15th, — : *Ki mi*-association (*A. tenericaulis* very rare).
Apr. 1st, — : *Din se pr*-association with *Sce arm* as subdominant (*A. tenericaulis* rare).
— 7th, — : *Din se pr*-association with *Chromulina pygmaea* as subdominant (*A. tenericaulis* very rare).
— 10th, 1930: *Din se pr*-association (*A. tenericaulis* rare).
— 22nd, — : *Din se pr*-association with *Ge mi* as subdominant (*A. tenericaulis* very rare).
— 26th, — : *Ge mi*-association with *Din se pr* as subdominant (*A. tenericaulis* rare).
May 1st, — : *Ge mi*-association (*A. tenericaulis* very rare).

May 10th, 1930: *Ge mi*-association (*A. tenericaulis* not infrequent).
— 16th, — : *Ank fa spa - Mio ho - Sce arm*-association (*A. tenericaulis* rather common).
— 21st, — : *Mio ho*-association with *Sce arm* as subdominant (*A. tenericaulis* not infrequent).
— 31st, — : *Mio ho*-association with *Sce arm* as subdominant (*A. tenericaulis* rare).
June 16th, — : *Mio ho*-association with *Ana si* and *Sce arm* as subdominants (*A. tenericaulis* rather common).

It appears from this that *Anabaena tenericaulis* is mainly found in blue-green algae associations of *Microcystis* species (with small cells) and *Anabaena*, and green algae associations of *Scenedesmus*, *Ankistrodesmus*, *Kirchneriella* and *Geminella*; besides it may occur in flagellate associations of *Dinobryon*.

The most constant associates were *Microcystis holsatica* and *Scenedesmus armatus*, which occurred in 97 % of the number of samples (29) that contained *Anabaena tenericaulis*; they are followed by *Ankistrodesmus falcatus* var. *spiralis* with 93 %, *Oscillatoria limnetica* and *Scenedesmus falcatus* with 90 %, *Chlamydomonas kakosmos* and *Oscillatoria limnetica* var. *acicularis* with 83 %, *Chlamydomonas retroversa* with 79 % and *Ankistrodesmus falcatus* and *Microcystis minutissima* with 76 %.

Ecology. Jægerbakke Dam is a small, highly eutrophic pond, sheltered from winds and with no inlets or outlets. It is conspicuous by its low calcium content. On the ecology of *Anabaena tenericaulis* the following data may be given: pH 6.6—9.8, calcium content 7.3—11.2 mg of CaO per litre, consumption of $KMnO_4$ 27—49 mg/l, contents of NH_3-N 0—0.75 mg/l, NO_3-N 0—0.015 mg/l, PO_4-P 0—0,015 mg/l and Fe 0.02—0.45 mg/l.

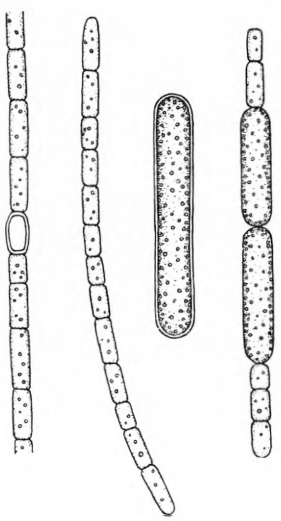


Fig. 123. *Anabaena tenericaulis* n. sp. var. *longispora* n. var. from Vedsted Sø, July 27th, 1926. 800×.

var. **longispora** nov. var.

Fig. nostra 123.

Diagnosis. Trichomatibus rectis vel leviter curvatis. Cellulis vegetativis cylindraceis, pallide aerugineis, 5—10 μ longis, 2—3 μ latis, protoplasmate subtiliter granuloso. Heterocystis orculaeformibus, 7 μ longis et 4 μ latis. Sporis solitariis vel binis, cylindraceis apicibus rotundatis, semper ab heterocystis remotis, in statu maturo ad 40 μ longis et 6 μ latis, ad 6.5 plo longioribus quam latiores.

Hab. In Vedsted Sø, Jutlandia meridiana, Dania, libere natans.

This euplanktic variety, which is somewhat robuster than the main species *Anabaena tenericaulis*, was observed in small quantities in the plankton of Vedsted Sø on July 27th, 1926. The lake is approximately oligotrophic. Its water is clear, Ca-deficient, and on the said date pH was 5.7.

The variety, the requirements of which are thus quite different from those of the main species, occurred in a typical *Ce hi*-association; as to the phytoplankton quotients see Table I.

Anabaena Viguieri Dénis et Frémy.

Geitler 1932, p. 878, fig. 560a.—*Fig. nostra* 124.

Systematics. The Danish individuals correspond completely to the diagnosis and figure cited above. The vegetative cells were spherical or barrel-shaped, 5—7 μ broad; the heterocysts were spherical, 5—7.5 μ in diameter; the spores according to 14 measurings were 1.2—1.4 times longer than broad, 13.5—18 μ long, 11—13 μ broad.

Distribution: Hesteskodam at Hillerød, pelagic.

Periodicity. The species was rare on July 17th, 1929 (temp. 23.5° C.), common on August 24th (temp. 17.5° C.) and abundant on September 10th (temp. 16.5° C.). On the date last-mentioned all trichomes were actively forming spores.

Sociology. *Anabaena Viguieri* was found in the following associations:

July 17th, 1929: *Mio fl ma*-association.
Aug. 24th, — : *Mio fl ma*-association.
Sep. 10th, — : *Ana Vi*-association with *Mio pu ra* as subdominant.

Beside in its self-formed association *Anabaena Viguieri* occurred only in myxophycean associations of *Microcystis*.

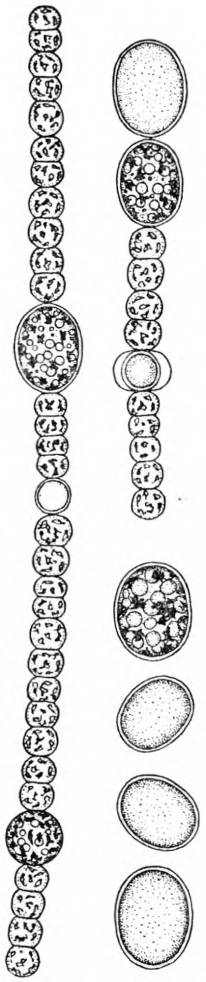


Fig. 124. *Anabaena Viguieri* Dénis et Frémy from Hesteskodam, September 10th, 1929. 800×.

Ecology. Hesteskodam is a highly eutrophicated pond, which in May 1930 at the margin was covered by neuston formed by a blood-red *Euglena* and *Euglena proxima*. On July 17th (nannoplankton, 25 species) the myxophycean quotient was $\frac{11}{2}$, the chlorophycean quotient $\frac{6}{2}$, the diatom quotient $\frac{0}{1}$, the euglenine quotient $\frac{3}{17}$ and the compound quotient $\frac{20}{2} = 10$. On September 10th the corresponding values (nannoplankton, 20 species) were $\frac{11}{2}$, $\frac{5}{2}$, $\frac{1}{0}$, $\frac{1}{16}$ and $\frac{18}{2} = 9$. The species was found at pH 8.8—9.4 and content of NO_3-N 0 mg/l.

var. **danica** nov. var.

Fig. nostra 125.

Diagnosis. A forma typica cellulis ellipsoideis et sporis majoribus differt. Cellulae vegetativae 5—11 μ longae, 5.5—7 μ latae; heterocystae sphaericae, 7—8.5 μ in diametro; sporae e 4 mensionibus 1.2—1.4 plo longiores quam latiores, 18—19 μ longae, 13—16 μ latae.

Hab. In Jægerbakke Dam prope Hillerød, Dania, libere natans.

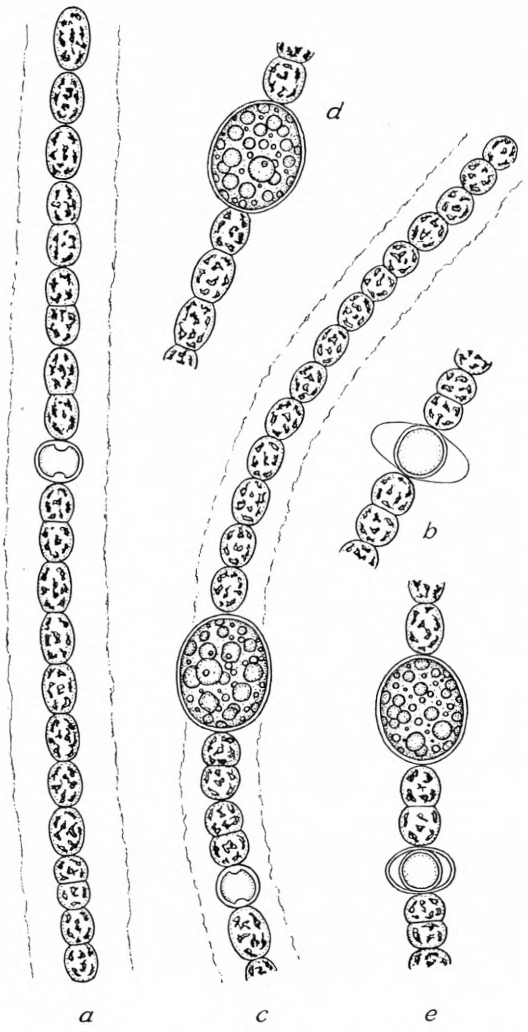


Fig. 125. *Anabaena Viguieri* Dénis et Frémy var. *danica* n. var. from Jægerbakke Dam; *a*—*c* from July 18th, *d*—*e* from September 13th, 1929. 800×.

Systematics. The trichomes are always surrounded by a thick gelatinous sheath; the cells are normally ellipsoidical, but spherical immediately after the division. The episporium may have a pale tawny colour. The spores figured in Fig. nostra 125 are not completely ripe; a ripe spore, characterized as usual by its homogeneous content, measured 18 μ in length and 13 μ in breadth.

Periodicity. Between June 12th and September 13th the variety was very common in the plankton. Strange to say this great and long maximum at temperatures between 17 and 28.5° C. did not end with an active formation of spores; nearly all of the very few spores observed were seen during the first half of September (temp. 17.5—19° C.). During the autumn the frequency of the variety decreased steadily, and on December 16th (temp. 3° C.) it was very rare. Apart from the problematic occurrence on February 17th, 1930 (temp. 1° C.) the variety was not found in the plankton of Jægerbakke Dam between December 16th and May 1st. In May it was very rare and at the end of the investigation on June 16th it was rare.

In other words *Anabaena Viguieri* var. *danica* is eurythermic with a temperature amplitude of 3—28.5° C. It was not observed with certainty in the months of January—April but reached a great and continuous maximum in June—September.

Sociology. The variety was found in the following associations:

June 12th, 1929: *Mio mi*-association with *Ana Vi da*, *Mio ho* and *Ra pe* as subdominants; see Table IV.
— 18th, — : *Mio mi*-association with *Ana te*, *Ana Vi da*, *Mio ho* and *Sce arm* as subdominants.
— 27th, — : *Mio mi*-association with *Ana Vi da* as subdominant.
July 4th, — : ditto.
— 11th, — : *Ana Vi da*-association with *Mio mi* as subdominant.
— 17th, — : *Ana Vi da - Sce arm*-association with *Mio mi*, *Mio ho* and *Os li* as subdominants.
— 27th, — : *Ana Vi da*-association with *Mio ho* as subdominant.
Aug. 10th, — : *Ana Vi da - Mio ho - Os li ac - Sce arm*-association.
— 21st, — : *Ana Vi da - Mio ho - Os li ac*-association.
Sep. 2nd, — : *Ana Vi da*-association with *Mio ho* as subdominant.
— 13th, — : *Ana Vi da - Mio ho*-association.
— 18th, — : *Mio ho*-indeterminable green alga-association (variety rather common); see Table IV.
— 23rd, — : *Mio ho*-association (variety rather common).
Oct. 3rd, — : ditto.
— 14th, — : *Mio ho*-association (variety rare).
— 23rd, — : *Mio ho*-association with *Sce arm* as subdominant (variety very rare).
Dec. 16th, 1929: *Ank fa se br - Ki mi*-association (variety very rare).
May 1st, 1930: *Ge mi*-association (variety very rare).
— 21st, — : *Mio ho*-association (variety very rare).
June 16th, — : *Mio ho*-association with *Ana si* and *Sce arm* as subdominants variety rare).

It appears from this that *Anabaena Viguieri* var. *danica* in the great majority of cases was found in myxophycean associations of *Microcystis* and *Oscillatoria* and could also form associations itself; it further occurred in chlorophycean associations of *Scenedesmus*, *Ankistrodesmus*, *Kirchneriella* and *Geminella*.

The most constant associates were *Scenedesmus armatus*, *Scenedesmus falcatus*, *Microcystis holsatica*, *Microcystis minutissima*, which occurred in 100 % of the number (20) of samples that contained *Anabaena Viguieri* var. *danica*. *Ankistrodesmus falcatus* var. *spirilliformis*, *Oscillatoria limnetica* and its var. *acicularis* occurred in 95 % of the samples, *Chlamydomonas retroversa* and *Ankistrodesmus falcatus* in 85 %, *Chlamydomonas kakosmos* and *Ankistrodesmus falcatus* var. *spiralis* in 80 %, *Selenastrum Westii* and *Sphaerozosma granulatum* in 75 % of the samples.

Ecology. Jægerbakke Dam is a very highly eutrophicated, but lime-deficient pond. This small, highly wind-sheltered pond is situated in a park at Hillerød. Its phytoplankton quotients appear from Table III.

The species was found at pH 7.05—9.8, content of CaO 7.3—10.9 mg/l, consumption of $KMnO_4$ 28—49 mg/l, contents of PO_4-P 0—0.015 mg/l, NH_3-N 0—0.01 mg/l, Fe 0.02 mg/l.

Addendum.

After the completion and translation of the manuscript I received two valuable papers, viz. H. Skuja's "Taxonomie des Phytoplanktons einiger Seen in Uppland, Schweden" (Symb. Bot. Upsal., vol. 9, 1948) and E. Teiling's "Staurodesmus, genus novum" (Bot. Notiser 1948).

During a short stay in Uppsala at Professor Skuja's and in Linköping at Dr. Teiling's I had an opportunity to discuss some of my new species with these two scientists. The following will render an account of the results of our discourses.

Euglena phacoides n. sp. (p. 163) is identical with *Euglena spathirhyncha* Skuja (1948, p. 196, t. 22, figs. 17—20).

Chlamydomonas clavata n. sp. (p. 30) is probably identical with *Chlamydomonas gloeophila* Skuja (1948, p. 85, t. 9, figs. 1 a—i).

Closterium polystictum Nyg. forma (Skuja 1948, p. 153, t. 18, figs. 1—3) is undoubtedly identical with *Closterium polystictum* Nyg. var. *breviusculum* n. var. (p. 60) even if the range of variation is larger (280—570 $\mu \times 6.5$—11.5 μ).

Skuja is of opinion that *Closterium Baillyanum* Breb. var. *parvulum* Grönblad f. *tenuis* n. f. (p. 56) ought to be named *Closterium Baillyanum* var. *tenue* n. var. I agree with Professor Skuja in this view.

The same author has referred *Closterium tortum* Griffiths to *Closterium parvulum* Näg. as var. *tortum* (Griff.) Skuja (1948, p. 154), while I have referred it to *Closterium Venus* Kg. as f. *torta* (Griff.) mihi (p. 63). In their Monograph of the British Desmidiaceae, vol. 1, p. 138, W. and G. S. West write: "The curvature of *Closterium Venus* (150—160° of arc) distinguishes it from *Closterium parvulum* (120—140° of arc), and it is invariably of smaller dimensions (51—81 $\mu \times 7$—10.5 μ, while those of *Closterium parvulum* are 96—121 $\mu \times 11$—14,5 μ) . . . . . and there are rarely more than two pyrenoids in each chloroplast." Skuja's specimens measured 90—160 μ in length thus being considerably longer than the Danish specimens (81—90 μ long). Griffiths states the measurements 90—100 $\mu \times 8$—10 μ for *Closterium tortum* Griff., consequently it is thinner than *Closterium parvulum*, but it has 3—4 pyrenoids per semicell. The Danish specimens evidently are more closely allied to *Closterium Venus* than to *Closterium parvulum* if we lay stress on their great curvature (151—164° of arc) and the dimensions.

Arthrodesmus incus Hass. var. *extensus* Anderss. (p. 71) is perhaps identical with *Staurodesmus Joshuae* Teiling (1948, p. 66, figs. 1—7, 9—10).

Arthrodesmus incus Hass. var. *extensus* Anderss. f. *minor* n. f. (p. 71) may be regarded as *Staurodesmus extensus* (Anderss.) Teiling f. *minor* mihi (see Teiling 1948, p. 67, fig. 11).

Staurastrum curvatum West f. *brevispina* n. f. (p. 89) may be named *Staurodesmus curvatus* (West) f. *brevispina* mihi.

Staurastrum cuspidatum Breb. var. *acuminatum* n. var. (p. 89) may be named *Staurodesmus cuspidatus* Ralfs subsp. *tricuspidatus* Teiling var. *acuminatus* mihi (see TEILING 1948, p. 60).

Staurastrum dejectum Breb. f. *mediocris* n. f. and f. *longispina* n. f. (p. 93—94) may be regarded as two local races of *Staurodesmus Spencerianus* Teiling subsp. *Spencerianus* Teiling (1948, p. 68, figs. 37—38, 42—43).

Dr. HUBER-PESTALOZZI is of opinion that my *Rhodomonas lacustris* (see p. 147) is a new species. I agree with him in this and propose to call it *Rhodomonas ovalis* n. sp.

The author's grateful thanks are due to Dr. HUBER-PESTALOZZI, Professor SKUJA and Dr. TEILING for advice and criticism.

5. A simple Micro-Manipulator.

For the isolation of one microscopical cell is often used a fine capillary tube, the point of which is inserted into the water-drop with the organisms; under microscopic control a single cell can then be sucked into the capillary tube. The difficulty of this operation consists in keeping the tube so quiet, that the point of it at a magnification of for instance 100 times can in fact be held quietly in front of the organism, which in many cases has a size of only 10—25 μ. I shall therefore describe a small invention, which I hope will meet a desideratum because the small apparatus can be fastened to the objective of the microscope; by means of the mechanical stage of the microscope the organism can be moved to the mouth of the fastened capillary tube and sucked up.

Construction. As shown in Fig. 126 the apparatus may consist of a block of metal, 55 mm long, 15 mm broad and 10 mm high, or, to avoid scratches on the side-walls of the objective, of a corresponding piece of ebonite or the kind of pressed material that is used for insulating purposes by the electric industry. In one end there is a vertical hole (diam. for instance 12 mm) for the objective and a deep incision, so that the walls of the hole can be fastened round the objective by means of a threaded bolt. On the side-wall of the other end is placed a retaining plate, so that the capillary tube can be pressed against one vertical wall of the block by means of 3 screws. Small pieces of felt or thin plates of cork glued to the walls of the block and the retaining plate prevent the breaking of the tube.

The capillary tube is a 5 mm glass tube, one end of which has been drawn into a long, thin point forming an angle of about 135° with the tube; at the other end of the tube a small but high nut with a threaded bolt to match is fastened by means of glass-cement. It is very important that the bolt should fit exactly into the thread

of the nut and that it is greased with a tough lubricant, for instance the kind used for the glass-taps of burettes because it is necessary to make the passage of the bolt through the nut completely air-tight. It is desirable to have a set of capillary tubes, the points of which are for instance 25, 50, 100 and 500 μ thick.

When the apparatus is to be used, the block is fastened to the objective, after which the capillary tube chosen is placed in such a position that the mouth of the

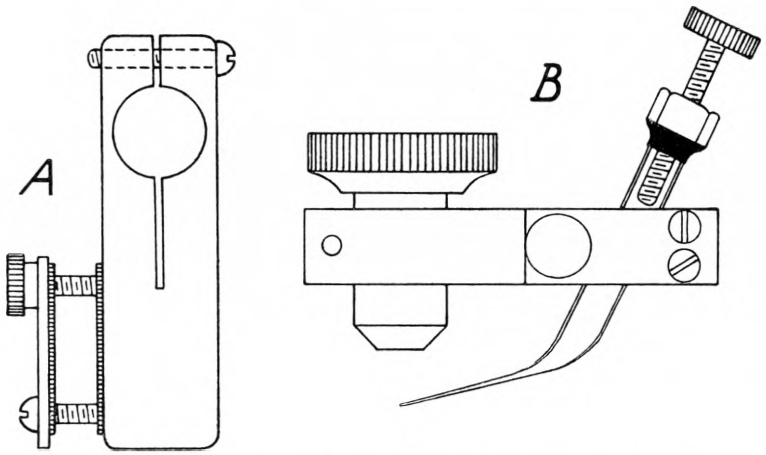


Fig. 126. *A*: the micro-manipulator in vertical view without the capillary tube; *B*: the micro-manipulator with the capillary tube in lateral view, mounted on the objective of the microscope.

tube is clearly visible in the centre of the field of vision (magnification about 100 times) and the point is nearly horizontal.

Application. If a single microscopical organism is to be selected from a suspension of organisms in water, it cannot be done by lowering the empty capillary tube into the drop on the slide. The capillary action, which increases with the diminishing diameter of the tube, will immediately carry water with numerous organisms into the tube. The tube must be allowed to suck up sterile water and by turning the threaded bolt a convenient column of water remains; if the tube is then let down into the suspension by lowering the tubus of the microscope, no organisms will be sucked up. By means of the mechanical stage the slide is now placed in such a position that the organism selected is situated before the mouth of the tube; a slight counter-clockwise turning of the threaded bolt of the capillary tube will then carry the cell into the tube, after which the capillary tube is removed from the suspension with the other organisms by raising the tubus of the microscope.

If one or several organisms are wanted for the cultivation of clones, the following procedure may be used. After the selection of one cell the slide with the suspension is replaced by a sterile slide, on which a sterile coverslip is placed. The tubus of the microscope is lowered until the point of the capillary tube touches the cover-

glass; a slight clockwise turning of the threaded bolt will now press a droplet of water containing the chosen cell on to the coverslip. At a magnification of for instance 200 times it should now be ascertained that the droplet contains one and only one cell. If this is the case, the coverglass can be slipped from the slide into the sterile fluid in which the species is to be cultivated.

The apparatus can also be used for the making of permanent slides of new or rare species, of which only a few individuals were found among many others, for instance desmid individuals in a plankton sample. Some drops of glycerine should be added to the sample, which is then placed on a watch-glass or in a salt-cellar to allow a slow evaporation of the water. The specimens wanted can now be selected from the glycerine suspension and placed in a droplet of pure glycerine on a slide for the usual ready-making of the slide.

If durable slides are wanted, the micro-organisms should not be mounted in a concentrated solution of potassium acetate. In 1930 I made more than 400 slides of plankton mounted in potassium acetate; all of them were sealed with the first class Rützow's Varnish. To-day nearly all of these slides have dried up, which would hardly have happened if glycerine had been used instead of potassium acetate.

In the literature the vapours of osmic acid are often recommended for the fixation of flagellates. I have tried to fix *Euglena gracilis* in this way, but the result was very poor because the long cells of this organism within a fraction of a second contracted into clots before they died. For such difficult kinds of objects I recommend the following method. A little of the *Euglena* suspension is spouted into 2—3 ml of $\frac{1}{2}$ % osmic acid, by which procedure the cells are fixed instantaneously. After a sedimentation of 5—10 minutes the osmic acid is sucked off, and the glass is filled with diluted formalin. After decantation repeatedly the rising water is replaced by 5—10 ml of 10 % glycerine with one drop of formalin. The suspension may now be poured into a watch-glass or a salt-cellar, so that the water may evaporate slowly, and it is now possible from the suspension in glycerine to make a first-class slide showing the *Euglena gracilis* individuals in exactly the same shape as when they were alive. Besides the chromatophores and the nucleus are very clearly visible in such a slide.

For plankton organisms of all sizes may be used a method invented at the Limnological Institute of Lund, Sweden. Small fragments of coverglass or mica are placed round a glycerine drop of a suitable size, containing one or several specimens of the organism. A slight heating will make the paraffin arranged in small grains along one of the edges of the coverslip melt and force its way under the coverglass where it surrounds the droplet of glycerine. After it has cooled down the slide is finished.

I should recommend to use minute spheres or pieces of modelling wax instead of splits of coverglass, 4 pieces of $\frac{1}{2}$—1 mm size around the droplet of glycerine. The advantage of this method is that the coverglass may be pressed close to the objects thus allowing the use of immersion objectives by the examination.

As it proved apparent that an air-bubble is formed in the glycerine in about three months, or even that the glycerine was totally absorbed by the paraffin, I should recommend to replace the paraffin by paraffin oil, at which the heating besides can be avoided. The slide should finally be sealed with e. g. Canada Balsam or Rützow's Varnish.

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6. List of new Localities.

Arreskov Sø, South Funen.
July 7th, 1946: Temp. 20°, nannoplankton.
Badstue-Ødam, NE-Seeland.
September 5th, 1941: netplankton and waterbloom (coll. by Jørgen Bock).
Ballegaard Mølledam at Avnbøl, North Sleswick.
February 11th, 1944: nannoplankton.
Bøllemosen, North Seeland.
September 5th, 1946: pH 4.9, nannoplankton.
May 17th, 1948: Temp. 22°, pH 4.2, netplankton.
Chara-pond in Bagmose E. of Aunslev, East Funen.
August 9th, 1926: pH 8.1, consumption of $KMnO_4$ 61 mg per l, netplankton.
Egen Mølledam, Als.
March 11th, 1943: oligohumic, nannoplankton.
February 25th, 1944: icebound, nannoplankton.
May 20th, 1945: temp. 12.5°, pH 8.4, nannoplankton.
November 21st, 1945: temp. 5.6°, pH 7.8, mesohumic, nannoplankton.
Emdrup Sø at Copengagen.
July 29th, 1941: nannoplankton (coll. by Jørgen Bock).
March 26th, 1946: temp. 5°, free from ice, nannoplankton.
November 29th, 1946: temp. 5.5°, pH 7.9, nannoplankton, 5 ml sample.
Eriophorum moor at Suserup, Seeland.
July 9th, 1947: pH 6,8, netplankton, 7 liter sample.
August 6th, 1947: temp. 19.5°, pH 6.8, netplankton, 1 ml sample.
September 6th, 1947: temp. 19°, pH 6.5—6.8, netplankton, 10 ml sample.
October 4th, 1947: temp. 13°, pH 6.6, netplankton, 10 ml sample.
November 15th, 1947: temp. 2.5°, pH 6.9, netplankton, 10 ml sample.
December 13th, 1947: temp. 3°, pH 6.6, netplankton, 10 ml sample.
January 10th, 1948: temp. 1°, partly icebound, pH 6.4, nannoplankton, 10 ml sample.
February 21st, 1948: temp. 2°, covered with 8 cm thick ice, pH 6.4, nannoplankton, 10 ml sample.
March 20th, 1948: temp. 7.5°, pH 6.6, net- and nannoplankton, 10 ml sample.
April 17th, 1948: temp. 15.5°, pH 6.8, net- and nannoplankton, 10 ml sample.
May 14th, 1948: temp. 20°, pH 6.9, net- and nannoplankton. 10 ml sample.
June 13th, 1948: temp. 20°, pH 6.6, net- and nannoplankton, 10 ml sample.
July 13th, 1948: temp. 22°, pH 6.8, net- and nannoplankton, 10 ml sample.
Field pond at the 32 km stone of main road 8, North Sleswick.
October, 4th 1942: temp. 16.5°, polyhumic, nannoplankton.
Field pond at Lysabild, Als.
March 11th, 1943: oligohumic, nannoplankton.
February 13th, 1944: nannoplankton.

Field pond between Sønderskoven and Høruphav, Als.
November 11th, 1944: temp. 4°, oligohumic, nannoplankton.
February 22nd, 1945: free from ice, oligohumic, nannoplankton.
Field pool North of Søndre Landevej at Sønderborg, North Sleswick.
February 27th, 1938: temp. 2.5°, icebound, nannoplankton.
March 25th, 1945: temp. 11°, pH 8.4, nannoplankton.
Field pool at the road from Aabenraa to Søgaard, North Sleswick.
September 14th, 1944: pH 7.9, nannoplankton.
Field watering pond at Augustenborg, Als.
December 21st, 1944: temp. 1°, pH 7.6, nannoplankton.
Graasten Slotssø, North Sleswick.
November 15th, 1942: nannoplankton.
Gurre Sø, North Seeland.
November 21st, 1945: nannoplankton.
April 2nd, 1946: nannoplankton.
October 28th, 1946: nannoplankton (all coll. by Lektor B. Asmund).
Hammersø, North Bornholm.
August 26th, 1947: nannoplankton.
Hulsø, North Seeland.
August 8th, 1946: netplankton.
December 23rd, 1946: ice 10 cm thick, temp. 0.5°, pH 7.5, nannoplankton, netplankton 20 ml sample, depth 3.9 m.
April 5th, 1947: temp. 3°, nearly quite icebound, pH 7.0, netplankton, nannoplankton.
September 4th, 1947: netplankton.
Hundslev Bydam, North Sleswick.
March 12th, 1943: temp. 3.5°, oligohumic, nannoplankton.
Jægerbakke Dam at Hillerød, North Seeland.
November 25th, 1944: temp. 1—2°, nannoplankton.
December 4th, 1944: temp. 2°, nannoplankton, 500 ml sample (coll. by Professor Kaj Berg).
Jægerdammen at Augustenborg, Als.
February 27th, 1944: oligohumic, nannoplankton.
Kidskelund Gadekær at Krusaa, North Sleswick.
August 18th, 1945: temp. 18.3°, pH 7.1, nannoplankton.
Klaresø in Teglstrup Hegn, North Seeland.
June 14th, 1947: pH 6.0, netplankton.
Klosterdam in Sønderborg, Als.
February 28th, 1945: temp. 7.5°, pH 8.4, nannoplankton.
March 25th, 1945: temp. 11°, pH 7.6, nannoplankton.
Krusaa-Dam (contaminated) near the 30 km stone at mainroad 8 (Sønderborg—Tønder), North Sleswick.
October 4th, 1942: temp. 16.5°, nannoplankton.
September 11th, 1944: pH 4.8, nannoplankton.
April 27th, 1945: temp. 9.5°, pH 4.8, neuston of Euglena, nannoplankton.
July 22nd, 1945: temp. 20.0°, pH 5.0, nannoplankton.
August 18th, 1945: temp. 18.5°, pH 4,9, 5.5 mg CaO per l, consumption of $KMnO_4$ 196 mg per l, neuston of Euglena, nannoplankton, 1000 ml sample.
September 21st, 1945: temp. 16°, nannoplankton.
October 28th, 1945: temp. 11.5°, pH 4.8, nannoplankton, 1000 ml sample.
November 30th, 1945: temp. 7.5°, pH 4.8, nannoplankton, 1000 ml sample.
December 30th, 1945: temp. 1.5°, partly icebound, pH 4.9, nannoplankton, 1000 ml sample.

Ladegaard Dam at Sønderborg, Als.
February, 17th 1938: temp. 2°, icebound, nannoplankton.
Lodne Mose at Broager, North Sleswick.
March 17th, 1943: oligohumic, nannoplankton.
February 26th, 1944: oligohumic, nannoplankton.
Lundesøen in Als.
February 20th, 1944: temp. 3.5°, nannoplankton.
Lundsø at Avnbøl, North Slewick.
March 14th, 1943: temp. 4°, oligohumic, nannoplankton.
Lyngby Sø, North Seeland.
March 25th, 1946: temp. 3.5°, partly icebound, nannoplankton.
Lynge Kirkedam at Sorø, Seeland.
November 15th, 1947: temp. 2°, partly covered with thin ice, pH 7.8, nannoplankton, 10 ml sample.
December 13th, 1947: temp. 3°, pH 7.6, nannoplankton, 10 ml sample.
January 10th, 1948: temp. 0.5°, pH 7.8, nannoplankton, 10 ml sample; partly icebound.
February 21st, 1948: temp. 1°, covered with 10 cm thick ice, pH 8.6, nannoplankton, 10 ml sample.
March 20th, 1948: temp. 7.5°, pH 8.6, nannoplankton, 10 ml sample.
April 17th, 1948: temp. 12.5°, pH 8.6, nannoplankton, 10 ml sample.
June 13th, 1948: temp. 20°, pH 7.6, nannoplankton.
Lynge Vandingsdam at Sorø, Seeland.
June 30th, 1947: 1000 ml sample.
August 6th, 1947: temp. 19.5°, pH 9.0, nannoplankton, 1 ml sample.
September 6th, 1947: quite dried up!
October 4th, 1947: 50—100 l water in the pond, temp. 13.5°, pH 7.8, nannoplankton, 10 ml sample.
November 15th, 1947: covered with thin ice, temp. 2°, pH 7.7, nannoplankton, 10 ml sample.
December 13th, 1947: temp. 3°, pH 7.8, nannoplankton, 10 ml sample.
January 10th, 1948: temp. 0.5°, pH 7.8, nannoplankton, 10 ml sample.
February 21st, 1948: temp. 1°, covered with 10 cm thick ice, pH 8.4, nannoplankton, 10 ml sample.
March 20th, 1948: temp. 7°, pH 8.3, net- and nannoplankton, 10 ml sample.
April 17th, 1948: temp. 14.5°, pH 8.5, net- and nannoplankton, 10 ml sample.
May 14th, 1948: temp. 18°, pH 8.8, nannoplankton, 10 ml sample; nearly overgrown with *Batr. aquatile*.
June 13th, 1948: temp. 20°, pH 9.2, nannoplankton, 10 ml sample. *Chara vulgaris* at the margin.
July 25th, 1948: temp. 24°, pH 9.1, nannoplankton, 10 ml sample. *Chara vulgaris* abundant everywhere in the pond together with *Batrachium aquatile* and *Batr. trichophyllum*.
Løvenholm Langsø, Jutland.
August 1st, 1948: temp. 27°, pH 4.1, netplankton, nannoplankton, 10 ml sample, superhumic!
Maribo Sø, Lolland.
October 27th, 1946: nannoplankton (coll. by Adjunkt K. Viderø).
Marl-pit at Økobbel, Als.
November 18th, 1941: icebound, pH 7.8, nannoplankton.
Mørksø in Salling, North Jutland.
July 6th, 1938: temp. 18.5°, pH 4.9, oligohumic, nannoplankton.
Mølledammen in Sønderborg, Als.
August 1st, 1937: water-bloom.

September 10th, 1941: nannoplankton.
August 30th, 1943: nannoplankton.
August 26th, 1944: nannoplankton.
November 25th, 1944: nannoplankton.
January 11th, 1945: nannoplankton.
July 4th, 1945: pH 9.4, nannoplankton.

Nordborg Sø, Als.
July 11th, 1938: nannoplankton.
July 19th, 1938: 1000 ml sample.
May 21st, 1940: nannoplankton.
September 23rd, 1940: nannoplankton.
December 9th, 1940: nannoplankton.

Pond I at Dybbøl Kirkegaard, North Sleswick.
March 10th, 1943: temp. 3.5°, oligohumic, nannoplankton.

Pond II at Dybbøl Kirkegaard, North Sleswick.
March 11th, 1943: temp. 4°, nannoplankton.

Pond at Mommark Færgegaard, Als.
February 15th, 1944: oligohumic, nannoplankton.

Pond at Mommark School, Als.
February 15th, 1944: oligohumic, nannoplankton.

Pond situated near the beginning of the Hokkerup road from the Graasten—Søgaard road, North Sleswick.
September 14th, 1944: pH 8.5, nannoplankton.

Pond at Høbbet NE of Faaborg, Funen.
July 7th, 1946: nannoplankton.

Pond in Ragebøl, North Sleswick.
August 30th, 1937: nannoplankton.
April 2nd, 1938: nannoplankton.
December 10th, 1940: covered with thin ice, nannoplankton.

Pond W of Rønhavegaard, Als.
March 12th, 1944: temp. 4.5°, nannoplankton.
December 17th, 1944: temp. 1°, icebound, nannoplankton.

Pond at Søndre Landevej, Sønderborg, Als.
January 3rd, 1937: temp. 4.5°, nannoplankton.
January 16th, 1937: icebound, netplankton.
January 1st, 1940: temp. 1.5°, pH 7.4, covered with 10 cm thick ice, nannoplankton.
July 12th, 1940: temp. 17°, pH 7.4, nannoplankton.
December 14th, 1941: temp. 5.5°, pH 7.7, nannoplankton.
October 23rd, 1943: temp. 11°, pH 7.4, 2000 ml sample.
December 29th, 1943: temp. 4.5°, nannoplankton.
February 6th, 1944: temp. 2°, 500 ml sample.
February 21st, 1944: temp. 0.5°, icebound, nannoplankton.
April 8th, 1944: temp. 6.5°, nannoplankton.
July 16th, 1944: nannoplankton.
November 17th, 1944: temp. 6°, pH 8.1, nannoplankton.
February 22nd, 1945: free from ice, nannoplankton.
March 25th, 1945: temp. 10°, pH 8.5, water level very high, nannoplankton.
August 10th, 1945: pH 7.6, nannoplankton.

Pond at Snogbæk, North Sleswick.
March 10th, 1943: temp. 4°, oligohumic, nannoplankton.

Pond in Sundsmark, Als.
November 8th, 1942: temp. 8.3°, pH 7.8, nannoplankton.
January 3rd, 1944: temp. 4°, nannoplankton.
July 20th, 1944: polyhumic, nannoplankton.
January 25th, 1945: covered with 7 cm thick ice, oligohumic, nannoplankton.
Pond (inundated grass field) W of Sønderskoven, Als.
March 13th, 1945: temp. 7.5°, pH 8.4, oligohumic, nannoplankton.
March 25th, 1945: temp. 11°, pH 8.1, nearly dried up, nannoplankton.
Pond W of Sønderskoven, Als.
March 25th, 1945: temp. 11°, pH 8.0, oligohumic, nannoplankton.
Pond (shallow) in the forest of Sønderskoven, Als.
December 14th, 1944: temp. 1.7°, pH 6.2, polyhumic, nannoplankton.
March 12th, 1945: nannoplankton.
Pond (small) in the new cemetery of Sønderborg, Als.
March 25th, 1945: temp. 11°, pH 8.4, oligohumic, nannoplankton.
Pool in the garden of Sønderborg Statsskole.
August 31st, 1944: temp. 18°, pH 8.5, nannoplankton.
September 11th, 1944: nannoplankton.
November 30th, 1944: temp. 6.5°, pH 7.1, polyhumic, nannoplankton.
Rønhavegaard Dam, Als.
March 12th, 1944: temp. 4.5°, pH 8.2, nannoplankton, 1000 ml sample.
March 19th, 1944: temp. 6°, nannoplankton.
December 10th, 1944: temp. 2.3°, pH 7.8, mesohumic, nannoplankton.
January 13th, 1945: temp. 1.5°, ice 3 cm thick, pH 7.9, oligohumic, nannoplankton.
March 8th, 1945: temp. 4°, pH 8.8, nannoplankton.
March 15th, 1945: temp. 7°, nannoplankton.
March 22nd, 1945: temp. 7.5°, pH 9.6, nannoplankton.
April 30th, 1945: temp. 10°, nannoplankton.
May 23rd, 1945: temp. 15.7°, pH 9.6, nannoplankton.
June 30th, 1945: temp. 17°, pH 9.3, nannoplankton.
July 20th, 1945: temp. 23.6°, pH 9.4, nannoplankton.
August 25th, 1945: temp. 17.3°, pH 9.8, nannoplankton, enormous production.
November 2nd, 1945: temp. 10.5°, nannoplankton.
Sandbjerg Sø at Alssund.
June 16th, 1925: temp. 17°, netplankton.
September 4th—10th, 1937: netplankton and nannoplankton.
August 14th, 1938: temp. 26.8°, pH 8.8, nannoplankton.
August 15th, 1938: 3000 ml sample.
September 4th, 1938: temp. 17°, pH 8.4, nannoplankton.
September 15th, 1938: temp. 14.5°, pH 8.3, nannoplankton.
October 1st, 1938: temp. 17.5°, pH 8.3, nannoplankton,
May 21st, 1939: nannoplankton.
August 6th, 1939: temp. 22°, nannoplankton.
September 3rd, 1939: temp. 21.6°, pH 8.4, nannoplankton.
May 15th, 1940: nannoplankton.
November 22nd, 1941: nannoplankton.
November 29th, 1941: nannoplankton.
February 27th, 1944: partly icebound, nannoplankton.
August 19th, 1944: water-bloom.
August 19th, 1945: 113.1 mg CaO per litre.

Skaansø in Salling, North Jutland.
July 4th, 1938: temp. 17.5°, pH 5.6, oligohumic, netplankton and nannoplankton.
Skørsø in Salling, North Jutland.
July 5th, 1938: temp. 18°, pH 4.6, nannoplankton.
Sorø Sø in Seeland.
June 30th, 1947: netplankton.
September 6th, 1947: temp. 19.5°, pH 7.9, netplankton, 1 ml sample.
Sortesø in Teglstrup Hegn, NE-Seeland.
June 14th, 1947: pH 4.7, netplankton.
Skovby Gadekær, Als.
November 9th, 1944: temp. 4.5°, pH 8.9, oligohumic, nannoplankton.
Sphagnum bog ("Cirkelsø") S of Søgaard Sø, North Sleswick.
July 16th, 1939: temp. 21.5°, pH 4.3, nannoplankton.
Steenstrup Skovdam S of Sorø, Seeland.
July 12th, 1947: netplankton.
Store Gribsø, NE-Seeland.
August 17th, 1946: temp. 19°, pH 4.3, 200 ml sample, netplankton.
January 4th, 1947: temp. 0°, ice 15 cm thick, pH 4.4, nannoplankton.
June 19th, 1947: netplankton, 100 ml sample.
May 6th, 1948: temp. 13°, pH 4.1, net- and nannoplankton, 10 ml sample.
Sædmose at Høgebjerg, Asserballe, Als.
November 10th, 1940: nannoplankton.
Tjustrup Sø in Seeland.
August 8th, 1941: netplankton.
July 30th, 1943: netplankton.
July 16th, 1946: netplankton, 20°.
July 2nd, 1947: netplankton.
Turf pit in Almsted Lyng, Als.
October 28th, 1940: polyhumic, nannoplankton.
Turf pit at Bromme Plantage, Seeland.
May 24th, 1947: netplankton.
July 3rd, 1947: netplankton.
Turf pit at Dødringe, Seeland.
May 24th, 1947: netplankton.
Turf pit in Hundslev, North Sleswick.
March 11th, 1943: temp. 3.5°, polyhumic, nannoplankton.
Turf pit 1 km W of Hvidemose in Salling, North Jutland.
July 4th, 1938: temp. 18°, pH 4.4, polyhumic, net- and nannoplankton.
Turf pit S of Kier, Als.
November 30th, 1944: temp. 5.5°, pH 7.4, mesohumic, nannoplankton.
Turf pit, nearly overgrown, NE of Skaansø in Salling, North Jutland.
July 4th, 1938: temp. 18.5°, pH 4.3, polyhumic, nannoplankton.
Turf pit near Suserup Skov, Seeland.
July 3rd, 1947: netplankton.
Turf pit N of Krusaa-Dam, North Sleswick.
August 18th, 1945: temp. 18.6°, pH 3.7, polyhumic, nannoplankton.
November 30th, 1945: temp. 7.5°, pH 3.8, polyhumic, nannoplankton.
Ulkebøl Gadekær, Als.
March 31st, 1943: nannoplankton.
Western village pond in Skovby, Als.
November 23rd, 1944: temp. 8°, pH 7.3, polyhumic, nannoplankton.

7. List of Abbreviations.

Act Ha = *Actinastrum Hantzschii* Lag.
Ana af in te = *Anabaena affinis* Lemm. var. *intermedia* Grif. f. *tenuis* n. f.
Ana ci = *Anabaena circinalis* Hansg.
Ana fl = *Anabaena flos aquae* Breb.
Ana Ha ma = *Anabaena Hassalii* Kg. var. *macrospora* Wittr.
Ana he = *Anabaena heterospora* n. sp.
Ana in = *Anabaena incrassata* Nyg.
Ana pl = *Anabaena planctonica* Brunnth.
Ana si = *Anabaena sigmoidea* n. sp.
Ana sp mi = *Anabaena spiroides* Kleb. var. *minima* Nyg.
Ana sp tu = *Anabaena spiroides* Kleb. var. *tumida* Nyg.
Ana su = *Anabaena subcylindrica* Borge
Ana te = *Anabaena tenericaulis* n. sp.
Ana te lo = *Anabaena tenericaulis* n. sp. var. *longispora* nov. var.
Ana Vi = *Anabaena Viguieri* Dénis et Frémy
Ana Vi da = *Anabaena Viguieri* Dénis et Frémy var. *danica* n. var.
Ank co mi = *Ankistrodesmus convolutus* Corda var. *minutus* Rabh.
Ank fa = *Ankistrodesmus falcatus* Ralfs
Ank fa mi du = *Ankistrodesmus falcatus* Ralfs var. *mirabilis* West f. *dulcis* Nyg.
Ank fa mi lo = *Ankistrodesmus falcatus* Ralfs var. *mirabilis* West f. *longiseta* Nyg.
Ank fa se br = *Ankistrodesmus falcatus* Ralfs var. *setiformis* Nyg. f. *brevis* Nyg.
Ank fa se el = *Ankistrodesmus falcatus* Ralfs var. *setiformis* Nyg. f. *elongata* Nyg.
Ank fa spa = *Ankistrodesmus falcatus* Ralfs var. *spiralis* G. S. West
Ank fa spi = *Ankistrodesmus falcatus* Ralfs var. *spirilliformis* West
Ank la = *Ankistrodesmus lacustris* Ostenf.
Api fl = *Aphanizomenon flos aquae* Ralfs
Api fl Kl = *Aphanizomenon flos aquae* Ralfs var. *Klebahnii* Elenk.
Ar cr lo = *Arthrodesmus crassus* West f. *longispina*
Ar in ex mi = *Arthrodesmus Incus* Hass. var. *extensus* Anders. f. *minor* n. f.
Asi fo = *Asterionella formosa* Hass.
Aso su = *Asterococcus superbus* Scherff.
Ba Bo = *Bambusina Borreri* Delp.
Bo Br = *Botryococcus Braunii* Kg.
Ca ag = *Carteria agloëformis* n. sp.
Ce co = *Ceratium cornutum* Clap. et Lachm.
Ce hi = *Ceratium hirundinella* Schrank
Ce hi si = *Ceratium hirundinella* Schrank f. *silesiacum* Schröder
Chla ac = *Chlamydomonas acidophila* Nyg.
Chla ci = *Chlamydomonas cingulata* Pascher
Chla ka = *Chlamydomonas kakosmos* Moewus

Chla ol = *Chlamydomonas oleosa* n. sp.
Chla ps = *Chlamydomonas pseudoplatyrhyncha* Pasch.
Chla Re = *Chlamydomonas Reinhardii* Dang.
Chla Re mi = *Chlamydomonas Reinhardii* Dang. var. *minor* Nyg.
Chrom No mi = *Chroomonas Nordstedtii* Hansg. f. *minor* n. f.
Chry ma = *Chrysococcus major* Nyg.
Chry mi = *Chrysococcus minutus* Nyg.
Cl ac va = *Closterium acutum* Breb. var. *variabile* Krieger
Cl Kü = *Closterium Kützingii* Breb.
Coa mi as = *Coelastrum microporum* Näg. f. *astroidea* (de Not.) mihi
Coo Kü = *Coelosphaerium Kützingianum* Näg.
Coo Nä = *Coelosphaerium Nägelianum* Unger
Cos as st = *Cosmarium asphaerosporum* Nordst. var. *strigosum* Nordst.
Cos de = *Cosmarium depressum* Lund.
Cos pu = *Cosmarium pusillum* Archer
Cru qu = *Crucigenia quadrata* Morren
Crym ov = *Cryptomonas ovata* Ehrb.
Crym ov cu = *Cryptomonas ovata* Ehrb. var. *curvata* Lemm.
Cyc co = *Cyclotella comta* Kg.
Cyc Kü ra = *Cyclotella Kützingiana* Twait. var. *radiosa* Fricke
Cyc Me = *Cyclotella Meneghiniana* Kg. emend. Nyg.
Cyc st su = *Cyclotella stelligera* Grun. var. *subglabra* n. var.
Dia el = *Diatoma elongatum* Ag.
Dia vu gr = *Diatoma vulgare* Bory var. *grandis* Grun.
Dic Eh = *Dictyosphaerium Ehrenbergianum* Näg.
Dic pu = *Dictyosphaerium pulchellum* Wood
Din cy al = *Dinobryon cylindricum* Imhof var. *alpinum* Bachm.
Din cy pa = *Dinobryon cylindricum* Imhof var. *palustre* Lemm.
Din di = *Dinobryon divergens* Imhof
Din se pr = *Dinobryon sertularia* Ehrb. var. *protuberans* Krieger
Din so = *Dinobryon sociale* Ehrb.
Din so am = *Dinobryon sociale* Ehrb. var. *americanum* Bachm.
Din so st = *Dinobryon sociale* Ehrb. var. *stipitatum* Lemm.
El ge = *Elakatothrix gelatinosa* Wille
El ge bi = *Elakatothrix gelatinosa* Wille f. *biplex* Nyg.
Eug ac = *Euglena acus* Ehrb.
Eug mi = *Euglena minima* Francé
Eug ob = *Euglena oblonga* Schm.
Eug pr = *Euglena proxima* Dang.
Eut gl = *Eutetramorus globosus* Walton
Frg cr = *Fragilaria crotonensis* Kitton
Frg ca = *Fragilaria capucina* Desm.
Ge mi = *Geminella minor* Heering
Gle ac = *Glenodinium aciculiferum* Lindem.
Gle Lo = *Glenodinium Lomnickii* Lindem.
Gos se = *Goniostomum semen* Diesing
Gy ex = *Gymnodinium excavatum* Nyg.
Gy ne = *Gymnodinium neglectum* Lindem.
Gy aer = *Gymnodinium aeruginosum* Stein
Ki mi = *Kirchneriella microscopica* Nyg.
La hy = *Lampropedia hyalina* Schröter

Le ps = *Lepocinclis pseudo-texta* Conrad
Le te = *Lepocinclis texta* Lemm.
Ly li = *Lyngbya limnetica* Lemm.
Ma ak = *Mallomonas akrokomos* Pascher et Ruttner
Ma ca = *Mallomonas caudata* Krieger, non Iwanoff
Ma pe ec = *Mallomonas pediculus* Teiling var. *echinospora* n. var.
Ma se = *Mallomonas semiglabra* n. sp.
Ma Te = *Mallomonas Teilingii* Conrad
Mel am = *Melosira ambigua* Müller
Mel gr = *Melosira granulata* Ralfs
Mel gr an = *Melosira granulata* Ralfs var. *angustissima* Müller
Mel it su = *Melosira italica* Kg. subsp. *subarctica* Müll.
Mer te = *Merismopedia tenuissima* Lemm.
Mia pu = *Micractinium pusillum* Fres.
Mio bo = *Microcystis Botrys* Teiling
Mio fl = *Microcystis flos aquae* Kirchner, emend. W.-L., Teiling
Mio fl ma = *Microcystis flos aquae* var. *major* n. var.
Mio ho = *Microcystis holsatica* Lemm.
Mio mi = *Microcystis minutissima* West
Mio pu = *Microcystis pulverea* Mig.
Mio pu ra = *Microcystis pulverea* Mig. var. *racemiformis* n. var.
Mio vi = *Microcystis viridis* Lemm., Teiling
Mio aer = *Microcystis aeruginosa* Kg. emend. W.-L., Teiling
Mio aer ma = *Microcystis aeruginosa* var. *major* Wittr.
Na be = *Nannokloster belonophorus* Pascher
Ni ac = *Nitzschia acicularis* Grun.
Oe It = *Oedogonium Itzigsohnii* de Bary
Oo cr = *Oocystis crassa* Wittr.
Oo cr mi = *Oocystis crassa* Wittr. var. *minor* n. var.
Oo Ma = *Oocystis Marssonii* Lemm.
Os Ag = *Oscillatoria Agardhii* Gom.
Os li = *Oscillatoria limnetica* Lemm.
Os li ac = *Oscillatoria limnetica* Lemm. var. *acicularis* n. var.
Pa mo = *Pandorina morum* Bary
Ped du = *Pediastrum duplex* Meyen
Per bi = *Peridinium bipes* Stein
Per pa = *Peridinium palatinum* Lautb.
Per Vo = *Peridinium Volzii* Lemm.
Per Wi = *Peridinium Willei* Huitf.-Kaas
Pho le = *Phacotus lenticularis* Ehrb.
Phu os = *Phacus oscillans* Klebs
Phu pl = *Phacus platyaulax* Pochm.
Phu py = *Phacus pyrum* Stein
Phu su = *Phacus suecicus* Lemm.
Ra pe = *Radiococcus pelagicus* Teiling
Rhi lo = *Rhizosolenia longiseta* Zach.
Sce arc ca = *Scenedesmus arcuatus* Lemm. var. *capitatus* G. M. Smith
Sce arm = *Scenedesmus armatus* Chodat
Sce arv = *Scenedesmus arvernensis* Chodat
Sce ec = *Scenedesmus ecornis* Chodat
Sce fa = *Scenedesmus falcatus* Chodat

Se ca = *Selenastrum capricornutum* Printz
Se We = *Selenastrum Westii* G. M. Smith
Spc Sc = *Sphaerocystis Schröteri* Chodat
Sta al = *Staurastrum alternans* Breb.
Sta Be = *Staurastrum Bergii* n. sp.
Sta br = *Staurastrum brachiatum* Ralfs
Sta de lo = *Staurastrum dejectum* Breb. f. *longispina* n. f.
Sta de me = *Staurastrum dejectum* Breb. f. *mediocris* n. f.
Sta pi tr = *Staurastrum pingue* Teiling var. *tridentatum* n. var.
Sta po di = *Staurastrum polymorphum* Breb. var. *divergens* n. var.
Ste As = *Stephanodiscus Astraea* Grun.
Ste du = *Stephanodiscus dubius* Hustedt
Ste Ha = *Stephanodiscus Hantzschii* Grun.
Sti ba = *Stichococcus bacillaris* Näg.
Sye ac = *Synedra acus* Kg.
Sye ac an = *Synedra acus* Kg. var. *angustissima* Grun.
Sye te = *Synedra tenera* Smith
Syu ec = *Synura echinulata* Korsch.
Syu Pe = *Synura Petersenii* Korsch.
Syu sp = *Synura spinosa* Korsch.
Ta fe as = *Tabellaria fenestrata* Kütz. var. *asterionelloides* Grun.
Teë mi = *Tetraëdron minimum* Hansg.
Teë mu = *Tetraëdron muticum* Kütz.
Tet st = *Tetrastrum staurogeniaeforme* Lemm.
Tra ch = *Trachelomonas chlamydophora* n. sp.
Tra hi = *Trachelomonas hispida* Stein
Tra in = *Trachelomonas intermedia* Dang.
Tra ve = *Trachelomonas verrucosa* Stokes
Tra vo = *Trachelomonas volvocina* Ehrb.
Trb tae = *Tribonema taeniatum* Pascher
Tsp Ny = *Tetraspora Nygaardii* Teiling
Tst st = *Tetrastrum staurogeniaeforme* Lemm.
Ul pe = *Ulothrix pelagica* n. sp.
Ura vo = *Uroglena volvox* Ehrb.
Ura am = *Uroglena americana* Calkins

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Indleveret til selskabet den 2. juni 1948.
Færdig fra trykkeriet den 10. januar 1950.

TABLE II

Table II. Composition of the phyto-

Species	(Dystrophic)														Oligo-
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø	
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29
Myxophyceæ															
Anabæna affinis var. intermedia	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— circinalis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— flos aquæ	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr
Anabæna Hassalii var. macrospora	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— incrassata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— planctonica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Anabæna Scheremetievii var. recta f. rotundospora	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— spiroides var. crassa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— subcylindrica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Anabæna tenericaulis var. longispora	..	..	..	..	..	..	..	..	..	..	..	r+	..	..	..
Aphanizomenon flos aquæ	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chroococcus limneticus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chroococcus limneticus var. carneus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— turgidus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Coelosphærium Kützingianum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Coelosphærium Nägelianum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Gomphosphæria aponina	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Lyngbya limnetica	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
Merismopedia elegans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— glauca	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
— tenuissima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Microcystis flos aquæ	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— minutissima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pulverea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Microcystis holsatica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— robusta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— stagnalis var. pulchra	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Microcystis viridis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— æruginosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. major	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Oscillatoria limnetica var. acicularis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Agardhii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Borneti f. tenuis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr

[1] f. tenuis. [2] var. limnetica. [3] Cells 3–4,5 μ. [4] Cells 4,5–6,5 μ: var. major nov. var. (p. 179). [5] Type: rr, var. major: c+.

(lankton from 16 Danish lakes,

tophic							Eutrophic																(Mixotrophic)					
Hampen Sø						Præstesø	Slaaen Sø	Nors Sø						Furesø					Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø	
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rr	..	rrr	..	..	..	..	..	..	..	..	rrr[1]	rr[1]
..	..	..	..	..	..	..	cc	rr	rrr	..	..	r	..	..	..	rrr	rrr	..	..	..	..	r	..	..	..	..	..
..	rrr	rrr	rr	..	cc	rrr	rr	cc	rrr	r	..	c	+	..	c	..	rr	..	..	r	rrr	..	..	rrr	..	..	..
..	r	..	rr	c	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	rr	..	..	..	..	..	..	..	..	..	..
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..	..	..	..	..	rrr	..	+	r	rr	r	..	rrr	..	..	..	rrr	rrr	rrr	rr	rr	rr	rr	r	r	+	..	r
..	..	..	..	..	..	..	..	..	rr	..	..	..	rrr	..	..	rr	rrr	..	..	..	..	r+	rr	..	..	..	..
..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	rr	..	r	rrr	..	r	..	+	..	..	rrr	r	rrr	rrr	..	rrr	..	rr	..	..	..	..	rr
..	+	rrr	rrr	rr	rr	..	rr	rrr	rrr	..	..	..	..	..	..	..	rrr	r+	..	rr	rr	+	rrr	cc	r	..	c
..	..	..	..	..	..	..	rrr	rrr	rrr	..	..	rrr	..	..	..	..	..	rrr[2]	..	..	..	..	..	..	..	..	..
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..	..	..	..	rrr	rrr	..	cc[4]	rr	rrr	rr	..	c	rr	..	rr	rr[3]	rr	r+[3]	r[3]	+[3]	c[5]	r	..	r	r	..	c[3,4]
..	..	..	..	rr	..	..	..	rrr	rr	..	..	rrr	..	..	..	rr	..	..	rrr	rrr	rrr	rrr	..	..	r	..	r
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Table I

Species	(Dystrophic)													Olig-	
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø	
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29
Oscillatoria limnetica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— neglecta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Phormidium mucicola	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Trichodesmium lacustre	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Euglenineæ															
Euglena acus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— oxyuris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Lepocinclis texta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Phacus caudata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— torta	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
— pleuronectes	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
Phacus circulatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Trachelomonas intermedia	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr
— nigra	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Trachelomonas superba	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— volvocina	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
Dinophyceae															
Amphidinium lacustre	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Ceratium hirundinella	rrr	rrr	..	..	..	..	rrr[1]	rrr[1]	..	..	..	+[5]	cc[5]	rr	r+
Diplopsalis acuta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Glenodinium dinobryonis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— edax	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— gymnodinium	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Glenodinium munusculum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Gymnodinium inversum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. elongatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Gymnodinium mirum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— paradoxum f. astigmosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Peridinium bipes	..	..	..	..	..	..	..	..	..	..	..	..	..	r	..
Peridinium cinctum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr
— eximium	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..
— Volzii (= guestrowiense)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Peridinium Willei	..	rrr	..	..	r+	+	rr	cc	r+	r	+	rrr	rr	..	rrr

[1] f. brachyceroides. [2] f. carinthiacum. [3] f. furcoides? [4] f. piburgense. [5] f. silesiacum. [6] forma with about 20—25 minute with 5 coarse striae pro 10 μ, striation in vertical view clockwise; cells basal flattened, 47 $\mu \times 45$ μ.

(continued).

trophic							Eutrophic															(Mixotrophic)					
		Hampen Sø				Præstesø	Slaaen Sø	Nors Sø						Furesø				Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø	
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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punctate striae pro 10 μ, striation in vertical view counter-clockwise; cells ovate, 29 $\mu \times 22$ μ. [7] Lepocinclis pseudotexta Conrad

Table II

Species	(Dystrophic)														Oligo-
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø	
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29
Cryptophyceæ															
Chroomonas Nordstedtii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cryptochrysis commutata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cryptomonas ovata	..	..	..	..	..	..	ccc[1]	..	..	..	..	..	..	..	..
Rhodomonas lacustris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Bacillariophyceae															
Asterionella formosa	..	..	..	r +	cc	..	..	..	..	..	..	..	..	..	..
Attheya Zachariasi	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
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Cyclotella Kützingiana var. radiosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Meneghiniana	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— stelligera var. subglabra	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cymatopleura elliptica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— solea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Diatoma elongatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Fragilaria capucina	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— construens	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— crotonensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Fragilaria Harrisonii var. dubia	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Melosira ambigua	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Stephanodiscus Binderanus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Melosira granulata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
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— — var. muzzanensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Melosira sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— islandica subsp. helvetica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— italica subsp. subarctica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Melosira varians	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Nitzschia acicularis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Rhizosolenia longiseta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Stephanodiscus Astræa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. minutula	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— dubius	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

[1] see p. 7. [2] var. mesolepta. [3] var. venter. [4] var. binodis. [5] also f. tenuis. [6] dead cells.

(continued).

trophic							Eutrophic																(Mixotrophic)					
Hampen Sø						Præstesø	Slaaen Sø	Nors Sø						Furesø					Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø	
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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Table II

Species	(Dystrophic)													Oligo-	
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø	
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29
Stephanodiscus Hantzschii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Surirella ovalis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Synedra acus var. angustissima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
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Tabellaria fenestrata	..	..	..	..	..	rrr[2]	..	..	..	..	..	..	..	c[3]	rrr[3]
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Chrysophyceæ															
Chrysococcus minutus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dinobryon bavaricum	..	..	..	..	..	rrr	..	..	..	..	..	..	..	rrr	rr
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Dinobryon cylindricum var. alpinum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. palustre	..	..	..	..	..	..	..	..	cc	..	c	rrr	..	..	..
— divergens	..	..	..	..	..	..	..	..	..	..	..	..	..	rr	r
Dinobryon divergens var. Schauinnslandii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pediforme	..	..	..	..	..	..	..	c	..	..	..	..	..	..	..
— sociale var. americanum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dinobryon sociale var. stipitatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Mallomonas caudata Krieg. non Iwan	r+	cc	rr	..	..	rrr	c	r+	..	..	..	..	..	..	..
— tessellata	..	rr	rrr	..	rr	..	rrr	..	..	..	..	..	..	..	..
Mallomonas tonsurata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Synura Petersenii	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr
— sphagnicola	rrr	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..
Synura spinosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Uroglena volvox	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— americana	..	..	..	..	..	..	..	..	..	cc	rrr	..	..	rrr	cc
Volvocales, Ulothricales, Oedogoniales, Xanthophyceae															
Asterococcus superbus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chlamydomonas bicocca	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— cingulata var. globulifera	..	..	..	rr	..	..	..	..	..	..	..	..	..	..	..

[1] and the main species: rrr. [2] var. intermedia. [3] var. asterionelloides and var. intermedia f. asterionelloides. [4] var. asterionel-

[continued).

trophic							Eutrophic																(Mixotrophic)					
Hampen Sø						Præstesø	Slaaen Sø	Nors Sø						Furesø					Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø	
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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Table II

Species	(Dystrophic)													Oligo-	
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø			
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29
Chlamydomonas clavata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Reinhardii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Eudorina elegans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Eutetramorus globosus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Gloeocystis gigas	..	..	rrr	..	..	..	..	..	..	rrr	..	..	..	..	..
— planctonica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Gloeocystis sp.	..	..	..	..	..	..	..	..	..	..	rrr	..	..	r+	..
Gonium pectorale	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Ophiocytium capitatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pandorina morum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Phacotus lenticularis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Schultziella pseudovolvox	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Sphærocystis Schroeteri	..	..	..	..	..	..	..	..	..	rrr	..	r	+	..	..
Tetraspora Nygaardii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tribonema taeniatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tribonema sp.$_1$	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— sp.$_2$	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Geminella minor	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Volvox aureus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chlorococcales															
Actinastrum Hantzschii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Ankistrodesmus falcatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. spirilliformis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. setiformis f. brevis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Ankistrodesmus lacustris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Botryococcus Braunii	rr	r+	c	..	..	..	..	r+	rrr	..	rrr	rrr	rrr	rrr	rrr
— protuberans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Coelastrum cambricum var. intermedium	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— microporum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— reticulatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Crucigenia quadrata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. minima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— rectangularis	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..

[1] forma with a regularly lobate surface.

(continued).

trophic						Eutrophic																		(Mixotrophic)					
Hampen Sø					Præstesø	Slaaen Sø	Nors Sø						Furesø					Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø			
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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Table II

Species	(Dystrophic)													Oligo-
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø	
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29
Crucigenia tetrapedia	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dictyosphærium Ehrenbergianum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pulchellum	..	..	..	..	..	..	..	..	..	..	..	rr	..	..	..
Elakatothrix gelatinosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr
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Kirchneriella contorta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— lunaris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— obesa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Lagerheimia quadriseta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Micractinium pusillum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Nephrocytium ecdysiscepanum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Oocystis Borgei	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— natans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Marssonii	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	rrr
Oocystis solitaria	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pediastrum alternans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— biradiatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pediastrum Boryanum	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. longicorne	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. perforatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pediastrum angulosum var. araneosum	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
— duplex	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..
— — var. brachylobum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pediastrum duplex var. clathratum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. pulchrum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. reticulatum	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
Pediastrum duplex var. subgranulatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— glanduliferum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Kawraiskyi	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Pediastrum muticum var. longicorne	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— simplex	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Tetras	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

[1] var. pygmæa. [2] f. glabra. [3] f. granulata. [4] var. tetraodon. [5] forma (see *Fig. nostra* 17).

continued).

rophic						Eutrophic																(Mixotrophic)					
Hampen Sø					Præstesø	Slaaen Sø	Nors Sø						Furesø					Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø	
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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Species	(Dystrophic)													Oligo-	
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø	
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29
Quadrigula closterioides	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Scenedesmus arcuatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— armatus	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	..
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— denticulatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— quadricauda	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Scenedesmus serratus	..	..	..	rrr	..	..	..	..	..	..	..	rrr	..	..	..
— spinoso-aculeolatus?	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Selenastrum Bibraianum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Sorastrum americanum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tetraëdron enorme f. minor	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— limneticum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tetraëdron limneticum var. simplex	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— minimum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— trigonum var. gracile	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tetrastrum apiculatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Westella botryoides	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Conjugales (Desmidieae)															
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— crassus	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rr
— triangularis	..	..	..	..	..	..	..	..	..	..	rrr	rr	rrr	rrr	..
Closterium aciculare	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— acutum var. variabile	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Baillyanum var. parvulum	..	..	..	..	..	rrr[1]	..	..	..	..	..	..	..	..	..
— intermedium forma	..	..	r	..	..	..	..	..	..	..	..	..	..	..	..
Closterium Kützingii	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..
— Leibleinii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Pritchardianum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— moniliferum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Closterium Venus f. torta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cosmarium angulosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Botrytis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cosmarium connatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Cucurbita	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..
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trophic							Eutrophic																(Mixotrophic)					
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11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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Species	(Dystrophic)														Oligo-	
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø		
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29	
Cosmarium depressum var. planctonicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
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— humile var. glabrum	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	
Cosmarium hyacinthi	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	
— pachydermum var. ætiopicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— punctulatum var. subpunctulatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Cosmarium pygmæum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— reniforme	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— subarctoum var. latum	..	..	..	..	..	..	..	..	..	..	..	..	..	r	rr	
Cosmarium subcrenatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— subtumidum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— — f. punctata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Cosmarium subtumidum f. parva	..	..	..	..	..	..	..	..	rrr	..	rrr	..	..	..	..	
— tetraophtalmum	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	
— Turpinii var. podolicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Desmidium Swartzii	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	
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Euastrum elegans	..	..	..	..	..	..	..	..	rrr	..	rrr	..	..	..	..	
Euastrum occidentale var. danicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— pinnatum	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	
— verrucosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
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trophic						Eutrophic																		(Mixotrophic)					
Hampen Sø					Præstesø	Slaaen Sø	Nors Sø						Furesø					Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø			
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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Table II

Species	(Dystrophic)														Oligo-
	Lovenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø	
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29
Sphærozosma vertebratum f. quadrata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Spondylosium planum	..	..	..	..	..	..	..	..	..	..	..	..	..	rr	rrr
Spondylosium pulchellum	..	..	..	..	..	..	..	..	rrr	rrr	..	..	..	..	..
Staurastrum alternans	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..
— anatinum	..	..	..	..	..	..	..	..	..	..	..	rrr	rr	rrr	rrr
Staurastrum apiculatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Arctiscon	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— avicula	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum pingue var. tridentatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Brebissonii	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..
— brevispinum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum Bullardii var. alandicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— cuspidatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. canadense	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..
Staurastrum cuspidatum var. acuminatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. maximum	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rr
— denticulatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum dejectum var. inflatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— furcigerum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— gracile	..	..	..	rrr	rrr	..	..	..	rrr	rr	r	..	..	..	..
Staurastrum crenulatum	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	..
— cingulum var. inflatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— cingulum var. obesum f. bibrachiata[1]	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum granulosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— hirsutum	..	..	rrr	..	..	..	..	..	..	..	rrr	..	..	..	..
— — f. minor	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..
Staurastrum inflexum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Iversenii	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	..
— Manfeldtii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum muticum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— oxyacantha	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— paradoxum?	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum pelagicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pendulum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

[1] Syn. Staurastrum Thunmarkii Teiling.

ontinued).

ophic							Eutrophic															(Mixotrophic)					
Hampen Sø					Præstesø	Slaaen Sø	Nors Sø						Furesø					Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø	
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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Table

Species	(Dystrophic)														Olig	
	Løvenholm Langsø			Store Øxsø		Store Gribsø			Madum Sø			Vedsted Sø		Kalgaard Sø		
	22.V.29	9.IX.29	1.VIII.48	10.IV.27	23.V.29	19.IX.26	18.VI.29	17.VIII.46	24.VI.28	23.V.29	24.VI.29	27.VII.26	2.VII.27	17.V.29	23.VI.29	
Staurastrum cingulum var. obesum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Staurastrum Sebaldii var. ornatum f. planctonica	..	..	..	..	..	..	..	..	..	..	..	rr	rr	..	..	
— planctonicum var. bullatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— tetracerum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Staurastrum Smithii var. verrucosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— uniseriatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— — f. bicornis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Staurastrum pingue	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— vestitum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Xanthidium antilopæum	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	rrr	
Xanthidium armatum	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	
— concinnum var. Boldtianum	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	

[1] var. validum.

(continued).

trophic							Eutrophic														(Mixotrophic)					
Hampen Sø						Præstesø	Slaaen Sø	Nors Sø						Furesø			Tissø		Mossø	Salten Langsø	Hostrup Sø				Hulsø	
11.IV.27	15.VIII.27	17.V.29	23.VI.29	23.IX.29	28.VI.30	4.IX.29	18.VII.25	13.VI.27	13.V.29	31.VIII.29	22.II.30	18.VIII.39	26.IX.26	7.V.31	7.VIII.32	21.VIII.43	1.IX.46	10.VIII.27	13.VII.29	18.VIII.29	19.VIII.29	23.VI.25	24.VII.26	5.VII.27	21.V.29	14.VI.28	8.VIII.46
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Table I. The phytoplankton quotients of 16 Danish lakes.

( ) round the figures for the calcium content denote that they are calculated from alkalinity (Boisen Bennike 1943). ( ) round the total number of species, the dominants and the quotients mean that only nannoplankton is at hand and that the material is moreover inconsiderable. [ ] round the dominant indicate that it is not very common in the sample.

Localities	Type	Substratum	Dates	pH	Content of Kalcium, mg CaO per l.	Consumption of $KMnO_4$, mg per l.	Phosphate mg P per l.	Ammonia mg N per l.	Nitrate mg N per l.	Total number of species	Phytoplankton association (dominants)	Frequency, per ml	Myxophyceæ / Desmidieæ	Chlorococcales / Desmidieæ	Centrales / Pennales	Euglenineæ / Myxophyceæ + Chlorococcales	*The Compound Quotient* = (Myx. + Chlor. + Centr. + Eugl.) / Desmidieæ	References
Løvenholm Langsø (Djursland)	oligotrophic (dystrophic phase)	stratified sand	11.IV.27	4.0	3	..	..	..	..	..	..	..	..	..	..	..	..	J. Iversen 1929, p. 307. G. Nygaard 1938, p. 685. Boisen Bennike 1943, p. 20.
			22.V.29	..	..	..	..	..	..	5	[Ma ca]	..	0/0	2/0	0/0	0/0 = 0	2/0	
			9.IX.29	4.1	..	..	0.03	0.5	0.025	7	Ma ca	..	1/0	2/0	0/0	0/3 = 0	3/0	
			27.VII.40	4.0	(7)	537!	..	..	..	..	..	..	..	..	..	..	..	
			1.VIII.48	4.1	..	..	..	..	..	7	Bo Br	..	0/3 = 0	1/3 = 0.3	0/0	0/1 = 0	1/3 = 0.3	
Store Øxsø (North Jutland)	oligotrophic (dystrophic phase)	stratified sand	10.IV.27	4.2	..	..	..	..	..	8	[As fo]	..	..	..	?1/3 = 0.3	..	..	J. Iversen 1929, p. 309. G. Nygaard 1938, p. 686. Boisen Bennike 1943, p. 20.
			18.VII.27	4.2	3	..	..	..	..	..	..	..	..	..	..	..	..	
			23.V.29	..	..	..	..	..	..	7	As fo	..	0/2 = 0	0/2 = 0	0/3 = 0	0/0	0/2 = 0	
			4.VII.40	4.0	(1)	99	..	..	..	..	..	..	..	..	..	..	..	
Store Gribsø (North Seeland)	oligotrophic (approximately dystrophic phase)	stratified sand	19.IX.26	5.4	..	..	..	..	..	6	[Per Wi]	..	0/1 = 0	0/1 = 0	0/2 = 0	0/0	0/1 = 0	Poulsen 1928: 15 mg CaO per l; pH 5.5—6.5. G. Nygaard 1938, p. 686. Boisen Bennike 1943, p. 20; Cl. Petersen: 12 mg CaO per l, pH 4.5—6.0, 33—63 mg $KMnO_4$ per l; 1943, p. 56.
			18.VI.29	4.7	..	..	0	..	0	5	Ma ca	..	0/1 = 0	0/1 = 0	0/0	0/0	0/1 = 0	
			10.II.31	4.3	..	..	..	..	..	..	..	..	..	..	..	..	..	
			15.VI.40	5.1	(6)	49	..	..	..	..	..	..	..	..	..	..	..	
			17.V.41	5.9	(4)	52	..	..	..	..	..	..	..	..	..	..	..	
			4.VIII.41	5.8	(4)	48	..	..	..	..	..	..	..	..	..	..	..	
			17.VIII.46	4.3	..	..	..	..	..	7	Per Wi	0.23 Per Wi	0/0	1/0	0/1 = 0	0/1 = 0	1/0	
Madum Sø (North Jutland)	oligotrophic (acidotrophic phase)	stratified sand	14.VII.26	4.5—4.8	3—3.5	4	..	..	..	..	..	..	..	..	..	..	..	Transparency > 8 m. J. Iversen 1929, p. 309. G. Nygaard 1938, p. 685. Boisen Bennike 1943, p. 20.
			18.VI.27															
			24.VI.28	..	..	..	..	..	..	12	Din cy pa	..	0/8 = 0	1/8 = 0.1	0/1 = 0	0/1 = 0	1/8 = 0.1	
			23.V.29	..	..	..	..	..	..	6	Ura am	0.48 colonies	0/2 = 0	0/2 = 0	0/0	0/0	0/2 = 0	
			24.VI.29	4.8	..	..	0	0	0	23	Din cy pa	..	0/15 = 0	2/15 = 0.1	0/2 = 0	0/2 = 0	2/15 = 0.1	
			9.IX.29	4.6	..	..	0	0	0	..	..	..	..	..	..	..	..	
			5.II.30	5.1	4	6.6	0	0	0.04	..	..	..	..	..	..	..	..	
			6.III.31	4.9	2.4	6.3	0	0.15	0.11	..	..	..	..	..	..	..	..	
			4.VII.40	4.8	(1)	24!	..	..	..	..	..	..	..	..	..	..	..	
Hampen Sø (Central Jutland)	(approximately) oligotrophic	stratified sand	11.IV.27	6.3	..	..	..	..	..	13	Ura am	..	..	..	0/2 = 0	..	..	J. Iversen 1929, p. 286 and 314. G. Nygaard 1938, p. 685. Boisen Bennike 1943, p. 20.
			15.VIII.27	5.4—8.5	6—6.5	..	..	..	..	27	Ta fe	..	3/13 = 0.2	3/13 = 0.2	0/1 = 0	0/6 = 0	6/13 = 0.5	
			17.V.29	..	..	..	..	..	..	20	Per bi + Ta fe	..	2/5 = 0.4	0/5 = 0	0/2 = 0	0/2 = 0	2/5 = 0.4	
			23.VI.29	6.9	..	..	0	0.05	0.01	25	Ura am	..	3/10 = 0.3	2/10 = 0.2	0/2 = 0	0/5 = 0	5/10 = 0.5	
			23.IX.29	7.2	..	..	0 m: 0 10 m: 0	0 m: 0.1 10 m: 0.08	0 m: 0 10 m: 0	33	Ta fe + Ana Ha	1.5 Ta-colonies 1.2 Ana-trich.	4/13 = 0.3	5/13 = 0.4	0/2 = 0	0/9 = 0	9/13 = 0.7	
			23.II.31	..	4	17	0.005	0.05	0.17	..	..	..	..	..	..	..	..	
			8.VII.40	6.7	(9)	21	..	..	..	..	..	..	..	..	..	..	..	
Vedsted Sø (North Sleswick)	approximately oligotrophic	stratified sand	27.VII.26	5.7	..	(oligo-humic)	..	..	..	25	[Ce hi]	..	2/9 = 0.2	6/9 = 0.7	0/1 = 0	1/8 = 0.1	9/9 = 1	J. Iversen 1929, p. 312. G. Nygaard 1938, p. 687.
			2.VII.27	6.0	..		..	..	..	12	Ce hi	..	0/6 = 0	3/6 = 0.5	0/0	0/3 = 0	3/6 = 0.5	
Kalgaard Sø (Central Jutland)	approximately oligotrophic	stratified sand	17.V.29	..	..	(oligo-humic)	..	..	..	21	Ta fe	..	1/8 = 0.1	1/8 = 0.1	0/3 = 0	0/2 = 0	2/8 = 0.25	G. Nygaard 1938, p. 685.
			23.VI.29	6.9	..		0	0	0	22	Ura am	..	2/6 = 0.3	3/6 = 0.5	0/2 = 0	1/5 = 0.2	6/6 = 1	
Præstesø (S.W. Jutland)	inter-mediate	dune-sand	28.VI.30	7.1	..	(rather oligohumic)	..	..	..	51	Ana fl	..	8/17 = 0.5	11/17 = 0.65	0/2 = 0	2/19 = 0.1	21/17 = 1.2	G. Nygaard 1938, p. 681. Boisen Bennike 1943, p. 34.
			18.VII.40	> 9.0	(12)	37	..	..	..	..	..	..	..	..	..	..	..	
Slaaen Sø (Central Jutland)	inter-mediate	stratified sand	4.IX.29	8.0	..	(oligohumic)	0 m: 0.07 10 m: 0.12	0 m: 0.05 10 m: 0.33	0 m: 0 10 m: 0.01	40	Ce hi	..	1/11 = 0.1	2/11 = 0.2	6/8 = 0.75	3/3 = 1	12/11 = 1.1	Transparency 8 m. G. Nygaard 1938, p. 686.
Nors Sø (Thy)	slightly eutrophic	Cretaceous, stratified sand and dune-sand	18.VII.25	..	..	..	..	..	..	51	Ana ci + Mio fl	..	12/12 = 1	13/12 = 1.1	2/4 = 0.5	0/25 = 0	27/12 = 2.25	J. Iversen 1929, p. 322. G. Nygaard 1938, p. 685. Boisen Bennike 1943, p. 20.
			13.VI.27	8.3	52	(oligohumic)	..	..	..	43	Ana fl	..	10/10 = 1	9/10 = 0.9	3/4 = 0.75	0/19 = 0	22/10 = 2.2	
			13.V.29	..	..	..	..	..	..	41	Din di	..	8/8 = 1	6/8 = 0.75	2/10 = 0.2	0/14 = 0	16/8 = 2	
			31.VIII.29	8.2	..	..	0	0.05	0	(20)	(Cyc Kü ra)	..	(4/5 = 0.8)	(4/5 = 0.8)	(2/2 = 1)	(1/8 = 0.1)	(11/5 = 2.2)	
			22.II.30	8.0	43.1	(oligohumic)	0	0	0.07	(7)	(As fo)	..	..	..	(2/2 = 1)	..	..	
			18.VIII.39	..	..	..	..	..	..	44	Ana fl + Mio fl	..	10/12 = 0.8	8/12 = 0.7	3/2 = 1.5	3/16 = 0.2	24/12 = 2	
			14.VII.40	8.3	(48)	22	..	..	..	..	..	..	..	..	..	..	..	
Furesø (North Seeland)	moderately eutrophic	moraine clay	26.IX.26	8.2	..	..	..	..	..	18	Frg cr	..	5/0	0/0	5/1 = 1	0/5 = 0	10/0	Brønsted and Wesenberg-Lund 1912: 54.5—65.4 mg CaO per l. G. Nygaard 1938, p. 684. Boisen Bennike 1943, p. 21. Sigurd Olsen 1944: pH 7.5—8.6.
			10.III.31	7.8	62	14	0.015	0.1	0.18	..	Ste Ha	..	..	..	..	..	..	
			7.V.31	..	..	..	..	..	..	24	As fo	..	0/0	0/0	6/8 = 0.75	1/0	7/0	
			7.VIII.32	..	..	..	..	..	..	36	Ana fl + As fo	..	10/5 = 2	7/5 = 1.4	5/3 = 1.7	0/17 = 0	22/5 = 4.4	
			3.VI.40	8.0	(68)	20	..	..	..	..	..	..	..	..	..	..	..	
			31.V.41	..	(67)	23	..	..	..	..	..	..	..	..	..	..	..	
			21.VIII.43	..	..	..	..	..	..	76	Mel gr an	..	17/12 = 1.4	17/12 = 1.4	8/11 = 0.7	0/34 = 0	42/12 = 3.5	
			1.IX.46	8.4	..	..	..	..	..	54	Ce hi	15 Ce hi	15/8 = 1.9	10/8 = 1.25	5/5 = 0.6	0/25 = 0	28/8 = 3.5	
Mossø (Central Jutland)	eutrophic	stratified sand	18.VIII.29	0 m: 8.0 15 m: 7.0	..	..	0 m: 0.005 15 m: 0.005	0 m: 0.2 15 m: 0.25	0 m: 0 15 m: 0.01	49	Api fl + Mio ær	..	12/6 = 2	16/6 = 2.7	7/5 = 1.4	0/25 = 0	35/6 = 5.8	Brønsted and Wesenberg-Lund 1912: 60 mg CaO per l. G. Nygaard 1938, p. 685. Boisen Bennike 1943, p. 21.
			24.VII.40	9.0	(59)	32	..	..	..	..	..	..	..	..	..	..	..	
Tissø (West Seeland)	eutrophic	moraine clay	10.VIII.27	0 m: 8.8 11 m: 8.4	125.6	..	..	..	..	58	Ly li	195 Ly-trich.	16/8 = 2	17/8 = 2.1	6/2 = 3	1/33 = 0	40/8 = 5	G. Nygaard 1938, p. 687.
			13.VII.29	8.4	..	..	0	0	0 m: 0 bottom: 0.35	40	As fo + Mel gr	..	7/6 = 1.2	14/6 = 2.3	3/4 = 1.25	0/20 = 0	26/6 = 4.3	
			19.II.31	..	107.8	48	0.02	0.15	1.5	..	..	..	..	..	..	..	..	
Salten Langsø (Central Jutland)	eutrophic	stratified sand	19.VIII.29	8.4	..	..	0.01	..	0.01	46	Ste As + Mio ær ma	..	12/4 = 3	14/4 = 3.5	9/4 = 2.25	0/22 = 0	35/4 = 8.75	Brønsted and Wesenberg-Lund 1912: 36.5 mg CaO per l. G. Nygaard 1938, p. 686.
Hostrup Sø (North Sleswick)	eutrophic (approximately mixotrophic phase)	stratified sand and gravel	23.VI.25	..	..	..	..	..	..	47	Api fl	..	16/6 = 2.7	13/6 = 2.2	2/4 = 0.5	1/29 = 0	32/6 = 5.3	J. Iversen 1929, p. 315. G. Nygaard 1938, p. 685.
			24.VII.26	7.3	..	50	..	..	..	37	Frg cr	..	6/7 = 0.9	16/7 = 2.3	1/2 = 0.5	0/22 = 0	23/7 = 3.3	
			5.VII.27	6.4—8.8	12	..	..	..	..	44	Coo Nä	..	11/6 = 1.8	15/6 = 2.5	1/5 = 0.2	0/26 = 0	27/6 = 4.5	
			21.V.29	..	..	..	..	..	..	31	Trb tae	..	7/4 = 1.75	10/4 = 2.5	1/4 = 0.25	0/17 = 0	18/4 = 4.5	
Hulsø (North Seeland)	eutrophic (mixotrophic phase)	moraine clay	14.VI.28	..	..	53	..	..	..	41	Din so am	..	3/1 = 3	9/1 = 9	9/6 = 1.5	4/12 = 0.3	25/1 = 25	J. Iversen 1929, p. 316. G. Nygaard 1938, p. 686. Boisen Bennike 1943, p. 35.
			8.VIII.46	..	..	..	..	..	..	57	Rhi lo	..	10/5 = 2	11/5 = 2.2	7/4 = 1.75	7/21 = 0.3	35/5 = 7	
			10.VI.40	7.7	(56)	69	..	..	..	..	..	..	..	..	..	..	..	
			2.VII.40	7.6	(81)	74	..	..	..	..	..	..	..	..	..	..	..	

Table III. The phytoplankton quotients of 20 Danish ponds.

Localities	Type	Substratum	Dates	pH	CaO mg per l	Consumption of $KMnO_4$ mg per l	PO_4-P mg per l	NH_3-N mg per l	NO_3-N mg per l	Sort of plankton	Total number of species	Phytoplankton assoc. (dominants)	Frequency individuals per ml	plankton quantity mg per l	average quantity of plankton for one year	Myxophyceæ / Desmidieæ	Chlorococcales / Desmidieæ	Centrales / Pennales	Euglinieæ / Myxophyceæ + Chlorococcales	*The Compound Quotient* = Myx. + Chlor. + Centr. + Eugl. / Desmidieæ	Contamination	Other plants
Bøndernes Mose I	oligotrophic (dystrophic phase)	stratified sand	28.VI.1929	4.2 yearly variation 3.7—4.3	5 yearly variation 0.3—5.9	yearly variation 136—205	yearly variation 0	yearly variation 0.75—1.5	yearly variation 0	netplankton	15	Crym ov cu		yearly variation 0.4—15.4	5.3 mg/l	$^0/_6 = 0$	$^1/_6 = 0.2$	$^0/_2 = 0$	$^1/_1 = 1$	$^2/_6 = 0.3$	naturally contaminated (by rotten leaves?); smell of H_2S, when icebound	Sphagnum cuspidatum
										nannoplankton	8	Crym ov cu	ca. 7500 Crym	3.6		$^0/_4 = 0$	$^1/_4 = 0.25$	$^0/_1 = 0$	$^0/_1 = 0$	$^1/_4 = 0.25$		
Bøndernes Mose II	oligotrophic (dystrophic phase)	stratified sand	22.VIII.1929	4.4 yearly variation 4.1—4.6	yearly variation 0.2—2.9	202 yearly variation 153—202	0 yearly variation 0	0.9 yearly variation 0.9—2.0	0 yearly variation 0	nannoplankton	19	Crym ov cu		2.7 yearly variation 0.4—4.9	2.2 mg/l	$^1/_8 = 0.1$	$^2/_8 = 0.25$	$^0/_1 = 0$	$^2/_3 = 0.7$	$^5/_8 = 0.6$		Sphagnum cuspidatum
			16.VI.1930	4.2		194				nannoplankton	19	Crym ov cu		3.5		$^2/_8 = 0.25$	$^1/_8 = 0.1$	$^0/_1 = 0$	$^2/_3 = 0.7$	$^5/_8 = 0.6$		
Store Jenshøj turf pit	oligotrophic (dystrophic phase)	dune sand	25.VI.1930	4.0		polyhumic				netplankton	14	Aso su				$^0/_{10} = 0$	$^1/_{10} = 0.1$	$^0/_0$	$^0/_1 = 0$	$^1/_{10} = 0.1$	÷	Batrachospermum vagum, Sphagnum cuspidatum
turf pit NE of Skaansø	oligotrophic (dystrophic phase)	fluvioglacial sand	4.VII.1938	4.3		polyhumic				netplankton	18	Sta br				$^0/_{10} = 0$	$^3/_{10} = 0.3$	$^0/_0$	$^0/_2 = 0$	$^3/_{10} = 0.3$	÷	Nearly overgrown with Sphagnum cuspidatum
Holmsø	oligotrophic (azidotrophic phase)	dune sand	26.VI.1930	4.6		oligohumic				nannoplankton	15	Per Wi				$^1/_{10} = 0.1$	$^3/_{10} = 0.3$	$^0/_0$	$^0/_4 = 0$	$^4/_{10} = 0.4$	÷	Lobelia Dortmanna very common
Skaansø	oligotrophic (azidotrophic phase)	fluvioglacial sand	4.VII.1938	5.6		oligohumic				netplankton	21	Din cy pa				$^1/_{10} = 0.1$	$^3/_{10} = 0.3$	$^0/_1 = 0$	$^0/_4 = 0$	$^4/_{10} = 0.4$	÷	
Mørkso	oligotrophic (azidotrophic phase)	fluvioglacial sand	6.VII.1938	4.9		oligohumic				netplankton	9	Per Wi				$^1/_4 = 0.25$	$^1/_4 = 0.25$	$^0/_2 = 0$	$^0/_2 = 0$	$^2/_4 = 0.5$	÷	Lobelia Dortmanna very common. Nuphar luteum
Klitsø at Højsande	oligotrophic (azidotrophic phase)	dune sand	30.VI.1925			oligohumic				netplankton	42	Tsp Ny				$^6/_{18} = 0.3$	$^8/_{18} = 0.45$	$^0/_1 = 0$	$^1/_{14} = 0.1$	$^{15}/_{18} = 0.8$	÷	Lobelia Dortmanna and Littorella uniflora very common
Lille Gribsø	approximately oligotrophic (intermediate)	stratified sand	28.VI.1929	4.9	yearly variation 1.1—4	yearly variation 33—47	yearly variation 0—0.02	yearly variation 0.05—0.2	yearly variation 0—0.02	netplankton	18	Ura am		yearly variation 2.0—9.6	5.1 mg/l	$^2/_7 = 0.3$	$^2/_5 = 0.3$	$^0/_1 = 0$	$^0/_4 = 0$	$^4/_7 = 0.6$	÷	Nuphar luteum and Potamogeton natans
			28.VI.1929	4.9 yearly variation 4.8—5.0?						nannoplankton	17	Se ca		2.9		$^2/_4 = 0.5$	$^5/_4 = 1.25$	$^0/_1 = 0$	$^0/_7 = 0$	$^7/_4 = 1.75$		
			28.VIII.1929							net + nannopl.	22	Cos as st				$^1/_9 = 0.1$	$^4/_9 = 0.45$	$^0/_1 = 0$	$^0/_5 = 0$	$^5/_9 = 0.55$		
Blankeborg I	slightly eutrophic (mixotrophic phase)	moraine clay	16.VIII.1925		according to 3 analyses 82—91	according to 4 analyses 49—81	according to 3 analyses 0—0.005	values between 0.2 and 0.35 observed	values between 0 and 0.17 observed	netplankton	38	Per Vo		yearly variation 1.19—12.85.	4.24 mg/l (2.VI.1927—20.V.1928).	$^3/_9 = 0.3$	$^9/_9 = 1$	$^2/_3 = 0.7$	$^2/_{12} = 0.2$	$^{16}/_9 = 1.8$	no appreciable contamination	Batrachium circinnatum, Polygonum amphibium, Chara fragilis
			15.VIII.1926	7.7						netplankton	45	Ce hi				$^5/_{10} = 0.5$	$^{11}/_{10} = 1.1$	$^1/_5 = 0.2$	$^5/_{16} = 0.3$	$^{22}/_{10} = 2.2$		
			17.VIII.1927	7.6						netplankton	60	Ce hi				$^3/_{12} = 0.25$	$^{15}/_{12} = 1.25$	$^2/_8 = 0.25$	$^6/_{18} = 0.3$	$^{26}/_{12} = 2.2$		
			17.VIII.1927	7.6 variation for 2 years 7.1—8.3						nannoplankton	55	Cos pu El ge bi		yearly variation 1.82—5.61.	3.51 mg/l (6.VI.1928—21.V.1929).	$^1/_9 = 0.1$	$^{15}/_9 = 1.7$	$^2/_9 = 0.2$	$^5/_{16} = 0.3$	$^{23}/_9 = 2.55$		
			18.VIII.1928	8.0						netplankton	51	Din di				$^4/_{14} = 0.3$	$^9/_{14} = 0.6$	$^2/_6 = 0.3$	$^5/_{13} = 0.4$	$^{20}/_{14} = 1.4$		
			18.VIII.1928	8.0					0	nannoplankton	71	green alga		yearly variation	4.99 mg/l (2.VI.1929—23.V.1930).	$^4/_{13} = 0.3$	$^{23}/_{13} = 1.8$	$^2/_8 = 0.25$	$^7/_{27} = 0.25$	$^{36}/_{13} = 2.8$		
			6.VIII.1929	8.2						nannoplankton	44	Din di		3.70 12.77	2.63—12.77.	$^6/_9 = 0.7$	$^{11}/_9 = 1.2$	$^1/_7 = 0.1$	$^2/_{17} = 0.1$	$^{20}/_9 = 2.2$		
			10.VI.1930							nannoplankton	61	Chrysophyceæ		5.24		$^5/_9 = 0.55$	$^{17}/_9 = 1.9$	$^4/_7 = 0.6$	$^6/_{22} = 0.3$	$^{32}/_9 = 3.55$		
Blankeborg II	eutrophic (mixotrophic phase)	moraine clay	15.VIII.1926	8.1						netplankton	28	Pa mo		yearly variation	5.49 mg/l (17.VII.1928—17.VI.1929), 10.73 mg/l (1.VII.1929—10.VI.1930).	$^2/_4 = 0.5$	$^7/_4 = 1.75$	$^2/_5 = 0.4$	$^1/_9 = 0.1$	$^{12}/_4 = 3$	soiled by ducks	Lemna minor, Potamogeton natans, Polygonum amphibium
			25.VII.1928	8.3				0.2	0.01	netplankton	17	Pa mo + Ste Ha				$^3/_1 = 3$	$^6/_1 = 6$	$^1/_2 = 0.5$	$^0/_9 = 0$	$^{10}/_1 = 10$		
			25.VII.1928	8.3 yearly variation 7.6—8.5				values between 0.2 and 0.9 observed	values between 0 and 1.3 observed	nannoplankton	24	Dic pu		4.41	1.58—18.79.	$^2/_0$	$^{12}/_0$	$^1/_1 = 1$	$^1/_{14} = 0.1$	$^{16}/_0$		
			28.VIII.1928	8.1						netplankton	20	Per pa Ste Ha		yearly variation		$^3/_1 = 3$	$^6/_1 = 6$	$^1/_1 = 1$	$^0/_9 = 0$	$^{10}/_1 = 10$		
			28.VIII.1928	8.1				0.3	0.025	nannoplankton	21	Ste Ha		2.51	2.51—27.55.	$^3/_1 = 3$	$^{11}/_1 = 11$	$^1/_1 = 1$	$^0/_{14} = 0$	$^{15}/_1 = 15$		
			10.VI.1930							nannoplankton	31	Ste Ha		5.92		$^3/_0$	$^{15}/_0$	$^1/_1 = 1$	$^1/_{18} = 0.05$	$^{20}/_0$		
Sortedam II	eutrophic (mixotrophic phase)	moraine clay	8.VI.1929		yearly variation 14.6—19.3	yearly variation 75—104	yearly variation 0—0.095	yearly variation 0.15—1.0	yearly variation 0—3	netplankton	49	Ce hi		yearly variation	5.9 mg/l	$^8/_{10} = 0.8$	$^{16}/_{10} = 1.6$	$^2/_4 = 0.5$	$^2/_{14} = 0.1$	$^{28}/_{10} = 2.8$	soiled by ducks	Lemna minor, L. trisulca, L. polyrrhiza, Pot. natans, Pot. obtusifolius, Cer. demersum, Hydrocharis morsus ranæ
			1.VII.1929	7.2	37.5 yearly variation 30.1—45.2					nannoplankton	43	Ce hi	95 Ce hi	3.7		$^1/_4 = 0.25$	$^{18}/_4 = 4.5$	$^1/_2 = 0.5$	$^{10}/_{19} = 0.5$	$^{30}/_4 = 7.5$		
			23.IX.1929	7.1						nannoplankton	41	Crym ov		4.1	0.4—18.2	$^2/_2 = 0.7$	$^{15}/_2 = 5$	$^2/_1 = 2$	$^8/_{17} = 0.5$	$^{27}/_3 = 9$		
Gadevang Mose	eutrophic (mixotrophic phase)	stratified sand	6.VII.1929		yearly variation 14.6—19.3	yearly variation 66—89	yearly variation 0.03—0.35	yearly variation 0.2—1.0	yearly variation 0—0.17	nannoplankton	39	Din di		2.4	yearly variation 0.6—11.2	3 mg/l	$^3/_1 = 3$	$^{16}/_1 = 16$	$^3/_2 = 1.5$	$^0/_{19} = 0$	$^{22}/_1 = 22$	contaminated by waste-water	Lemna minor, Nymphæa alba, Potam. natans, Riccia fluitans, Calla palustris
			10.VII.1929	6.3	6.3—8.6					netplankton	21	Din di Syn sp				$^2/_1 = 2$	$^8/_1 = 8$	$^1/_1 = 1$	$^0/_{10} = 0$	$^{11}/_1 = 11$		
Vandingsdam	eutrophic (mixotrophic phase)	stratified sand	28.V.1929	7.7	yearly variation 14.3—27	yearly variation 51—92	yearly variation 0—0.075	yearly variation 0.08—1.0	yearly variation 0—0.55	netplankton	30	Chla Re		yearly variation	24.6 mg/l	$^1/_1 = 1$	$^{14}/_1 = 14$	$^2/_1 = 2$	$^6/_{15} = 0.4$	$^{23}/_1 = 23$	soiled by cattle and ducks	No limnophytes but Cladophora on stones
			28.V.1929	7.7						nannoplankton	41	Dic pu		18.4		$^2/_1 = 2$	$^{23}/_1 = 25$	$^2/_0$	$^4/_{27} = 0.15$	$^{33}/_1 = 33$		
			24.VIII.1929	7.0	87					nannoplankton	35	Tee mi		59.8	0.9—92.4	$^3/_1 = 3$	$^{15}/_1 = 15$	$^2/_1 = 2$	$^6/_{18} = 0.3$	$^{26}/_1 = 26$		
Badstue-Ødam	eutrophic	moraine clay and stratified sand	6.VI.1929	7.6 yearly variation 7.4—9.0	yearly variation 68.4—82.2	54 yearly variation 40—57	yearly variation 0—0.035	yearly variation 0.05—0.3	yearly variation 0—3.0	netplankton	36	Mel gr an		yearly variation 1.6—11	5.5 mg/l[1]	$^7/_2 = 3.5$	$^7/_2 = 3.5$	$^5/_5 = 1$	$^1/_{14} = 0.1$	$^{20}/_2 = 10$	contaminated	Batrachium circinnatum, Nuphar luteum
			23.VIII.1929	8.5						nannoplankton	61	Frg cr		8.8		$^9/_3 = 3$	$^{18}/_3 = 6$	$^4/_6 = 0.7$	$^7/_{27} = 0.25$	$^{38}/_3 = 12.7$		
Frederiksborg Slotssø	eutrophic	moraine clay and stratified sand	11.VI.1929	9.2 yearly variation 7.6—9.7	yearly variation 64.4—72.2	yearly variation 39—53	yearly variation 0.015—1.5	yearly variation 0—1.25	yearly variation 0—1.1	netplankton	35	Ana in		yearly variation 1—21.4	10.6 mg/l[1]	$^{13}/_3 = 4.3$	$^6/_5 = 2$	$^5/_2 = 2.5$	$^0/_{19} = 0$	$^{24}/_3 = 8$	contaminated by waste-water	Potamogeton crispus, Myrioph. spicatum, Polygonum amphibium
			11.VI.1929	9.2						nannoplankton	49	Sce arm		11.2		$^{11}/_4 = 2.75$	$^{17}/_4 = 4.25$	$^7/_3 = 2.3$	$^1/_{28} = 0$	$^{36}/_4 = 9$		
			23.IX.1929							nannoplankton	54	Os Ag	12400 Os Ag			$^{16}/_4 = 4$	$^{15}/_4 = 3.75$	$^6/_1 = 6$	$^3/_{31} = 0.1$	$^{40}/_4 = 10$		
Jægerbakke Dam	eutrophic	stratified sand	12.VI.1929	9.4 yearly variation 6.6—9.8	yearly variation 7.3—11.2	yearly variation 27—49	yearly variation 0—0.015	yearly variation 0—0.75	yearly variation 0—0.01	net + nannopl.	42	Mio mi		22.9	yearly variation 3.9—93.2	44.2 mg/l	$^7/_7 = 1$	$^{21}/_3 = 3$	$^0/_0$	$^2/_{28} = 0.1$	$^{30}/_7 = 4.3$	contaminated	Helodea canadensis, Polygonum amphibium
			17.IX.1929	8.9						nannoplankton	46	Mio ho				$^8/_3 = 2.7$	$^{17}/_3 = 5.7$	$^0/_0$	$^6/_{25} = 0.25$	$^{31}/_3 = 10.3$		
			16.V.1930							nannoplankton	53					$^5/_2 = 2.5$	$^{28}/_2 = 14$	$^0/_0$	$^2/_{33} = 0.1$	$^{35}/_2 = 17.5$		
Flødegaardens Dam	eutrophic	moraine clay	1.VII.1926	8.2						nannoplankton	44	Sce ec		yearly variation 3.1—81.4.	22.22 mg/l (2.VI.1927—21.V.1928). 62.96 mg/l (5.VI.1928—22.V.1929).	$^4/_4 = 4$	$^{21}/_1 = 21$	$^2/_3 = 0.7$	$^7/_{25} = 0.3$	$^{34}/_1 = 34$	soiled by cattle	Potamogeton crispus, Pot. natans, Polygonum amphibium, Batrachium circinnatum. Stratiotes aloides (♀) invaded the pond in the period of 1940—43
			28.VII.1926	8.2						netplankton	42	Din di				$^5/_1 = 5$	$^{19}/_1 = 19$		$^2/_5 = 0.4$	$^{29}/_1 = 29$		
			20.VII.1927		according to 2 analyses 82—90	47 on November 6th, 1929		values between 0.3 and 1.5 observed	values between 0 and 0.35 observed	nannoplankton	58	Mio ho		31.5	yearly variation 8.6—173.8.	$^3/_1 = 3$	$^{31}/_1 = 31$	$^2/_2 = 1$	$^7/_{24} = 0.2$	$^{43}/_1 = 43$		
			7.IX.1928	8.1 variation for 2 years 7.6—9.2						nannoplankton	50	Mio ho		108.4		$^3/_0$	$^{29}/_0$	$^3/_2 = 1.5$	$^6/_{32} = 0.2$	$^{41}/_0$		
			19.VIII.1929				0.25 on July 31st, 1929			nannoplankton	51	Mio ho		68.4	yearly variation 47.3 mg/l (2.VI.1929—23.V.1930).	$^4/_1 = 4$	$^{31}/_1 = 31$	$^2/_2 = 1$	$^4/_{35} = 0.1$	$^{41}/_1 = 41$		
			10.VI.1930							nannoplankton	67	green algæ		33.9	6.1—137.3.	$^4/_2 = 2$	$^{33}/_2 = 16.5$	$^3/_2 = 1.5$	$^6/_{37} = 0.2$	$^{46}/_2 = 23$		
			3.VIII.1939							nannoplankton	45	Dic pu		small quantity		$^2/_4 = 0.5$	$^{21}/_4 = 5.25$	$^2/_4 = 0.5$	$^{10}/_{23} = 0.4$	$^{33}/_4 = 8.75$		
Lynge Vandingsdam	eutrophic (approximately saprotrophic phase)	moraine clay	30.VI.1947			paper-filtered water pale green-brownish				nannoplankton	42	Tra vo				$^0/_1 = 0$	$^{12}/_1 = 12$	$^1/_2 = 0.5$	$^{18}/_{12} = 1.5$	$^{31}/_1 = 31$	soiled by cattle	Potamogeton natans
			6.VIII.1947	9.0						nannoplankton	33	Eug ob	43000 Eugl.[2])	> 500		$^0/_0$	$^7/_0$	$^1/_2 = 0.5$	$^{21}/_7 = 3$			
Bistrup Dam	eutrophic (saprotrophic phase)	moraine clay	12.VIII.1929	7.8	118.7	water pale green-brownish	6.0	12.0	0.25	nannoplankton	5	Bacteria				$^0/_0$	$^1/_0$	$^0/_0$	$^3/_1 = 3$	$^4/_0$	strongly soiled by inflow from a stable	No limnophytes
			24.X.1929							nannoplankton	10	Bacteria	8 Eug ph 6 Phu pl			$^1/_0$	$^0/_0$	$^0/_0$	$^8/_1 = 8$	$^9/_0$		
			16.XI.1929							nannoplankton	10	Bacteria	60 Eug ph 9 Phu pl			$^0/_0$	$^0/_0$	$^0/_0$	$^8/_0$	$^8/_0$		

[1] The average value is in reality a little larger the samples from may and one from april not being counted.
[2] 23300 Euglena oblonga, 9900 E. gracilis, 7600 E. granulata, 1700 E. acus and 300 E. oxyuris per ml.

TABLE IV

Table IV. Composition of the phyto-

Species	(Dystrophic)				Oligotrophic							Blankeborg I							
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø									
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30
Bacteria																				
Lampropedia hyalina	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
"Chlorobacteria"	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Myxophyceae																				
Anabaena affinis var. intermedia f. tenuis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— augustumalis var. marchica	..	rrr	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— sigmoidea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Anabaena flos aquae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— heterospora	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— incrassata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Anabaena planctonica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— spiroides var. crassa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— tenericaulis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Anabaena Viguieri var. danica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— spp. (sterile)	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	rrr	..	rrr	..	..
Aphanizomenon flos aquae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Aphanocapsa elachista	..	..	..	..	..	..	..	..	rr	..	..	..	..	..	..	..	..	..	..	..
— — var. conferta	..	..	rrr	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..
Arthrospira Jenneri	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chroococcus limneticus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr
— — var. carneus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. elegans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chroococcus turgidus	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
Coelosphaerium dubium	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..
— Kützingianum	..	..	..	..	..	..	..	..	rrr	..	..	..	..	rrr	..	..	..	rrr	rrr	..
Coelosphaerium Nägelianum	..	..	..	..	..	..	..	..	..	..	..	..	c	+	rr	..	rrr	rrr	+	+ rrr
Eucapsis alpina	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Gloeothece distans	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
Gomphosphaeria aponina	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— lacustris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Lyngbya limnetica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..

[1] When the same date is given twice against the same pond, the left-hand date stands for the nannoplankton

plankton from 20 Danish ponds.[1]

| (Mixotrophic) | | |

Table IV

Species	(Dystrophic)				Oligotrophic																
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø			Blankeborg 1								
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30	
Merismopedia Marssonii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— punctata	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	
— tenuissima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Microcystis elabens	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	
Microcystis flos aquae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Microcystis flos aquae var. major	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— holsatica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	
— minutissima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	r	..	c	rr	rrr	rrr	
Microcystis pulverea	..	..	..	..	..	..	..	..	..	r	rrr	..	..	..	..	..	..	..	..	..	
— — var. racemiformis	..	..	..	..	..	..	..	..	..	rr	rrr	..	..	..	..	..	..	..	..	..	
— robusta?	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	
Microcystis viridis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— aeruginosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— — var. major	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	..	..	rrr	rrr	..	
Oscillatoria limnetica var. acicularis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— Agardhii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— chlorina	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Oscillatoria limnetica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	rrr	
— neglecta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Phormidium mucicola	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Rhabdoderma Gorskii var. spiralis	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	
Trichodesmium lacustre	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Euglenineae																					
Euglena acus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	..	..	
— Ehrenbergii	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	..	..	..	..	
— gracilis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Euglena granulata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— oblonga	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— oxyuris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Euglena phacoides	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— pisciformis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— proxima	rrr	rrr	r	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	rrr	rrr	..	

(continued).

| (Mixotrophic) | | |

Table IV

Species	(Dystrophic)				Oligotrophic							Blankeborg I							
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø									
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30
Euglena rubra?	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— sanguinea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— spirogyra	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Euglena viridis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— sp. (scarlet)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Lepocinclis fusiformis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— ovum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	rrr
— pseudo-texta	..	..	..	..	..	..	..	..	..	..	..	..	rr	rrr	..	..	..	..	..	rrr
Lepocinclis Steinii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Phacus acuminata var. americana	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr
— curvicauda	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	rrr	..	rrr
Phacus caudata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— circulatus	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..
— helikoides	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	rrr	rrr	rrr	rrr	..
Phacus longicauda var. cordata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr
— Manginii var. inflatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— orbicularis	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	rrr	..	..	..
Phacus oscillans	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— platyaulax	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pleuronectes	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Phacus anomala var. pullus gallinae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pyrum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
— suecica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Phacus suecica var. inermis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— torta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	..	..	..
— Zingeri (ovoidea?)	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Phacus aenigmatica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Trachelomonas acuminata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— armata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— crebea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Trachelomonas cylindrica var. decollata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— granulata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— hispida	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

[1] var. coronata.

(continued).

(Mixotrophic)						Eutrophic																								(Saprotrophic)		
Blankeborg II						Sortedam II			Gadevang Mose		Vandingsdam			Badstue-Ødam		Frederiksborg Slotssø			Jægerbakke Dam			Flødegaardens Dam								Lynge Vandingsdam		Bistrup Dam		
15.VIII.26	25.VII.28	25.VI.28	28.VIII.28	28.VIII.28	10.VI.30	8.VI.29	1.VII.29	23.IX.29	6.VII.29	10.VII.29	28.VI.29	28.VI.29	24.VIII.29	6.VI.29	23.VIII.29	11.VI.29	11.VI.29	23.IX.29	12.VI.29	17.IX.29	16.V.30	1.VII.26	28.VII.26	20.VII.27	7.IX.28	19.VIII.29	10.VI.30	3.VIII.39	30.VI. 47	6.VIII.47	12.VIII.29	24.X.29	16.XI.29
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Table IV

| Species | (Dystrophic) | | | | Oligotrophic | | | |

(continued).

(Mixotrophic)						Eutrophic																				(Saprotrophic)		
Blankeborg II						Sortedam II			Gadevang Mose		Vandingsdam			Badstue-Ødam		Frederiksborg Slotssø			Jægerbakke Dam			Flødegaardens Dam							Lynge Vandingsdam		Bistrup Dam		
15.VIII.28	25.VII.28	25.VII.28	28.VIII.28	28.VIII.28	10.VI.30	8.VI.29	1.VII.29	23.IX.29	6.VII.29	10.VII.29	28.VI.29	28.VI.29	24.VIII.29	6.VI.29	23.VIII.29	11.VI.29	11.VI.29	23.IX.29	12.VI.29	17.IX.29	16.V.30	1.VII.26	28.VII.26	20.VII.27	7.IX.28	19.VIII.29	10.VI.30	3.VIII.39	30.VI.47	6.VIII.47	12.VIII.29	24.X.29	16.XI.29
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Table IV

Species	(Dystrophic)				Oligotrophic					Blankeborg 1							
	Bøndernes Mose I	Bøndernes Mose II	Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø								
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28
Chloromonadineae																	
Gonyostomum semen	r	rr	r+	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cryptophyceae																	
Chroomonas acuta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cryptomonas ovata	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	rrr
— — var. curvata	+	cc	cc	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cyanomonas americana	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Bacillariophyceae																	
Asterionella formosa	..	..	..	..	..	..	..	..	..	..	..	..	r	rr	rr	r+	r
Cyclotella comta	..	..	..	..	..	..	..	..	..	..	..	..	rr	rrr	r	rrr	r
— Kützingiana var. parva	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cyclotella Meneghiniana	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	..	rrr
— pseudostelligera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— stelligera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cyclotella stelligera var. subglabra	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cymatopleura elliptica	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	rrr
Diatoma elongatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..
Diatoma vulgare	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Eunotia alpina	rrr	rr	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— formica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Eunotia lunaris var. capitata	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— robusta var. diadema	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..
Fragilaria capucina	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr[2]	..	rrr[2]
Fragilaria construens var. subsalsa	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
— — var. venter	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..
— crotonensis	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	rrr	rrr
Melosira ambigua	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— granulata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — var. angustissima	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— varians	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

Species	Blankeborg 1								
	18.VIII.28	6.VIII.29	10.VI.30						
Chloromonadineae									
Gonyostomum semen	..	..	..						
Cryptophyceae									
Chroomonas acuta	..	..	..						
Cryptomonas ovata	rrr	..	rrr						
— — var. curvata	..	..	..						
Cyanomonas americana	..	..	..						
Bacillariophyceae									
Asterionella formosa	r	rr	rrr						
Cyclotella comta	r	rr	c						
— Kützingiana var. parva	..	..	..						
Cyclotella Meneghiniana	rrr	..	rrr						
— pseudostelligera	..	..	..						
— stelligera	..	..	..						
Cyclotella stelligera var. subglabra	..	..	..						
Cymatopleura elliptica	rrr	..	..						
Diatoma elongatum	..	..	..						
Diatoma vulgare	..	..	..						
Eunotia alpina	..	..	..						
— formica	..	..	..						
Eunotia lunaris var. capitata	..	..	..						
— robusta var. diadema	..	..	..						
Fragilaria capucina	rrr[2]	rrr[2]	rrr[2]						
Fragilaria construens var. subsalsa	rrr	..	..						
— — var. venter	..	..	..						
— crotonensis	rrr	rrr	rrr						
Melosira ambigua	..	..	rrr						
— granulata	..	..	..						
— — var. angustissima	..	..	..						
— varians	..	..	..						

[1] determination not sure. [2] var. mesolepta.

continued).

(Mixotrophic) Eutrophic (Saprotrophic)

Blankeborg II						Sortedam II			Gadevang Mose		Vandingsdam			Badstue-Odam		Frederiksborg Slotssø			Jægerbakke Dam			Flødegaardens Dam							Lynge Vandingsdam		Bistrup Dam		
15.VIII.26	25.VII.28	25.VII.28	28.VIII.28	28.VIII.28	10.VI.30	8.VI.29	1.VII.29	23.IX.29	6.VII.29	10.VII.29	28.VI.29	28.VI.29	24.VIII.29	6.VI.29	23.VIII.29	11.VI.29	11.VI.29	23.IX.29	12.VI.29	17.IX.29	16.V.30	1.VII.26	28.VII.26	20.VII.27	7.IX.28	19.VIII.29	10.VI.30	3.VIII.39	30.VI.47	6.VIII.47	12.VIII.29	24.X.29	16.XI.29
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Table IV

Species	(Dystrophic)					Oligotrophic							Blankeborg I							
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Morksø	Klitsø at Højsande	Lille Gribsø										
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30
Nitzschia acicularis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
— palea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— sigmoidea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Nitzschia vermicularis	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	rrr	rrr	..	rrr	..
Rhizosolenia longiseta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Stephanodiscus Astraea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	rrr
Stephanodiscus dubius	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Hantzschii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Synedra acus var. angustissima	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	r	rrr	rrr	rrr
Synedra capitata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	rrr	rrr	rrr
— ulna	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	..	..	rrr	rrr
Tabellaria binalis	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..
Tabellaria fenestrata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..
— flocculosa	..	..	..	..	..	..	rr	..	..	rrr	rr	rr	..	..	..	..	rrr	..	..	..
Chrysophyceae																				
Chromulina pygmaea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chrysococcus major	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— minutus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Dinobryon bavaricum	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
— cylindricum var. palustre	..	..	..	..	..	..	c	..	..	..	..	..	..	..	..	..	..	..	..	..
— divergens	..	..	..	..	..	..	..	..	..	..	..	..	r+	r	rr	c	rr	cc	ccc	r
Dinobryon divergens var. Schauinnslandii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr
— pediforme	rrr	rrr	rrr	rrr	rrr	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..
— sertularia	..	..	..	..	..	..	..	..	..	..	..	..	rr	rrr	..	r	rr	rr	..	..
Dinobryon sociale	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rr	..	..	..	..	..
— — var. americanum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	+	..	..	..	..
— suecicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Hymenomonas stagnicola	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Mallomonas akrokomos	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— caudata[1]	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— reginae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

[1] *Mallomonas caudata* Krieger (non Iwanoff).

((continued).

| ((Mixotrophic) | | |

Table IV

Species	(Dystrophic)					Oligotrophic							Blankeborg I							
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshoj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Morksø	Klitsø at Højsande	Lille Gribsø										
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30
Mallomonas sphagnicola	..	rrr	r	..	r	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— tonsurata	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	rrr	..	..
— tridentata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Mallomonas sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Synura Petersenii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— sphagnicola	rrr	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Synura spinosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Uroglena volvox	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— americana	..	..	..	..	..	..	..	..	r +	c +	+	..	..	..	..	..	..	..	..	..
Undeterm. Chrysophyceae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	cc
Volvocales, Ulothricales, Oedogoniales, Xanthophyceae																				
Asterococcus superbus	..	..	..	r	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Carteria cordiformis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— fornicata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Carteria globulosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— stellifera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chlamydomonas acidophila	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chlamydomonas capitis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— cingulata	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— clathrata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chlamydomonas clavata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Dinobryonis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— gloeocystiformis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chlamydomonas kakosmos	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— latifrons	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— longistigma	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chlamydomonas oleosa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pseudoplatyrhyncha	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr
— Reinhardii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	rrr	..
Chlamydomonas Reinhardii var. minor	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— retroversa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Chlorogonium acus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

[1] Only cysts. [2] The main species + var. globulifera.

continued).

Mixotrophic)						Eutrophic																						(Saprotrophic)		
Blankeborg II						Sortedam II			Gadevang Mose		Vandingsdam			Badstue-Ødam		Frederiksborg Slotsso		Jægerbakke Dam			Flødegaardens Dam							Lynge Vandingsdam		Bistrup Dam		
15.VIII.26	25.VII.28	25.VII.28	28.VIII.28	28.VIII.28	10.VI.30	8.VI.29	1.VII.29	23.IX.29	6.VII.29	10.VII.29	28.VI.29	28.VI.29	24.VIII.29	6.VI.29	23.VIII.29	11.VI.29	11.VI.29	23.IX.29	12.VI.29	17.IX.29	16.V.30	1.VII.26	28.VII.26	20.VII.27	7.IX.28	19.VIII.29	10.VI.30	3.VIII.39	30.VI.47	6.VIII.47	12.VIII.29	24.X.29	16.XI.29
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Table IV

Species	(Dystrophic)				Oligotrophic					Blankeborg I							
	Bøndernes Mose I	Bøndernes Mose II	Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø								
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28
Chlorogonium minimum	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Coccomonas sp.	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Dysmorphococcus Fritschii	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Eudorina elegans	..	.. ..	..	..	..	..	..	..	rr	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Eutetramorus globosus	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	+	rrr	rrr	rr	rr
Gemellicystis neglecta	..	.. ..	..	..	..	..	..	..	..	..	r	..	.. ..	.. ..	.. ..	.. ..	.. ..
Gloeocystis ampla	..	.. ..	..	..	..	..	..	..	rrr	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
— gigas	..	.. ..	..	..	..	rrr	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
— planctonica	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	rr	..	rr
Gonium pectorale	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
— sociale	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Oedogonium Itzigsohnii	..	.. ..	..	r	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Ophiocytium capitatum	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	rrr	rrr	rrr
— longispinum	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Pandorina morum	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Phacotus angustus?	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
— lenticularis	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Pteromonas aculeata	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Pteromonas angulosa	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
— spinosa	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Spermatozopsis exultans	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Sphaerocystis Schröteri	..	.. ..	..	..	..	rrr	..	rr	.. ..	..	..	..	.. ..	.. ..	rrr	.. ..	.. ..
Stichococcus bacillaris	..	.. ..	..	..	..	..	..	..	+	..	..	cc	.. ..	.. ..	.. ..	.. ..	.. ..
Tetraspora Nygaardii	..	.. ..	..	..	..	..	..	c +	.. ..	..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Geminella minor	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Ulothrix pelagica	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Chlorococcales																	
Actinastrum Hantzschii	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	.. ..	.. ..
Ankistrodesmus convolutus var. minutus	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	rrr	..	r
— falcatus	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	..	rrr
Ank. falcatus var. acicularis f. longissima	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	rrr	..	..
— — — mirabilis f. dulcis	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	..	..
— — — — f. longiseta	..	.. ..	..	..	..	..	..	..	..	.. ..	..	..	.. ..	.. ..	.. ..	..	rrr

[1] determination not sure.

(continued).

| (Mixotrophic) | | |

Table IV

Species	(Dystrophic)				Oligotrophic																
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørkso	Klitsø at Højsande	Lille Gribsø			Blankeborg I								
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30	
Ank. falcatus var. setiformis f. brevis	..	..	..	..	..	..	..	..	..	+	rr	r	..	..	..	..	..	..	..	..	
— — — — f. elongata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— — — spiralis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Ank. falcatus var. spirilliformis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	..	..	rrr	
— lacustris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— longissimus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Botryococcus Braunii	..	..	..	rrr	rrr	rrr	rr	rrr	rrr	..	..	rrr	rrr	rrr	..	rrr	rrr	rrr	rrr	..	
Coelastrum microporum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	
— — f. astroidea	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	
Coelastrum reticulatum	..	..	..	..	..	..	..	..	..	..	..	..	r	rrr	rrr	rrr	rr	rrr	r+	+	
Crucigenia quadrata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— — var. minima[1]	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	r	rrr	rrr	rrr	
Crucigenia rectangularis	..	..	..	..	..	..	..	..	rr	..	..	..	..	..	..	..	..	..	..	..	
— tetrapedia[2]	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Desmatractum indutum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Dictyosphærium pulchellum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	..	rr	..	
Elakatothrix gelatinosa	..	..	..	..	rrr	..	r	..	r+	..	..	..	..	..	..	..	..	..	..	..	
— — f. biplex	..	..	..	..	..	..	..	..	..	rr	..	..	..	rrr	c+	rrr	r	..	..	..	
Eremosphæra viridis	..	..	..	..	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Franceia geminata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Golenkinia radiata	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Hofmania Lauterbornii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Kirchneriella contorta	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	
— lunaris	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	
Kirchneriella lunaris var. Dianae	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— microscopica	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— obesa	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Lagerheimia ciliata	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	rrr	rrr	..	..	rrr	
— quadriseta	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— subsalsa	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	..	..	..	..	..	
Lagerheimia wratislaviensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Micractinium pusillum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Nannokloster belonophorus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	

[1] Syn.: Cr. minima Brunnth. [2] incl. Crucigenia fenestrata.

(continued).

(Mixotrophic)						Eutrophic																				(Saprotrophic)					
Blankeborg II						Sortedam II			Gadevang Mose		Vandingsdam			Badstue-Ødam		Frederiksborg Slotsso			Jægerbakke Dam			Flødegaardens Dam						Lynge Vandingsdam		Bistrup Dam		
15.VIII.26	25.VII.28	25.VII.28	28.VIII.28	28.VIII.28	10.VI.30	8.VI.29	1.VII.29	23.IX.29	6.VII.29	10.VII.29	28.VI.29	28.VI.29	24.VIII.29	6.VI.29	23.VIII.29	11.VI.29	11.VI.29	23.IX.29	12.VI.29	17.IX.29	16.V.30	1.VII.26	28.VII.26	20.VII.27	7.IX.28	19.VIII.29	10.VI.30	3.VIII.39	30.VI. 47	6.VIII.47	12.VIII.29	24.X.29	16.XI.29
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Table IV

Species	(Dystrophic)					Oligotrophic															
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø			Blankeborg I								
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30	
Nephrocytium Agardhianum	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	rrr	
— lunatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	
Oocystis Marssonii	..	..	..	..	..	..	rr	..	rrr	rr	..	..	rrr	rrr	rr	rrr	r	rrr	rrr	rr	
Oocystis solitaria	r	rrr	rrr	..	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Pediastrum angulosum var. araneosum	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	
— biradiatum	..	..	..	..	..	rrr[1]	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Pediastrum Boryanum	..	..	..	..	..	..	..	..	rrr	..	..	..	rrr	rrr	..	rrr	rrr	rr	rrr	rrr	
— — var. brevicorne	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— — — longicorne	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Pediastrum Boryanum var. rugulosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— duplex	..	..	..	..	..	..	..	..	rrr	..	..	..	..	rr	..	rrr	..	..	..	..	
— — var. clathratum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Pediastrum duplex var. coronatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— — — reticulatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— Kawraiskyi	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	
Pediastrum tetras	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Quadrigula closterioides	..	..	..	..	..	rrr	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	
Radiococcus pelagicus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Scenedesmus acutus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	..	rrr	rrr	
— arcuatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rr	..	..	..	
— — var. capitatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Scenedesmus armatus	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	rr	..	rr	..	rrr	rrr	
— arvernensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	
— brasiliensis var. norvegica	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	
Scenedesmus brevispina	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— dimorphus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— ecornis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	rrr	rrr	..	
Scenedesmus falcatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— incrassatulus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— opoliensis	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
Scenedesmus ovalternus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
? — — var. Graevenitzii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	
— quadricauda	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	
? — tetradesmus var. parenchymaticus	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	

[1] determination not sure.

continued).

| Mixotrophic) | | | | | | | Eutrophic | | | | | | |

Table IV

Species	(Dystrophic)					Oligotrophic							Blankeborg I							
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø										
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30
Schroederia setigera	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Selenastrum Bibraianum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— capricornutum	..	..	..	..	..	..	..	..	..	ccc	..	rr	..	..	r	..	rr	..	..	rrr
Selenastrum gracile	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Westii	..	..	..	..	..	..	..	..	..	+	rr	rr	..	..	..	..	..	..	..	..
Tetraedron caudatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr
Tetraedron hastatum var. palatinum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— limneticum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..
— — var. simplex	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tetraedron minimum	..	..	..	..	..	..	..	..	..	..	..	..	r	rrr	r+	rrr	r	rr	r	c
— muticum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— planctonicum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	rrr
Tetraedron regulare Incus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Schmidlei var. euryacanthum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— trigonum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rrr	..	..
Tetraedron trigonum var. crassum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	rrr	..
— — — gracile	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr
— — — setigerum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tetrallantos Lagerheimii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tetrastrum apiculatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— heteracanthum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Tetrastrum staurogeniæforme	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..
Westella botryoides	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
Undeterm. green algae	rrr	..	..	..	..	..	..	..	..	r+	r	rrr	..	..	r	..	cc	..	..	..
Conjugales (Desmidieae)																				
Arthrodesmus convergens	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
— Incus var. extensus f. minor	..	rrr	rrr	..	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Arthrodesmus octocornis	..	..	..	rrr	..	rrr	rrr	rrr	..	..	..	..	..	..	..	..	..	..	..	..
— triangularis	..	..	..	..	..	..	..	..	..	rrr	..	rrr	..	..	..	..	..	..	..	..
Closterium abruptum	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..
Closterium aciculare	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..
— acutum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	rrr	rrr
— — var. Linea	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..

(continued).

| (Mixotrophic) | | |

Table IV

Species	(Dystrophic)				Oligotrophic							Blankeborg I							
	Bondernes Mose I	Bondernes Mose II		Store Jenshoj turf pit	turf pit NE of Skaanso	Holmsø	Skaanso	Morkso	Klitso at Højsande	Lille Gribsø									
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30
Closterium acutum var. variabile	rrr	rrr	rrr	rrr	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	rrr
— Baillyanum var. parvulum	..	..	..	..	..	..	..	..	..	..	rrr	rr	..	..	..	..	..	..	..	..
— Ehrenbergii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Closterium gracile	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..
— idiosporum	..	..	..	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— incurvum	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
Closterium Kützingii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— moniliferum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— parvulum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Closterium striolatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— subulatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Venus	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
Cosmarium angulosum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— asphærosporum var. strigosum	..	..	..	..	rrr	..	..	..	..	r	..	ccc	..	..	..	..	rrr	..	..	..
— bioculatum f. depressa	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	rrr	..	rrr	rrr
Cosmarium Blyttii var. Novæ-Sylviae	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
— contractum var. ellipsoideum	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
— — — minutum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cosmarium humile var. glabrum	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	rrr	..	..	rrr	..	..
— Kjellmannii var. grande	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— læve var. septentrionale	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cosmarium Majæ	..	..	..	..	..	..	..	..	..	+	..	+	..	..	..	..	..	..	..	..
— Meneghinii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Nymannianum	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cosmarium præmorsum	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
— punctulatum var. subpunctulatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— pusillum	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	c+	rr	+	rrr	..	rrr
Cosmarium pygmæum	..	..	..	..	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— reniforme	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	rrr	..	..	..
— Sinostegos var. obtusius	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Cosmarium subarctoum f. minor	..	..	..	..	..	..	..	..	..	rrr	..	rr	..	..	..	..	..	..	..	..
— subprotumidum var. Gregorii	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— subtumidum	..	..	..	rr	rrr	..	rrr	..	rrr	..	..	..	..	rrr	..	rrr	..	rrr	..	..

[1] f. latiuscula.

(continued).

| (Mixotrophic) | | |

Table IV

Species	(Dystrophic)					Oligotrophic															
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø			Blankeborg I								
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30
Euastrum bidentatum	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..
— binale	..	..	..	rrr	rrr	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — f. Gutwinskii	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Euastrum denticulatum	..	..	..	..	..	rrr	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
— elegans	..	..	..	..	..	rrr	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
— pinnatum	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	..	..	..	..	..	..	..
Euastrum verrucosum	..	..	.	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
— sp.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..
Bambusina Borreri	..	rrr	..	rrr	rrr	..	rrr	..	..	..	rrr	..	..	..	..	..	..	..	..	..
Gonatozygon Brebissonii	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..
Gonatozygon Kinahani	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Micrasterias truncata	..	..	..	rrr	..	..	..	..	..	..	rrr	rrr	..	..	..	..	..	..	..	..
Pleurotænium Ehrenbergii	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..
— trabecula	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..
Sphærozosma granulatum	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	rr	..	rrr	..
Spondylosium pulchellum	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum alternans	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— apiculatum	..	..	..	..	..	..	..	..	rrr	..	..	..	rrr	..	..	rrr	rrr	rrr	..	rrr
Staurastrum Arachne	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
— avicula[1]	..	..	..	..	..	..	..	..	..	..	..	..	rr	rrr	..	rrr	..	rr	rrr	..
— barbulae	..	..	..	..	..	..	rrr	rrr	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum brachiatum	..	..	..	..	c	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— cingulum var. inflatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— crenulum var. brittannicum	..	..	..	..	..	..	..	..	rrr	..	..	..	rrr	rrr	rrr	rrr	rrr	rrr	rrr	rrr
Staurastrum curvatum f. brevispina	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
— cuspidatum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	..	rrr
— — var. divergens	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
Staurastrum danicum	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— — forma	..	..	..	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— dejectum[2]	..	rrr	rrr	rrr	+	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum Dickiei	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
— erasum[3]	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	rrr	rrr	rrr
— furcigerum	..	..	..	..	..	..	..	..	..	..	..	..	rr	rr	rrr	rr	rrr	rrr	rrr	..

[1] see Nygaard 1945, fig. 80 (sub nomine Staurastrum lunatum). [2] f. mediocris and f. longispina, see p. 93 and 94.

(continued).

(Mixotrophic)						Eutrophic																					(Saprotrophic)		
Blankeborg II						Sortedam II			Gadevang Mose		Vandingsdam			Badstue-Ødam		Frederiksborg Slotssø			Jægerbakke Dam			Flødegaardens Dam						Lynge Vandingsdam		Bistrup Dam		
15.VIII.26	25.VII.28	25.VII.28	28.VIII.28	28.VIII.28	10.VI.30	8.VI.29	1.VII.29	23.IX.29	6.VII.29	10.VII.29	28.VI.29	28.VI.29	24.VIII.29	6.VI.29	23.VIII.29	11.VI.29	11.VI.29	23.IX.29	12.VI.29	17.IX.29	16.V.30	1.VII.26	28.VII.26	20.VII.27	7.IX.28	19.VIII.29	10.VI.30	3.VIII.39	30.VI. 47	6.VIII.47	12.VIII.29	24.X.29	16.XI.29
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[3] see R. Grönblad 1942, p. 40—41, t. 4, fig. 14.

Table IV

Species	(Dystrophic)					Oligotrophic							Blankeborg 1							
	Bøndernes Mose I	Bøndernes Mose II		Store Jenshøj turf pit	turf pit NE of Skaansø	Holmsø	Skaansø	Mørksø	Klitsø at Højsande	Lille Gribsø										
	28.VI.29	22.VIII.29	16.VI.30	25.VI.30	4.VII.38	26.VI.30	4.VII.38	6.VII.38	30.VI.25	28.VI.29	28.VI.29	28.VIII.29	16.VIII.25	15.VIII.26	17.VIII.27	17.VIII.27	18.VIII.28	18.VIII.28	6.VIII.29	10.VI.30
Staurastrum gracile	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	rr	..	rrr	rrr	..
— longiradiatum var.	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..
— laeve	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
Staurastrum Manfeldtii[1]	..	..	..	..	..	..	..	..	..	..	..	..	rrr	r	rrr	r +	rrr	r	..	..
— monticulosum var. pulchrum	rr	rr	rrr	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— paradoxum var. parvum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Staurastrum polymorphum var. divergens	rrr	rrr	rr	..	rr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— Pseudosebaldii var. simplicius	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— teliferum	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..
Staurastrum tetracerum var. biverruciferum	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rr	r	rr	+	rr	..	rrr
— — — validum	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— uniseriatum	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	..	..	..	..	..	..
Staurastrum vestitum var. parvum	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..
— sp.	rrr	..	..	..	..	..	..	..	..	..	..	rrr	..	..	..	..	..	..	..	..
Tetmemorus granulatus	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Xanthidium antilopæum	..	rrr	rrr	..	..	..	rrr	..	rrr	..	..	rrr	..	..	..	..	..	..	..	..
— concinnum var. Boldtianum	rrr	..	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..

[1] see Nygaard 1945, fig. 79.

(continued).

(Mixotrophic)						Eutrophic															(Saprotrophic)		
Blankeborg II						Sortedam II			Gadevang Mose			Vandingsdam			Badstue-Odam		Frederiksborg Slotssø			Jægerbakke Dam			Flødegaardens Dam							Lynge Vandingsdam		Bistrup Dam		
15.VIII.26	25.VII.28	25.VII.28	28.VIII.28	28.VIII.28	10.VI.30	8.VI.29	1.VII.29	23.IX.29	6.VII.29	10.VII.29	28.VI.29	28.VI.29	24.VIII.29	6.VI.29	23.VIII.29	11.VI.29	11.VI.29	23.IX.29	12.VI.29	17.IX.29	16.V.30	1.VII.26	28.VII.26	20.VII.27	7.IX.28	19.VIII.29	10.VI.30	3.VIII.39	30.VI.47	6.VIII.47	12.VIII.29	24.X.29	16.XI.29
..	..	..	..	..	..	rrr	rrr	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
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..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	rrr	rrr	rrr	rrr	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
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(FAM. *COCHLIDIDAE, LEPIDOPTERA*)

VON

PAUL J. HOLST CHRISTENSEN

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
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A. Einleitung.

Bei meinen Studien über die Embryologie bei *Orgyia antiqua* L. (Holst Christensen 1937, 1942 und 1943) habe ich oft die Erfahrung gemacht, dass die Untersuchung der sehr dickschaligen und vollständig undurchsichtigen Eier dieses Schmetterlings mit grossen Schwierigkeiten verbunden ist. Bei meiner Suche nach einem geeigneteren Objekte blieb ich unter anderen bei den eigentümlichen, flachen, durchsichtigen Eiern des Nachtfalters, *Cochlidion limacodes* Hufn., (s. Holst Christensen 1943, S. 212 und Tafeln IV und V) stehen. Um für diesen in Dänemark recht seltenen Schmetterling reichliches Material zu beschaffen, war es nötig, Züchtungen in grösserer Zahl vorzunehmen; hierbei war es unvermeidlich, dass mich das eigentümliche Aussehen der Raupen dieser Art in grösste Verwunderung versetzte. Da in der Literatur, soweit mir bekannt, keine genauere Schilderung des Aussehens und der Biologie der verschiedenen Larvenstadien samt der Anzahl der Häutungen vorliegt, dürfte es interessant sein, einiges darüber mitzuteilen. Ich möchte an dieser Stelle dem Rask-Ørsted Fond, der die Kosten der Übersetzung bestritten hat, und dem Carlsbergfond, ohne dessen Unterstützung die Durchführung der vorliegenden Untersuchung unmöglich gewesen wäre, meinen wärmsten Dank aussprechen. Auch Frau Bodil Strubberg, die unter meiner Anleitung den grössten Teil der Zeichnungen ausgeführt hat, danke ich für ihre schöne und sorgfältige Arbeit.

B. Material und Methoden.

Die Beschaffung des Materials war mit den grössten Schwierigkeiten verbunden, und ohne die bereitwillige Hilfe von seiten verschiedener Schmetterlingssammler hätte sich die Untersuchung nicht durchführen lassen. Für die Zusendung von Eiern, Raupen und Schmetterlingen möchte ich den Herren Gutsbesitzer Erling Pedersen, Lehrer H. P. S. Sønderup, Gärtner A. Møller und Zivilingenieur N. L. Wolff bestens danken. Auch für die ausgezeichnete Hilfe, die mir Gutsbesitzer Erling Pedersen dadurch erwiesen hat, dass er meine Tiere bis nach der Kopulation, die in der Gefangenschaft oft misslingt, bei sich in Pflege behalten hat, spreche ich ihm meinen aufrichtigen Dank aus.

Die befruchteten Weibchen wurden einzeln, entweder in Präparatgläsern mit flachem Boden (8 × 2 cm) oder in runden Glasdosen mit geschliffenem Glasdeckel, (6 × 3,5 cm) aufbewahrt. Auf dem Boden oder an den Wänden dieser Behälter legten die Tiere sehr bereitwillig ihre Eier ab. Um während der Embryonalentwicklung einen passenden Feuchtigkeitsgrad aufrechtzuerhalten, wurde jeden Tag ein frisches Eichenblatt in den Glasbehälter gelegt. Ab und zu wurden die Eier vorsichtig aus einer Pipette mit Wasser bespritzt, wonach dieses wieder entfernt wurde. Die Züchtungen wurden in einem Zimmer mit einer Temperatur von etwa 18—23° C durchgeführt. Bei dieser Temperatur[1] machen die Eier ihre Entwicklung im Laufe von etwa 10 Tagen durch. Die Räupchen wurden auf einem frischen Eichenblatt angebracht, dessen Stiel mit feuchter Watte umbunden war, um sowohl für Haltbarkeit als für einen passenden Feuchtigkeitsgrad zu sorgen. Gewöhnlich wurden je 10 Räupchen in eine Glasdose gelegt. Das Futter wurde täglich gewechselt, abgesehen von der Zeit, während der sich die Tiere im Häutungsstadium befanden und deshalb am liebsten nicht gestört werden sollten. Die Züchtung der Räupchen war übrigens, wie sich erwies, deshalb mit einigen Schwierigkeiten verbunden, weil die Tiere bei der Überführung zu neuem Futter oft zu Grunde gehen. Dem kann aber leicht dadurch abgeholfen werden, dass man ein Stück abgerissenes Karduspapier mit faserigem Rande benutzt, auf welchem die Räupchen festgehalten werden, von dem sie sich jedoch später leicht wieder abnehmen lassen. Zu weiteren Untersuchungen wurden die Tiere nach der Häutung in Petrunkewitsch's Flüssigkeit oder bloss in 70 % Alkohol fixiert. Dagegen wurden die Zeichnungen immer nach frischen Tieren gemacht. Damit sie sich ruhig verhielten, mussten sie vorsichtig mit Äther betäubt werden; diesem Betäubungsmittel gegenüber erwiesen sich die Raupen als sehr empfindlich. Während der Zeichenarbeit musste oft ein Glas, in dem mit Äther angefeuchtete Watte lag, vor oder über sie gehalten werden, damit sie ruhig blieben. Gewöhnlich gingen die Tiere aber nach der Betäubung später doch noch zu Grunde, und wenn sie gleich am Anfang eine zu grosse Dosis bekommen hatten, mussten sie wegen der eingetretenen Farbenveränderungen als Zeichenobjekt verworfen werden. Statt dessen wurden sie dann in 70 % Alkohol zu anderem Gebrauch aufbewahrt.

C. Allgemeines über *Cochlidion limacodes* Hufn.

Zum leichteren Verständnis der folgenden Darstellung dürfte es angebracht sein, einiges über das Aussehen der Imago, die Systematik und die Biologie mitzuteilen. *Cochlidion limacodes* Hufn. ist ein kleiner, unansehnlicher, recht seltener Nachtfalter, der hauptsächlich in den südlicheren Teilen von Dänemark, wie zum Beispiel in Südseeland, Möen und Lolland-Falster, heimisch ist. Die ockergelben Oberflügel sind mit einem Paar deutlicher, dunkelbrauner, quergehender »Zwischenlinien« versehen;

[1] Bei 24—27° C dagegen dauert die Eientwicklung nur 8—9 Tage.

die Flügellänge beträgt beim Männchen etwa 1 cm, beim Weibchen etwas mehr (1,3 cm). Die Unterflügel sind, namentlich beim Männchen, schwarzbraun mit hellerem Rand. In Dänemark – und auch im übrigen Europa – ist die Familie *Cochlididae* nur mit den Gattungen *Cochlidion* Hb. mit der Art *limacodes* Hufn. und *Heterogenea* Knoch mit ihrer Art *asella* Schiff. vertreten. In Amerika dagegen (Packard 1893 und Dyar 1894—99 und 1907) kommen zahlreiche Gattungen und viele Arten vor, und in der ganzen Welt rechnet man mit etwa 400 Arten auf etwa 100 Gattungen verteilt. Die Flugzeit der Imago fällt in die Monate Juni und Juli; in der Gefangenschaft habe ich das Tier gewöhnlich um den 22. Juni herum gezüchtet. Im Gegensatz zu den meisten anderen Nachtfaltern tritt dieser bei vollem Tageslicht auf, ebenso wie es mit *Orgyia antiqua* L. der Fall ist. So gibt South (1909, Ser. II, p. 345) an, dass man beide Geschlechter im Sonnenschein lebhaft um die Kronen der Eichen herumschwärmen sehen kann. Das Weibchen legt seine flachen, gelblich-weissen Eier auf verschiedenen Laubbäumen (Eichen, Buchen, Kastanien und Weissdorn) ab, und die vollständig erwachsenen Raupen sind den Nacktschnecken ähnlich, weshalb sie auf englisch »slug-caterpillars« (s. auch Seite 12) genannt werden. Die Überwinterung geht in einem ovoiden, mit einem Deckel versehenen Kokon vor sich, der gern an einem Blatt festgesponnen ist, das später auf die Erde fällt (s. Klöcker 1917, S. 33). Erst spät im Frühling verwandelt sich die Raupe in eine bleiche, graugelbe Puppe (s. S. 28 und Tafel IX, Abb. 32, 33 und 34).

Nach dieser allgemeinen Übersicht gehen wir nun auf eine genauere Besprechung der Paarungsbiologie, der Eiablage samt der Metamorphose über.

D. Biologie der Begattung und Eiablage.

I. Biologie der Begattung.

Wie oben erwähnt, ist es äusserst schwierig, gezüchtete Exemplare von *Cochlidion limacodes* in der Gefangenschaft zur Begattung zu bringen (s. S. 3). Wenn man nämlich einige frisch ausgeschlüpfte Männchen und Weibchen in Drahtkäfigen einsperrt (siehe die Fussnote), erweist es sich, dass die Tiere einander ununterbrochen stören, indem sie herumfliegen und sich gegenseitig stossen, wodurch eine Begattung ganz unmöglich gemacht wird. Deshalb ging ich dazu über nur ein einziges Pärchen in einem Käfig[1] einzusperren, der an einer kleinen Buche in meinem Garten aufgehängt wurde, damit die Umgebung so anziehend wie möglich sein sollte. Auch diese Veranstaltung gab kein positives Resultat, und ich fand keinen anderen Ausweg, als meine Puppen an den stets hilfsbereiten Spezialisten, Herrn Erling

[1] Der Käfig war zylindrisch und an jedem Ende mit einem kreisrunden, 1,2 cm dicken Holzboden versehen, an dem das Drahtnetz befestigt war. Er war 21 × 15 cm gross; der Boden war ausserdem in der Mitte mit einem 4 cm grossen Loch versehen, in dem ein zum Öffnen und Schliessen des Käfigs bestimmter, abnehmbarer Kork sass.

Pedersen, zu senden, der trotz grosser Schwierigkeiten eine Begattung zu Stande brachte. Nach überstandener Kopulation wurden die befruchteten Weibchen an mich zurückgesandt; sehr oft hatten sie einen Teil ihrer Eier bereits vor der Ankunft gelegt. Besonders häufig war dies bei solchen Weibchen der Fall, bei denen eine verspätete Begattung stattgefunden hatte. Wenn die Kopulation dagegen mit neu ausgebrüteten Tieren vor sich gegangen war, verging oft erst einige Zeit, bevor das Weibchen seine Eier ablegte. Die Begattung in der freien Natur kann auf einem Stamm, einem Zweig oder in gewissen Fällen auf einem Zaunpfahl stattfinden; dabei werden die Köpfe in diametral entgegengesetzter Richtung gehalten, also gerade so wie bei den Nachtfaltern allgemein üblich; sie dauert gewöhnlich längere Zeit. Während der Kopulation in der Gefangenschaft muss man äusserst vorsichtig sein, damit die sehr scheuen Tiere nicht erschrecken; bei der kleinsten Störung wird nämlich die Begattung sofort abgebrochen.

II. Die Eiablage.

Leider habe ich keine Möglichkeit gehabt zu beobachten, wie die Eiablage in der Natur vor sich geht, aber es besteht Grund zu der Annahme, dass der Vorgang nicht in wesentlichen Punkten von den Beobachtungen abweicht, die ich bei Tieren in der Gefangenschaft gemacht habe. Wird ein befruchtetes Weibchen in einem Präparatglas, einer Glasdose oder bloss in einer Streichholzschachtel eingesperrt, findet eine Eiablage gewöhnlich bald statt — in letzterer am raschesten, weil es hier dunkel ist. Die Eiablage geschieht nämlich bevorzugt im Laufe der Nacht. Am Tage verhält sich das Tier meist ruhig, gegen Abend aber wird es unruhig, fliegt oft auf und schwirrt im Glase oder in der Glasdose herum. Wenn das Weibchen zur Ruhe gekommen ist, kann man oft sehen, dass es eine Art pumpender Bewegungen mit dem Hinterkörper vornimmt, wonach es diesen gegen die Unterlage drückt und die Eier absetzt. Wenn man nicht gut aufpasst, ist es garnicht so leicht dies festzustellen, weil das Ei einer kleinen, flachen und teilweise klaren Schale, gewöhnlich von ovaler Form, ähnlich ist. Das nächste Ei wird oft in unmittelbarer Nähe des ersten abgelegt — es kann aber auch so angebracht werden, dass es dieses teilweise deckt. Am nächsten Tag sieht das Innere des Glases aus als sei es dicht mit ganz kleinen Wassertropfen besetzt. Betrachtet man die Eier unter schwacher Lupenvergrösserung, erweist es sich, dass oft einige der charakteristischen Schuppen des Weibchens an ihnen kleben (Tafel I, Abb. 2). Ich habe den Eindruck, dass etwa 100—200 Eier abgelegt werden können, obgleich ich keine Gelegenheit gehabt habe, die genaue Zahl festzustellen. Nach den oben erwähnten Beobachtungen ist anzunehmen, dass *Cochlidion limacodes* Hufn. auch in der Natur die Eier immer einzeln ablegt, im Gegensatz zu der verwandten Art, *Heterogenea asella* Schiff., welche sie in Klumpen auf den Blättern anbringt (s. Klöcker 1917, S. 33).

E. Die Metamorphose.

I. Das Ei.

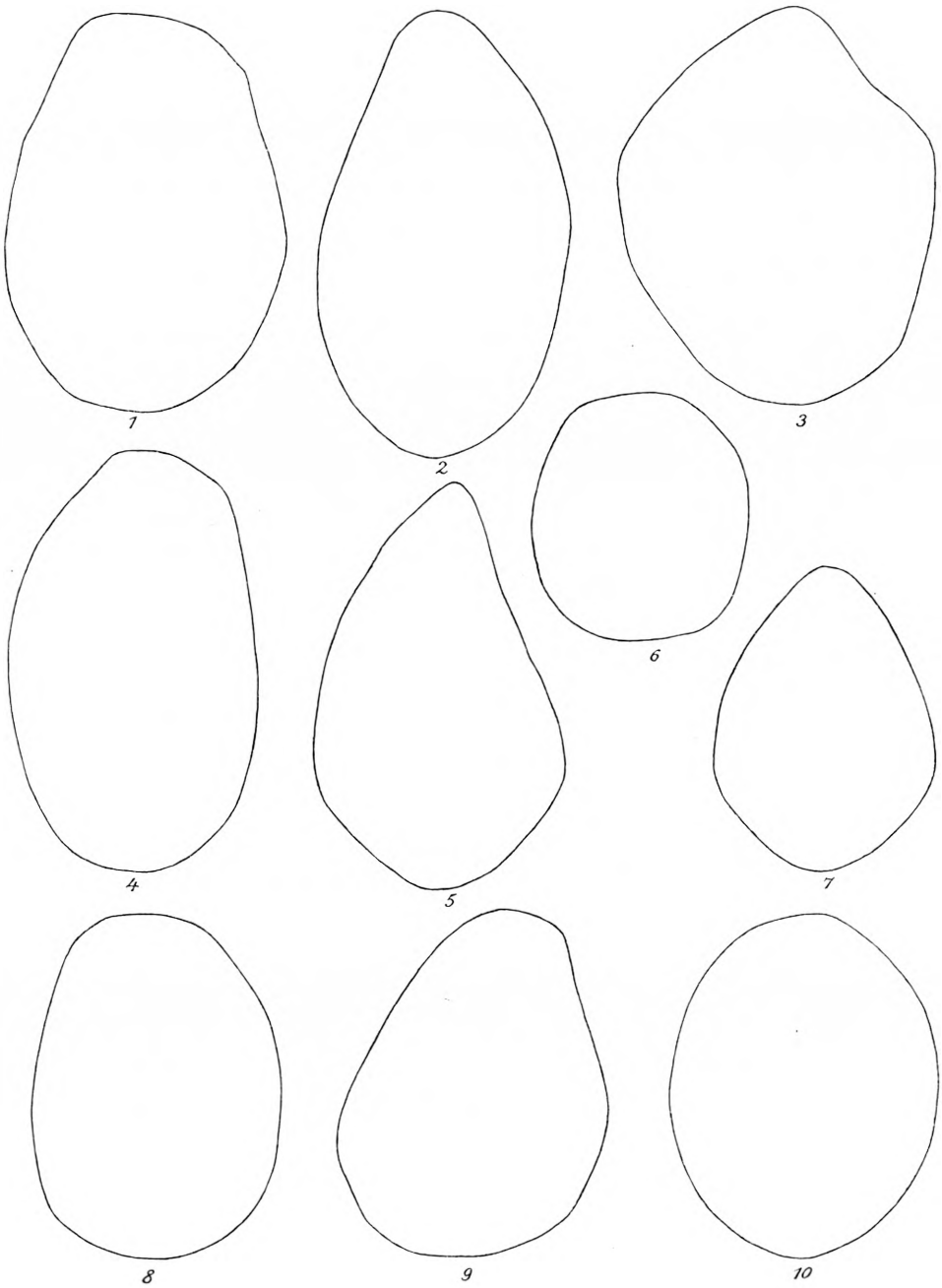
Das Ei von *Cochlidion limacodes* HUFN. ist so oft in der Literatur beschrieben und abgebildet worden, dass hier im wesentlichen nur angeführt werden soll, was zur Ergänzung und Erläuterung der folgenden Darstellung dienen kann. Das Ei ist, wie schon auf S. 6 erwähnt, flach, schuppenähnlich und gewöhnlich von ovaler Form (s. Textabb. 1). Es ist, wie Tabelle 1 zeigt, durchschnittlich 0,90 mm lang und 0,65 mm breit.

Tabelle 1.

Die Grösse 20 verschiedener Eier in einer Eiablage von *Cochlidion limacodes* HUFN.

Nummer des Eies	Maximallänge in mm	Maximalbreite in mm
1	1,14	0,63
2	1,09	0,64
3	0,93	0,71
4	0,92	0,61
5	0,80	0,54
6	1,03	0,83
7	1,07	0,63
8	0,89	0,64
9	1,01	0,71
10	1,03	0,81
11	0,79	0,64
12	0,83	0,54
13	0,83	0,59
14	0,86	0,64
15	0,66	0,56
16	0,89	0,64
17	0,86	0,59
18	0,79	0,64
19	0,84	0,69
20	0,79	0,69
Im ganzen 20 Eier	Durchschnitt: $0{,}90 \pm 0{,}12$	Durchschnitt: $0{,}65 \pm 0{,}08$

Grösse und Form des Eies sind übrigens ziemlich verschieden. So trifft man nicht bloss kleine Eier, die nur 0,66 mm lang und 0,56 mm breit sind (s. Tab. 1, Ei No. 15, samt Textabb. 1, Abb. 6), sondern auch grosse, deren Länge 1,03 mm und deren Breite 0,83 mm beträgt (s. Tab. 1, Ei No. 6, samt Textabb. 1, Abb. 3). Ebenso kann sich die Form ändern, so dass sie einem Hühnerei (s. Textabb. 1, Abb. 7 und 9) oder einem »flachgedrückten« Tropfen (s. Textabb. 1, Abb. 5) ähnlich ist. Längs der Peripherie des Eies und etwas nach innen zu ist der Rand ausserordentlich dünn, aber danach steigt die Höhe schnell zur Mitte hinan, so dass ein flacher,



Textabb. 1. Umrisszeichnungen 10 verschiedener Eier einer Eiablage von *Cochlidion limacodes* HUFN. Vergr. 52,5 ×.

ovaler Wall entsteht. Ab und zu ist die Steigung zum einen Ende des Eies hin ganz bedeutend, und wir bekommen dann »tropfenförmige« Eier. Die Eierschale, das Chorion, ist sehr dünn und durchsichtig, und wenn die Raupe das Ei verlassen hat, schillert die leere Schale in perlmutterartigem Glanz. Schon bei schwächerer Mikroskopvergrösserung zeigt die Eierschale eine typische, an ein Stahldrahtnetz erinnernde Textur (Tafel I, Abb. 1 und 2, Ch). An dem einen (spitzen) Ende des Eies befindet sich ein charakteristischer Mikropylapparat (Tafel I, Abb. 1 und 2, Mi), der dem der *Orgyia antiqua* L. (Holst Christensen 1937, Tafel 7, Abb. 1; 1942, Tafel 1, Abb. 1 und Tafel 2, Abb. 3—6) sehr ähnlich ist. Ebenso wie dort besteht er hier aus einer zentralen Grube, welche von 2 Kreisen von »Blättern« umgeben ist. In der inneren Spitze der innersten Blätter befinden sich etwa 6—8 sehr feine Mikropylkanäle, die zum Durchgang der Spermien während der Befruchtung des Eies bestimmt sind.

Das frisch abgelegte Ei ist von gelblich-weisser Farbe, die während der Entwicklung allmählich in einen mehr milchartigen Ton übergeht. Gegen Ende der Entwicklung füllt die Raupe fast das ganze Innere des Eies (Tafel I, Abb. 2) aus. Der grösste Teil der Nahrungsmasse, des Deutoplasmas, ist verzehrt; nur längs des Rückens und vor dem Kopfe ist noch ein kleinerer Teil zu beobachten. Auf dem Kopf sind 2 deutliche »Augen« (s. S. 10) zu sehen. Das schön verzweigte Trachéensystem ist in Form von silberglänzenden Kanälen im Inneren der Raupe zu bemerken. Gegen Ende der Embryonalperiode ist die Segmentierung besonders deutlich, allmählich wird sie aber etwas undeutlich. Die bräunlichen Mundteile der Raupe kann man oft in Bewegung sehen, und es ist fernerhin zu beobachten, wie das Tier das Deutoplasma rhythmisch in einem feinen Strom durch den Mund aufnimmt. Wenn die Nahrungsmasse ganz verbraucht ist und die dünnen Embryonalhüllen verzehrt sind, ist der Zeitpunkt für das Ausschlüpfen der Raupe gekommen. Mittels der Oberkiefer nagt sie nun ein ovales Loch in das Chorion, und hierauf arbeitet sie sich, den Körper sehr energisch hin und her bewegend, aus der Eierschale heraus. Gleichzeitig macht das Tier mit der Unterseite des Körpers krampfartige Bewegungen in der Richtung von hinten nach vorn, was an eine Art »peristaltische Welle« erinnert. Obgleich, wie auf S. 7 erwähnt, die einzelnen Eier (vgl. Textabb. 1) von ganz verschiedener Grösse sind, sind die ausgeschlüpften Räupchen fast alle gleich gross.

II. Larvenstadien und Häutungen.

1. Die Raupe vor der 1. Häutung.

(Larvenstadien Ia, Ib und Ic).

Charakteristisch für die Räupchen vor der 1. Häutung ist ihr sehr verschiedenes Aussehen, je nachdem ob es sich um junge oder alte Raupen handelt. Der Unterschied ist tatsächlich so bedeutend, dass es oft mit den grössten Schwierigkeiten verbunden ist, festzustellen, ob eine Häutung eingetreten ist oder nicht. Nur nach sehr gründlicher

Untersuchung und unter Berücksichtigung ganz bestimmter, anatomischer Eigentümlichkeiten kann die Frage mit Sicherheit entschieden werden. Es erschien mir deshalb zweckmässig, zwischen drei verschiedenen »Stadien« zu unterscheiden, die ich als Stadien Ia, Ib und Ic bezeichne. Stadium Ia bedeutet hiernach die frisch ausgeschlüpfte Raupe, Stadium Ib die etwas ältere Raupe (= die junge »Igelraupe«) und Stadium Ic die Raupe am Ende der Periode vor der 1. Häutung (= die ältere »Igelraupe«).

Stadium Ia.

(Die frisch ausgeschlüpfte Raupe).

Die kleine Raupe, die aus dem *limacodes*-Ei kriecht, zeichnet sich durch ein ganz eigentümliches Aussehen aus, das ziemlich stark von dem abweicht, das wir bei den Raupen der Nachtfalter sonst antreffen. Je nach dem Zustande der Kontraktion ist das Tier etwa 0,88 mm—etwa 1,02 mm lang. Wie aus Tafel I, Abb. 3, zu ersehen, ist die Raupe von konischer Form, d. h. das Vorderende ist breiter, während der Körper nach hinten zu allmählich schmäler wird; ausserdem ist das Tier etwas flachgedrückt walzenförmig, etwa 0,40 mm breit und etwa 0,34 mm hoch. Die Farbe ist auf der oberen Seite hellgrün, doch zieht sich in der Mitte, den Rücken entlang, ein dunklerer grüner Streifen hin, der nach hinten zu noch dunkler wirkt; er erstreckt sich ungefähr vom Vorderrande des 4. Paares der Rückenwarzen zum 8. Paar. Die untere Seite dagegen ist von ganz heller, fast glasklarer Farbe. Wenn man die frisch ausgeschlüpfte Raupe von oben betrachtet (Tafel I, Abb. 3), sieht es aus, als habe sie keinen Kopf, weil dieser gewöhnlich unter die breite, halbmondförmige Vorderbrust eingezogen ist. Wenn man die Raupe wendet, streckt sie bald den Kopf heraus, und man bemerkt dann, dass dieser ziemlich klein und von hellbrauner Farbe ist. Von oben gesehen, besteht er (Tafel I, Abb. 4) aus 2 deutlichen, langgestreckt-ovalen, in der Mitte beinahe zusammenstossenden Chitinhälften (*Ep*); er ist nur etwa 0,31 mm lang und etwa 0,23 mm breit. Zu beiden Seiten des Kopfes sind 2 schwarze, ovale »Augen«, die etwa 43 μ hoch und etwa 26 μ breit sind; sie bestehen aus je 6 kleinen, dicht nebeneinander stehenden Ozellen (*Oc*). Innerhalb der Augen kann man 2 deutliche, dunkelbraune Linien (*S.l.*) beobachten, die sich oben der Mittellinie nähern und vom oberen, inneren Rand der beiden erwähnten Chitinhälften gebildet werden. Vor den Augen sind die verhältnismässig gut entwickelten 3-gliedrigen Fühler (*Antennae, An*) zu sehen, welche an der Spitze Fühlzäpfchen und Fühlhärchen haben, von denen eines besonders lang ist[1]. Im Mittelfeld des Kopfes (*Frons, Fr*), zwischen den Fühlern, hinter der Oberlippe (*Labrum, Lbr*) und dem Kopfschild (*Clypeus, Cl*), scheinen die beiden, mit mehreren Zähnen

[1] Es ist meine Absicht, später eine eingehendere Beschreibung der Anatomie der Raupe zu geben, weshalb in dieser Arbeit nur solche Einzelheiten angeführt werden, die für die Schilderung der Metamorphose von unmittelbarer Bedeutung sind.

versehenen Oberkiefer (*Mandibulae, Md*) durch, und vor diesen kann man auf jeder Seite die recht gut entwickelten Unterkiefer (*Maxillae* I, *Mx*) beobachten, deren Bau im Zusammenhang mit den anderen Mundteilen später, bei der Besprechung einer älteren Raupe (s. S. 16), eingehend behandelt wird. Die ganz vorn in der Mittellinie befindliche Unterlippe (*Labium, Lb*) hat eine höchst sonderbare Form: sie endet nämlich nicht in einen konusförmigen Spinnzapfen, wie dies gewöhnlich bei den Raupen der Schmetterlinge der Fall ist, sondern ist flach und erinnert stark an einen Fischschwanz. Infolge dieser ungewöhnlichen Form ist die von der Raupe abgesonderte Seide nicht faden-, sondern bandförmig (s. S. 25). Wie bereits erwähnt, ist die Vorderbrust (*Prothorax*) sehr gut entwickelt, und wenn man ein Hautpräparat derselben in starker Vergrösserung von oben betrachtet, entdeckt man eine Chitinverdickung von der Form eines Andreaskreuzes (Tafel II, Abb. 5). Die stärkste Chitinisierung ist kaudal gerichtet; bei gewöhnlicher Lupenvergrösserung erscheint die Prothoraxzeichnung von schmutziggrüner Farbe. Längs dem Vorderrande der Vorderbrust befinden sich 14 lange Haare, von denen einige etwa 0,29 mm lang sein können. Am auffallendsten an der neu ausgeschlüpften Raupe ist aber eine Reihe von paarweise verteilten, lampenkuppelförmigen Warzen zu beiden Seiten der Mittellinie, den Rücken entlang. Unten sind die Warzen etwa 77 μ, oben dagegen nur 34 μ breit. Besonders gut entwickelt sind die beiden vordersten Rückenwarzen auf dem Mesothorax, deren Höhe etwa 68 μ beträgt, wogegen die folgenden nur etwa 51 μ hoch sind. Im ganzen kommen 11 Paar solcher in der Mitte befindlichen Rückenwarzen vor, die das Tier so bewegen kann, dass ihre Spitzen nicht immer auf einer geraden Linie liegen, sondern zuweilen eine Wellenlinie bilden. Auf dem Meso- und Metathorax ist ausserdem unten, auf jeder Seite, noch eine Warze angebracht, und darunter, mit den Rückenwarzen interferierend, haben wir im ganzen 10 Paar Seitenwarzen. Oben auf diesen Seitenwarzen, und noch deutlicher an der Oberseite der Rückenwarzen, ist ein kleiner, dunkler Ring mit einem Durchmesser von etwa 17 μ zu unterscheiden. Betrachtet man die Warze auf einem Tiere, das in 70 $^0/_0$ Alkohol fixiert ist, unter starker Vergrösserung, so erweist sich, dass der Ring an eine kleine »Königskrone« mit etwa 8 Zäckchen erinnert; von der Seite gesehen ist die Krone etwas unter der Spitze der Warze versenkt, und 2 divergierende Linien gehen bis zu ihrem Rande hinauf. Mit anderen Worten: die Krone bildet den Abschluss eines in der Warze angebrachten, konusförmigen Rohres (s. S. 13). An jeder Längsseite der Raupe sitzen etwa 10 gut entwickelte Haare, die etwa 20 μ lang sind, wogegen die Härchen am Hinterende des Tieres nur etwa ein Drittel so lang sind. Auf der Unterseite der Raupe sitzt, wie schon erwähnt, der tief in den Prothorax versenkte Kopf (vgl. auch Tafel III, Abb. 11). Die Brustfüsse sind nur sehr schwach entwickelt, fast rudimentär; sie sind kegelförmig und laufen in einen kleinen, krummen Haken aus. Ihre Länge beträgt etwa 34 μ und die Breite etwa 26 μ. Auf dem Hinterleib (*Abdomen*) sind überhaupt keine »Warzenfüsse« (= Afterfüsse), ein für Schmetterlingsraupen recht ungewöhnlicher Befund; statt dessen bewegt sich das Tier in einer Art »peristaltischen Welle« fort, was deutlich beobachtet werden

kann, wenn die Raupe auf der Unterseite einer Glasplatte kriecht. Ihr Gang wird dadurch eigentümlich gleitend und schneckenartig, was sicher einer der Gründe ist, weshalb die Raupen der *Cochlididen* auf englisch »slug-caterpillars« genannt werden (s. S. 5).

Stadium I b.

(Die junge »Igelraupe«).

Was mich bei der Untersuchung meiner Glasschalen (s. S. 4) mit den neu ausgeschlüpften Raupen zuerst und am meisten verwunderte, war der Umstand, dass kurz nach dem Ausschlüpfen plötzlich zwei ganz verschieden aussehende Tiere vorhanden waren. Einerseits konnte man die bereits beschriebenen, mit Stadium Ia bezeichneten Raupen (Tafel I, Abb. 3) bemerken, anderseits aber auch andere, höchst merkwürdige, auf dem Rücken und den Seiten mit ungewöhnlich langen, beweglichen Haaren versehene »igelähnliche« Raupen (Tafel II, Abb. 6 und 7). So grundverschieden sahen diese Tiere aus, dass ich lange Zeit der Meinung war, dass tatsächlich eine Häutung stattgefunden habe, obgleich sich diese Verwandlung im Laufe von $^3/_4$ Stunden oder noch kürzerer Zeit vollzogen haben musste. Die »Igelraupen« waren etwa so gross wie die in Stadium Ia befindlichen Raupen — nur mit dem Unterschied, dass sie infolge ihrer eigentümlichen Haarbekleidung selbstverständlich viel grösser aussahen. Aus diesem Grunde war die Theorie einer stattgefundenen Häutung wenig wahrscheinlich, und die Tatsache, dass ich weder am Hinterende der Tiere noch in den Zwerg-Reagenzgläsern, worin einige Raupen isoliert gehalten wurden, jemals die kleinste Andeutung einer abgeworfenen Larvenhaut habe finden können, deutete auch nicht in dieser Richtung. Das einzig sichere Kriterium, das man tatsächlich anwenden konnte, war eine ganz genaue Untersuchung von Kopf und Prothorax. Hierbei erwies sich mit unverkennbarer Sicherheit, dass keine Häutung stattgefunden hatte, da sowohl Form und Grösse des Kopfes als auch die Prothoraxzeichnung ganz denen der Ia-Raupen entsprachen. Wie sollte man nun aber dieses plötzliche, rätselhafte Auftauchen der langen Haare erklären? Als ich die Raupen durch das binokulare Mikroskop betrachtete, machte ich die merkwürdige Feststellung, dass die Haare augenscheinlich an Grösse zunahmen. Anfangs waren sie recht kurz, allmählich wurden sie aber länger, und zuletzt hatten sie in ausgewachsenem Zustand (Tafel II, Abb. 6) eine Länge erreicht, die ungefähr der Breite der Raupe entsprach. Wie sollte man dieses schnelle Wachsen erklären?

Hier dürfte es zweckmässig sein, diese sonderbaren Raupenhaare zunächst etwas genauer zu beschreiben. Wie aus Tafel II, Abb. 6, 7 und 8, hervorgeht, haben sie eine ganz eigentümliche Form, die nicht weniger sonderbar ist als die der merkwürdigen Haare, welche A. S. Packard (1893) bei amerikanischen *Cochlididen* beschrieben und abgebildet hat. Die Raupenhaare von *Cochlidion limacodes* erinnern etwas an eine

nach unten hin allmählich dicker werdende Stecknadel. Ihre Farbe ist grünlichweiss — in der Nähe der Spitze wirken sie jedoch eher kristallklar; sie sind mit einer kleinen, hirschgeweihähnlichen, etwa 21 μ langen und etwa 13 μ breiten Seitenspitze versehen, welche in einer Entfernung von etwa 56 μ von ihrer Ausgangsstelle auf der Warze sitzt. Durch diesen Seitenauswuchs werden die etwa 260 μ langen Raupenhaare eigentlich in 3 Teile geteilt: 1. ein etwa 30 μ dickes und glattes Anfangsstück, das mit dem »Seitengeweih« endet; 2. ein schlankeres, ebenfalls glattes Zwischenstück, welches an der dünnsten Stelle etwa 9,5 μ dick ist und mit einer nicht immer gleich deutlichen Querlinie (»dem Gelenk«) endet, und 3. ein Endstück, das mit dem »Gelenk« beginnt und oben in eine keulenförmige Erweiterung von etwa 19 μ ausläuft. Im Gegensatz zu den beiden anderen Teilen des Haares ist das Endstück nicht glatt, sondern mit kleinen, nach oben gewendeten Dörnchen versehen, die an »die Zacken« auf der Haarkutikula der Haare von Säugetieren erinnern. In der Mitte des Raupenhaares bemerkt man ein deutliches, zur Spitze hin allmählich schmäler werdendes Rohr. Im dünnsten Teil des Haares wird es bedeutend schmäler und in der Nähe der Spitze wieder ampullenförmig breiter. Direkt unter der bereits erwähnten »Königskrone«, die das obere Ende des Haares bildet, wird das Rohr wieder zu einem kapillarfeinen Kanal eingeengt, der in einen kesselförmigen Boden unter der Krone auszumünden scheint. Die Seitenzacke ist an der Spitze abgerundet und sieht aus, als ob sie aus 2 zusammengekniffenen »Schnäbeln« bestehe, von welchen der obere etwas kleiner als der untere ist. Im Innern kann das Vorhandensein eines Rohres deutlich festgestellt werden, das ein gutes Stück isoliert läuft, bevor es ins Hauptrohr mündet.

Das Erscheinen dieser merkwürdigen Raupenhaare muss folgendermassen erklärt werden: zuerst stecken sie eingezogen im Boden der früher erwähnten Warzen, nur ihre Spitze erreicht ungefähr das Niveau der äusseren Haut der Raupe. Wie der eingestülpte Finger eines Gummihandschuhs durch Füllen mit Wasser wieder ausgestreckt wird, so muss man sich vorstellen, dass die erwähnten, eingestülpten Haare durch den Blutdruck herausgepresst und allmählich glatt ausgestreckt werden. Über den Zweck dieser eigentümlichen Haare[1] kann man sich nur sehr schwer eine bestimmte Meinung bilden; die wahrscheinlichste Erklärung ist wohl die, dass sie zum Schutz gegen Angriffe von seiten feindlicher Tiere dienen.

Es ist bereits erwähnt worden, dass die Raupe im Stande ist, die Haare zu bewegen, weil die Warzen, auf denen die Haare sitzen, ihre Stellung verändern können. Schon eine kleine Bewegung der Warzen kann auch die mit diesen verbundenen, langen Raupenhaare in Bewegung versetzen, da diese wie ein langer Hebel wirken. Dieser Vorgang kann an den kriechenden Raupen deutlich beobachtet werden; ihre Haare bewegen sich oft lebhaft in verschiedenen Richtungen. Von einem etwas stärkeren Farbton auf dem Rücken und dem Bauch abgesehen, haben die jungen »Igelraupen« dieselbe Farbe wie die Raupen im Stadium Ia; allmählich

[1] Ab und zu kann man auf der Spitze einiger Haare ein Flüssigkeitströpfchen beobachten.

aber geht auch, entsprechend der Zunahme der Nahrungsaufnahme, eine merkbare Veränderung inbezug auf Farbe und Form vor sich, wodurch die jungen zu den älteren »Igelraupen« übergehen.

Stadium I c.

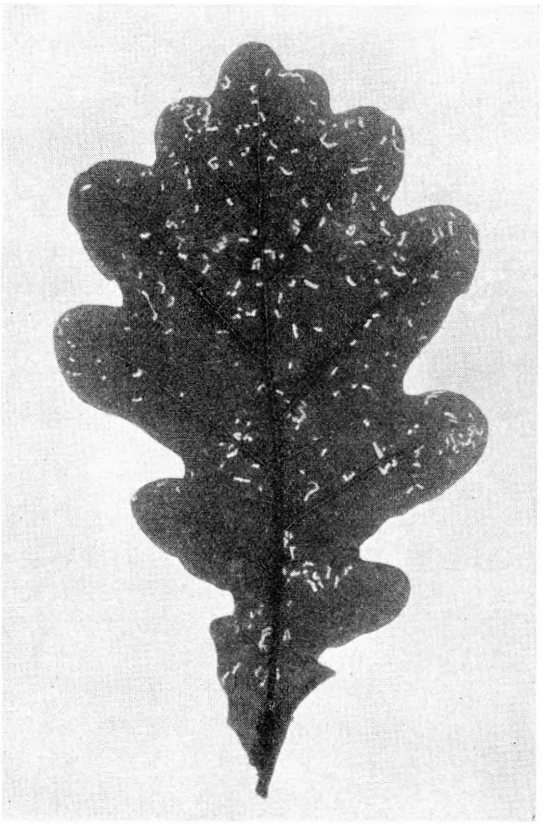
(Die ältere »Igelraupe«).

Was an den älteren »Igelraupen« (Tafel II, Abb. 8) besonders auffällt, sind ausser ihrer Grösse die eigentümlichen, grossen und kräftigen Warzen auf dem Rücken und den Seiten; danach auch die charakteristischen, mit Seitenzacken versehenen Raupenhaare, die nunmehr ihre Maximallänge erreicht haben. Die Raupenhaare sind grünlich-weiss, während die Warzen hellgrün sind. Allmählich zeigt sich auf den Rückenwarzen ein kleiner, dunkler, grünlicher Fleck, der auf der inneren Seite am Grunde der Warze deutlich durchscheint. In der Mitte des Rückens zieht sich der gewöhnliche dunkel-grünliche Streifen hin, und sowohl unter den oberen Warzenreihen als auch unter den Seitenwarzen sieht man ausserdem einen etwas undeutlichen grünlich-weissen Streifen. Im hinteren Teil des Mittelstreifens, auf der Höhe der Segmentgrenzen, ist oft auch eine Reihe kleiner, perlenförmiger, glänzend-grüner Flecke zu bemerken. Für die Warzen, deren Anzahl, Grösse und Verteilung aus Tafel II, Abb. 8, hervorgeht, ist es charakteristisch, dass sie von wenigen Ausnahmen (siehe z. B. vorn auf dem Tiere) abgesehen nur mit einem einzigen Raupenhaar versehen sind. Im Gegensatz hierzu hat die Raupe nach der 1. Häutung meist zwei Haare (Tafel II, Abb. 9). Am Ende der Periode vor der 1. Häutung tritt eine charakteristische Farbenveränderung des Raupenhaares ein; es wird nämlich bräunlich, da sich das neue Haar innerhalb des alten entwickelt. Es ist als ein dunkles, stachelförmiges Gebilde, welches die Höhe der Seitenzacke erreicht, zu sehen. Über dieser ist die Farbe auch bräunlich, was sicher auf eine degenerative Wirksamkeit in diesem Teil des Raupenhaares zurückzuführen ist. Bezüglich ihrer anderen Eigenschaften gleicht die Raupe ganz den Tieren in den beiden früheren Stadien (I a und I b). Das hellbraune Köpfchen, das fast immer ganz unter den Prothorax eingezogen ist, sieht jetzt im Verhältnis zu der Grösse des Tieres viel kleiner aus. Der Prothorax trägt, wie gewöhnlich, die charakteristische, dunkle Zeichnung, die an ein Andreaskreuz erinnert (Tafel II, Abb. 5). Auf der Unterseite bemerkt man 3 Paar kleine Thorakalbeine sowie den Hinterleib ohne Warzenfüsse. Der Bauch ist hell gelblichgrün, mit Ausnahme jener Stellen, an denen die dunklen Exkremente durchscheinen.

Biologie.

Allmählich, während die Raupe älter wird, nimmt sie eine mehr gelblich-grüne Farbe an, und wenn der Zeitpunkt der Häutung gekommen ist, ist ihre Farbe ganz blass. Die Raupe hat ausserdem eine andere Form bekommen; sie sieht kürzer und aufgeschwollener aus, und der Kopf erscheint jetzt ungewöhnlich klein. Ein Versuch,

die Raupe von ihrer Unterlage zu entfernen, kann nur schwierig durchgeführt werden, weil sie an ihrem ausgenagten Loche festgesaugt sitzt. Dies kann überall dort, wo sich die Raupen auf dem Blatte aufgehalten haben, genauer studiert werden. Gewöhnlich nagen sie auf der Oberseite der Eichenblätter, ab und zu auch auf ihrer Unterseite. Zuerst wird die Epidermis weggenagt, dann die darunter befindlichen Schichten, während die Epidermis auf der entgegengesetzten Seite immer intakt bleibt. Nur die allerfeinsten Rippen werden verzehrt, wogegen die gröberen stehen bleiben, so selbstverständlich auch alle grossen Seitenrippen und die Mittelrippe. Das Resultat der Wirksamkeit der Raupen wird deutlich sichtbar, wenn man ein benagtes Eichenblatt gegen das Licht hält (Textabb. 2). Rund um das Blatt herum sind die unregelmässigen, 1—2 mm breiten Nagespuren zu sehen, die wie silberglänzende Punkte, Striche oder Kommata aufleuchten. Am Ende der Larvengänge bemerkt man oft die kleinen, schwarzen, kugelförmigen Exkremente, welche zuweilen auch zwischen den Haaren auf dem Hinterteil der Tiere sitzen. Am Ende der Wachstumsperiode, im Stadium Ic, haben die Raupen eine Länge von etwa 1,4 mm und eine Breite von etwa 0,5 mm erreicht, und es sind ungefähr 7—8 Tage vergangen seit dem Augenblick, wo sie aus dem Ei geschlüpft sind. Nach der jetzt stattfindenden 1. Häutung sind oft die an den Blättern haften gebliebenen oder etwa noch am Hinterteile der Raupen sitzenden alten, abgelegten Larvenhäute zu sehen.



Textabb. 2. Ein von ganz jungen *Cochlidion*-Raupen benagtes Eichenblatt. Nat. Grösse.

2. Die Raupe nach der 1. Häutung.

(Larvenstadium II).

Man kann sich schwer eine phantastischere Raupe vorstellen als die nach der 1. Häutung. Das Tier, welches langgestreckt-oval ist, hat eine Länge von etwa 1,88 mm und eine Breite von 0,83 mm; die Höhe ist dagegen etwa 0,78 mm. Von oben betrachtet (Tafel II, Abb. 9) erinnert es mit seinen vielen, mit Haaren versehenen

Warzen an einen Panzerwagen mit einer Serie von Panzertürmen, die mit 1 oder 2 Kanonen ausgerüstet sind. Von der Seite gesehen (Tafel III, Abb. 10) hat die Raupe fast die Form eines hohen Brotes, von der Unterseite (Tafel III, Abb. 11) erinnert sie an eine Mumie. Wenn man das Tier von oben betrachtet (Tafel II, Abb. 9), ist der Kopf der Raupe, wie gewöhnlich, nicht zu sehen. Von der Seite kann man ihn teilweise (Tafel III, Abb. 10) erkennen, und von der Unterseite (Tafel III, Abb. 11) wird er noch deutlicher sichtbar, trotzdem er auch hier tief unter den Prothorax eingezogen ist. Der etwa 0,44 mm lange und 0,31 mm breite Kopf[1] (Tafel III, Abb. 12) ist von bräunlicher Farbe — auf beiden Seiten befinden sich jedoch 2 grössere, schmutzig-grüne Ausbreitungen (*U*). Durch die Mittellinie zieht sich eine deutliche, epikraniale Mittelfurche (*Epf*), und vor dieser liegt die dreieckige Frons (*Fr*), die an den Seiten von 2 starken, bräunlichen Linien (*S.l.*) und 2 schmalen, adfrontalen Skleriten (*ad.Scl.*) begrenzt wird. Ausserhalb, zu beiden Seiten der Frons, liegen, mit 2 ovalen, kohlschwarzen Flecken als Hintergrund, die 6 fast in einer Reihe aufgestellten Ozellen (*Oc*). Vor der Frons sieht man den Clypeus (*Cl*), wo die mit mehreren Zähnen versehenen Mandibeln (*Md*) durchscheinen. Weiter nach vorn, über den vorgeschobenen Mundteilen, ist die zungenförmige Oberlippe (*Labrum, Lbr*) zu bemerken. Unter und vor dieser sieht man wieder die charakteristische, fischschwanzförmige Unterlippe (*Labium, Lb*), welche fein längsgeriffelt und ausserdem mit 2 kleinen Unterlippenpalpen (*Palpi labiales, Lbp*) versehen ist. An den Seiten erscheinen die Unterkiefer (*Maxillae* I, *Mx*) mit ihren deutlichen Tastern (*Mxp*) auf der äusseren und den beiden Laden (*Lob*) (der äusseren Lade, *Lobus externus,* und der inneren Lade, *Lobus internus*) auf der inneren Seite. Vor den Augen sitzen die fast ganz ausgestreckten, 3-gliedrigen Antennen (*An*), die an der Spitze ausser mit mehreren kleinen Härchen mit einem langen Haar versehen sind.

Der sehr gut entwickelte Prothorax hat eine klare Farbe, erscheint aber, von oben betrachtet, dunkel, weil der Kopf durchscheint. Die Vorderbrust ist auch mit einer charakteristischen Zeichnung versehen, die ganz deutlich von jener abweicht, welche bei der Raupe vor der 1. Häutung (vgl. Tafel II, Abb. 5) zu beobachten ist. Ein mikroskopisches Präparat der Prothoraxhaut (Tafel III, Abb. 13) zeigt 2 deutliche, bräunliche Zeichnungen. Mehr nach vorne ist, in der Mitte, zuerst ein wurstförmiger, grösserer, an jedem Ende mit einer kleinen Verlängerung versehener Fleck zu sehen; dahinter befindet sich ein beinahe viereckiger Fleck, der sich nach hinten durch 2 flügelartige Verlängerungen ausdehnt. In der Mitte, längs des Rückens (Tafel II, Abb. 9), zieht sich ein tiefer, grünlicher Graben hin, der zuweilen auch einen bräunlichen Ton bekommt, da der Darminhalt durchscheint. In der Mittellinie, in der Nähe der Segmentgrenzen, sieht man im ganzen 8 weissliche Flecke, von denen der erste und letzte ziemlich undeutlich sind. Über den in der Mitte befindlichen Flecken sind ausserdem 2 mehr oder weniger deutliche Seitenflecke. Unter den 11 Paar grossen, grünen Rückenwarzen bemerkt man einen deutlichen, weisslichen Streifen (Tafel III, Abb.10), der sich in jeder Warze wie eine Mittelsäule etwas hinauf erstreckt, während die helleren

[1] Der Kopf ist mit ausgestreckten Mundteilen gemessen worden.

oder weisslich-grünen Seitenwarzen unten einen schwächeren, grünlich-weissen Streifen haben. Sowohl die Rücken- als auch die Seitenwarzen sind quergeriffelt, und die ersteren sind ausserdem mit sehr kleinen, dunkelgrünen Dörnchen versehen. Die Seitenwarzen sind dagegen mit weisslichen, keulenförmigen Härchen besetzt (Tafel II, Abb. 9; Tafel III, Abb. 10 und 11). Sowohl die Rückenwarzen als die 2 vorderen, lateral gestellten Warzen (»die Frontwarzen«) und auch die 11 Paar anderen Seitenwarzen sind mit 1 oder 2 gelbbraunen Haaren versehen, welche in ihrem äussersten Drittel braunschwarz sind. Im Gegensatz zu den Haaren der »Igelraupe« sind diese vollkommen zweiglos und stachelförmig. Alle Rückenwarzen tragen 2 solche etwa 188 μ langen Haare, während die Seitenwarzen gewöhnlich nur 1 haben. Bei den ersteren gehen ausserdem die 2 Haare von einer kleinen Warze aus, die sich wieder oben auf jeder grossen Rückenwarze befindet.

Der Bauch ist, wie bereits erwähnt, gelbbraun, und der Darminhalt scheint oft in der Mittellinie des Tieres bräunlich durch (Tafel III, Abb. 11). Man sieht den Kopf tief eingezogen hinter einem ringförmigen, faltenartigen Kragen, und der ganze Vorderteil des Tieres ist so stark zusammengezogen, dass man die 6 rudimentären Thorakalbeine nicht beobachten kann. Der gut entwickelte Hinterkörper, der zusammen mit dem Kopf und der Vorderbrust, wie bereits früher erwähnt, an eine Mumie erinnert, besitzt keine Warzenfüsse.

Biologie.

Die Raupen nach der 1. Häutung sind sehr gefrässig, und infolgedessen entstehen auf den Blättern nach ihrer Wirksamkeit viel grössere Flecken. Während die Raupen vor der 1. Häutung Nagespuren in Form von Punkten, Kommata oder Strichen hinterliessen, handelt es sich jetzt um grössere Flecken von mehr oder weniger regelmässiger Form (Tafel III, Abb. 14). Vor das Licht gehalten erscheinen sie als sehr deutliche, silberglänzende Felder im Blatt. Wenn die Raupe vor der 2. Häutung ihre maximale Grösse erreicht hat, ist sie etwa 2 mm lang und etwa 1 mm breit. Sie stellt nun die Nahrungsaufnahme eine Zeitlang ein, und die Farbe des Tieres wird merkbar bleicher, beinahe graugelb. Zuletzt, etwa 7 Tage nach der ersten Häutung, findet die 2. Häutung statt, und es sieht aus, als ob sie der Raupe grosse Anstrengungen bereite. Der Vorgang ist nämlich mit den gewaltsamsten, konvulsivischen Zusammenziehungen verbunden, die auch noch nach Ablage der Haut fortsetzen. So kann man oft beobachten, dass die alte Haut mit allen ihren vielen, stachelförmigen Haaren vor dem Tiere liegt, während dieses infolge der gewaltsamen Kontraktionen des Körpers, abwechselnd im vorderen und hinteren Drittel der Raupe je eine querlaufende, dorsoventrale Einbuchtung zeigt. Zuerst entsteht eine Einbuchtung vorn, dann eine hinten, und wieder umgekehrt. Oft sitzt die alte, abgestossene Haut mit der Kopfkapsel auf den neuen, stachelförmigen Haaren fest, ebenso wie man auch zuweilen bemerken kann, dass die alte Haut fest und breit auf der Blattfläche klebt.

3. Die Raupe nach der 2. Häutung.

(Larvenstadium III).

Nach der 2. Häutung ist die Raupe (Tafel IV, Abb. 15) etwa 2,66 mm lang, etwa 1,78 mm breit und etwa 1,44 mm hoch. Die Form ist oval oder besser eiförmig, und das Tier sieht etwas flacher aus als im vorigen Larvenstadium. Die Grundfarbe der Raupe ist grünlich, und der Kopf ist wie gewöhnlich nicht zu sehen, wenn das Tier von oben betrachtet wird. Sieht man die Raupe dagegen von der Seite (Tafel IV, Abb. 16), so wird etwas vom alleruntersten Teile des Kopfes sichtbar. Dieser (Tafel IV, Abb. 17), der eine Länge von etwa 0,58 mm und oben eine Breite von etwa 0,51 mm hat, wirkt am ehesten bräunlich. Oben, in der Mitte, ist er aber grün, und nach den Seiten hinaus befinden sich zwei grössere, graugrüne Ausbreitungen (*U*). Die epikraniale Mittelfurche (*Epf*) ist hier stark verwischt, während die vorn liegende Frons (*Fr*) an den Seiten durch 2 starke, braune Linien (*S.l.*) abgegrenzt ist. Nach der Frons folgen der Clypeus (*Cl*) und die Oberlippe (*Lbr*), die beide sehr breit und kurz sind. Vor der Oberlippe sind die beiden kräftigen, mit mehreren Zähnen versehenen Mandibeln (*Md*). An den Seiten, ausserhalb der Frons, befinden sich 2 schwarze Augenflecke mit 6 kleinen Ozellen (*Oc*). Vor diesen liegen die nur teilweise ausgestreckten Fühler (*An*) und Unterkiefer (*Mx*). Die Unterlippe ist dagegen nicht zu sehen, weil sie ganz eingezogen ist.

Die gut entwickelte Vorderbrust ist grünlich und hinten von einem weisslichgrünen Mesothorax-Vorderrand abgegrenzt; sie hat 2 gut ausgebildete und 2 schwach entwickelte Flecke. Eine Abbildung dieser Prothoraxzeichnung, so wie sie im Mikroskop zu sehen ist, bringen wir auf Tafel IV, Abb. 18. Man kann sowohl einen grösseren V-förmigen als auch einen kleineren, dahinterliegenden, fledermausähnlichen Fleck bemerken. An den Seiten, ungefähr mitten zwischen den beiden grösseren Figuren, erscheinen 2 kleine, teilweise undeutliche Flecke.

Die Farbe ist oben auf dem Rücken grün, an den Seiten jedoch heller grün. Zu beiden Seiten der Mittellinie befindet sich die gewöhnliche Doppelreihe von 11 Paar grossen, gut entwickelten, hellgrünen Wärzchen. Sie sind — mit Ausnahme des hintersten, das 3 hat — mit je 2 steifen, stachelförmigen Haaren versehen, die oft zur Spitze hin gebogen sind. Das eine Haar ist oft nach innen oder nach oben gerichtet, das andere nach aussen, und sie entspringen aus je einer kleinen, quergeriffelten Warze. Da sie sehr gut entwickelt sind, sieht es tatsächlich aus, als ob die Rückenwarzen doppelt wären. Oben in der Mitte jeder Warze befindet sich ein weisslichgrüner, zuweilen sahnefarbiger Kegel (Tafel IV, Abb. 16), welcher, von der Seite gesehen, an eine kleine Warze erinnert. Alle Warzen zusammen sind unter den grossen Rückenwarzen zu einem wellenförmigen Streifen vereinigt. In der Mittellinie, innerhalb des Warzenpaares No. 2 (Tafel IV, Abb. 15), ist ein kleiner, weisslichgrüner Fleck; vor diesem liegen 2 teilweise undeutliche Flecke. Zwischen dem 3. und 4. Warzenpaar befindet sich ein grösserer, deutlicherer, rhombischer Fleck, welcher 2 an den

Seiten befindliche kleinere Flecke vor sich hat. Die Flecke sind am ehesten hellgrün, und der grosse Fleck in der Mitte hat in seinem Innern ein quergestelltes Mittelfeld von dunklerem Grün. Im ganzen kommen 10 Mittelflecke vor, von denen der erste und der letzte sehr undeutlich, die 8 übrigen aber deutlich sind. Die 7 ersten sind von zunehmender Grösse, und die Flecke 3—8 sind besonders gross. Wenn man die Raupe von der Seite betrachtet (Tafel IV, Abb. 16), sind ausserhalb eines jeden Zwischenraumes zwischen den grossen Rückenwarzen, jedoch unter dem wellenförmigen Seitenstreifen, im ganzen 9 hellgrüne, fast dreieckige Flecke zu sehen. Am weitesten aussen befinden sich die 11 Paar grossen Seitenwarzen und die 2 Frontwarzen. Sie sind alle mit je einem grossen, stachelförmigen Haar versehen, das von der gleichen Beschaffenheit ist wie das der Rückenwarzen. Die Frontwarzen sind ausserdem mit einem sehr langen, bürstenförmigen Haar ausgestattet, und das zweite Seitenwarzenpaar hat ausser dem grossen auch noch ein kleineres, stachelförmiges Haar. Sowohl die Front- als die Seitenwarzen sind quergefurcht, glasklar und hellgrün; sie sind mit kleinen, weisslichen, keulenförmigen Haaren besetzt, im Gegensatz zu den Rückenwarzen, die mit sehr kleinen, dunkelgrünen, tropfenförmigen Flecken übersät sind von derselben Art wie die der Raupe nach der 1. Häutung. In den Zwischenräumen unter den Seitenwarzen sind etwa 8 gelblich-weisse Schrägstriche, worauf ein weisslicher, mehr oder weniger zusammenhängender Streifen folgt.

Auf der hell-grasgrünen Bauchseite sieht man oft den Darminhalt dunkel durchscheinen. Die 6 Thorakalbeine sind, wie gewöhnlich, sehr schwach entwickelt, ebenso wie auch jede Andeutung von Warzenfüssen fehlt.

Biologie.

Die Nahrungsaufnahme der Raupen ist nunmehr ganz bedeutend gestiegen, immer häufiger werden auch quer durch das Blatt Löcher genagt und grössere Blattrippen verzehrt. Das Wachstum schreitet schnell fort, und etwa 8 Tage nach der 2. findet die 3. Häutung statt.

4. Die Raupe nach der 3. Häutung.

(Larvenstadium IV).

Wenn die Raupe die 3. Häutung hinter sich hat (Tafel IV, Abb. 19), ist sie etwa 3,81 mm lang, etwa 2,31 mm breit und etwa 1,66 mm hoch. Sie ist ellipsenförmig und sieht, von der Seite betrachtet (Tafel V, Abb 20), bedeutend flacher aus. Sonst ist das Tier der Raupe in der vorigen Häutung sehr ähnlich — die Farbe ist aber oben, zwischen den beiden Warzenreihen, kräftiger grasgrün.

Wie gewöhnlich ist der Kopf (Tafel V, Abb. 21) von oben nicht zu sehen (Tafel IV, Abb. 19), und auch wenn man das Tier von der Seite betrachtet (Tafel V, Abb. 20), sieht man ihn oft nicht. Der etwa 1,49 mm lange und etwa 1,21 mm breite Kopf ist

von hellgrüner Farbe, während die Seitenteile (*U*), die jedoch einen viel kleineren Umfang haben als bei der vorigen Häutung (s. Tafel IV, Abb. 17), olivgrün sind. Als eine feine Mittellinie auf der Kopfkapsel (*Ep*) ist die epikraniale Mittelfurche (*Epf*) zu sehen, die bis zur beinahe dreieckigen, scharf abgegrenzten Frons (*Fr*) vorstösst, welche kranial mit 2 deutlichen, punktförmigen Flecken versehen ist. Kranial zur Frons sieht man den halbmondförmigen Clypeus (*Cl*) und vor diesem wieder die 2-lippige Oberlippe (*Lbr*). Diese bedeckt 2 kräftige, mehrzähnige Mandibeln (*Md*) von dunkelbrauner Farbe. Ausserhalb der Oberkiefer sitzen die gut entwickelten Unterkiefer (*Mx*), die mit je einem bedeutenden Kiefertaster (*Mxp*) samt einer mit Fühlhärchen und Fühlzäpfchen besetzten äusseren und inneren Lade (*Lobus externus* und *Lobus internus*, *Lob*) versehen sind. Weiter lateral bemerkt man die verhältnismässig kräftigen, 3-gliedrigen Antennen (*An*), welche an der Spitze ausser mit kürzeren Härchen mit einem sehr langen Haar ausgerüstet sind. Am weitesten kranial, in der Mittellinie, befindet sich die fein ausgeformte, fischschwanzähnliche Unterlippe (*Lb*). Sie ist der Länge nach deutlich fein gestreift und besitzt ausserdem lateral auf jeder Seite eine kleine Lippenpalpe (*Lbp*). In der Nähe der Fühler, ganz aussen auf der Lateralseite der Hauptkapsel, sind, mit einem schwarzen Fleck als Hintergrund, auf jeder Seite 6 fast in einer Reihe aufgestellte Ozellen (*Oc*) zu sehen.

Die gut entwickelte Vorderbrust ist von grasgrüner Farbe, und auf jeder Seite des Vorderrandes sitzen 7 weissliche Haare, von denen 2 ganz dicht nebeneinander stehen. Die Mittelbrust ist vorn sahnefarbig und mit einem orangeroten Frontstreifen und kleinen, langgestreckten Frontwarzen versehen. Oben bemerkt man eine charakteristische, olivfarbige Prothoraxzeichnung, die hinten (kaudal) mit 2 kleinen, dicht nebeneinander liegenden Flecken versehen ist. Wenn man ein Glyzerin-Gelatine-Präparat der Prothoraxhaut unter starker Vergrösserung (Tafel V, Abb. 22) betrachtet, bemerkt man eine kräftige, braune Verdickung des Chitins, die der Form nach an ein W erinnert. Hinten sind auch die 2 kleinen, quergelegenen und nicht immer deutlichen Flecke im Chitin zu sehen.

Zu beiden Seiten der Mittellinie bemerkt man die gewöhnlichen 11 Paar grossen, grünen, quergeriffelten Rückenwarzen (Tafel IV, Abb. 19), die, ebenso wie der ganze Rücken, mit den früher erwähnten, sehr kleinen, dunkelgrünen Wärzchen dicht übersät sind. Oben auf den Rückenwarzen sind 2 etwa 0,31 mm lange, stachelförmige, in ihrem äussersten Drittel schwarze Haare, die selbst aus je einem besonderen kuppelförmigen Teil der Rückenwarze entspringen, so dass diese tatsächlich aussieht, als sei sie an der Spitze doppelt. In der Mittellinie, im grasgrünen Mittelfeld, bemerkt man 10 weissliche, fast rhombische Flecke, welche in der Mitte mit je einem gräulich-grünen Querstreifen versehen sind, von dem radiäre Streifen nach unten hin ausstrahlen. Der 1. Mittelfleck, der klein ist, befindet sich vor dem 2. Rückenwarzenpaar; zwischen dem 2. und 3. sieht man einen grösseren, und zwischen dem 3. und 4. einen noch grösseren Fleck. Die Flecke 4—9 sind ziemlich gross und zwar beinahe gleich gross. Auf dem Hinterrande der Warzenpaare 2—9 einschliesslich bemerkt man einen kleineren, weisslich-grünen, länglichen, querliegenden Fleck, der

mit den grossen Mittelflecken interferiert. Die Seitenteile des Tieres sind von mehr bläulich-grüner Farbe, und man bemerkt im ganzen etwa 11 Paar quergeriffelte und mit weissen, keulenförmigen Härchen versehene Seitenwarzen, ausser dem ersten Paar, den früher erwähnten Frontwarzen. Diese sind — ebenso wie das nächste Paar (2) — mit je einem stachelförmigen Haar versehen, besitzen aber ausserdem ein langes, bürstenförmiges Haar. Die Seitenwarzen-Paare 4—12 haben auch nur ein einziges stachelförmiges Haar, das ähnlich aussieht wie die Haare der Rückenwarzen, während das 3. Paar 2 hat, die dicht nebeneinander stehen. Am Hinterende des Tieres finden sich 2 Warzen mit je 3 stachelförmigen Haaren und einer langen Bürste. Das grasgrüne Mittelfeld oben wird auf beiden Seiten von einem wellenförmigen, sahnefarbigen Streifen umrahmt, der sich auch bei dieser Häutung in jede grosse Rückenwarze kegelförmig hinaufstreckt (Tafel V, Abb. 20). Auf den Seiten bemerkt man 9 tropfenförmige, weisslich-grüne Löcher, die in der Mitte mit je einem grasgrünen Querstreifen versehen sind, von dem Radiärstreifen ausstrahlen. Oben, über diesen Seitenflecken und vor dem ersten, liegt ein kleiner, weissgelber Fleck, dann folgt einer zwischen den nächsten und hinter dem letzten. Im ganzen kommen so 10 kleinere Flecke vor, von denen der 4., 5. und 6. sehr deutlich sind. Unten erscheinen auch 9 Flecke derselben Farbe; diese sind deutlicher, insbesondere 2—7. Zwischen den grossen Seitenwarzen finden sich 9 grössere, weissliche Flecke, die aber nur etwa $^1/_3$ so gross wie die grossen Seitenflecke sind; 7 sind sehr deutlich. Unter den Seitenwarzen sieht man undeutlich auf jeder Seite 8 kleine Atemlöcher (Stigmen), und unter diesen wieder einen milchfarbigen Streifen, der in den sahnefarbigen Vorderrand des Mesothorax hinübergeht.

Die Unterseite des Tieres ist hell-seegrün, kristallglänzend und mit 3 Paar Thorakalbeinchen versehen. In der Mittellinie scheint oft der gräulich-grüne Darminhalt durch, und hier beobachtet man auch eine Furche, die zwischen einer Reihe gepaarter, von einander durch deutliche Querfurchen getrennter Wülste die Grenze zieht (vgl. die Bauchseite der Raupe nach der letzten Häutung (Tafel VII, Abb. 29)). Die Wülste müssen sicher als eine Art Ersatzorgane für die fehlenden Warzenfüsse aufgefasst werden.

Biologie.

Im Larvenstadium IV ist die Nahrungsaufnahme noch lebhafter geworden, wodurch das Wachstum ausserordentlich schnell fortschreitet. Man trifft nunmehr die Tiere nicht nur innen auf der Blättfläche an, sondern auch am Rande der Blätter, wo sie tiefe Einbuchtungen ausnagen (s. S. 24). Am Ende der Fressperiode, vor der 4. Häutung, hat die Raupe allmählich eine Grösse von etwa 6 mm Länge, etwa 3,5 mm in der Breite und etwa 2,5 mm in der Höhe erreicht. Zuletzt findet die Häutung statt — etwa 7 Tage nach der vorigen — und die abgestreifte, stark zusammengeschrumpfte, alte Larvenhaut mit ihren vielen, stachelförmigen Haaren hängt entweder auf den Blättern oder am Hinterende der neuen Haare.

5. Die Raupe nach der 4. Häutung.

(Larvenstadium V).

Die Raupen im 5. Larvenstadium sehen ganz verschieden aus, je nachdem ob es sich um junge oder alte Tiere handelt. Da man bei flüchtiger Betrachtung glauben könnte, dass inbezug auf die ältere Raupe eine Häutung vorliegt, habe ich es für zweckmässig gehalten, das Larvenstadium V in 2 Abschnitte einzuteilen: Larvenstadium Va und Vb. Wir beginnen mit der Besprechung der jungen Raupe nach der 4. Häutung.

Larvenstadium Va.

Wenn die Raupe die 4. Häutung durchgemacht hat (Tafel V, Abb. 23), ist ihre Länge auf etwa 6,21 mm, ihre Breite auf etwa 3,57 mm und ihre Höhe auf etwa 2,43 mm angewachsen. Die Form ist ellipsenähnlich oder eiförmig, wobei das Vorderende bei einem bestimmten Kontraktionszustand, wie deutlich zu sehen ist, breiter als das übrige Tier ist. Flüchtig betrachtet kann die Raupe an einen Chiton erinnern, besonders wenn man sie von der Seite sieht (Tafel VI, Abb. 24); ihre Grundfarbe ist grünlich.

Wie bei den früheren Larvenstadien ist der Kopf (Tafel VI, Abb. 25) von oben nicht zu sehen (Tafel V, Abb. 23) — betrachtet man dagegen das Tier von der Seite (Tafel VI, Abb. 24), kann man oft einen beträchtlichen Teil des Kopfes erkennen. Der Kopf (Tafel VI, Abb. 25) ist etwa 1,72 mm lang und etwa 1,38 mm breit und von hellgrüner Farbe; die Seitenteile (*U*), besonders um die Augen herum, sind olivfarbig. Die Mittellinie ist mit einer epikranialen Mittelfurche (*Epf*) versehen, die kaudal am deutlichsten ist. Kranial zu dieser ist die beinahe dreieckige Frons (*Fr*), die auf beiden Seiten von 2 starken, nach vorn auseinanderlaufenden Linien abgegrenzt wird (*S.l.*). Danach bemerkt man den bikonvexen Clypeus (*Cl*) und vor diesem wieder die herzförmige Oberlippe (*Lbr*). Ganz aussen kranial auf der Kopfkapsel (*Ep*) sind, auf schwarzem Hintergrunde, auf jeder Seite 6 dicht aneinanderliegende Ozellen (*Oc*) zu sehen. Innerhalb dieser bemerkt man die gut entwickelten 3-gliedrigen Antennen (*An*), welche an den äussersten Spitzen mehrere Haare tragen, von denen eines besonders lang ist. Unter der Oberlippe sieht man die 2 grossen, mit mehreren Zähnen ausgerüsteten, kastanienbraunen Mandibeln (*Md*). Lateral hierzu liegen die Unterkiefer (*Mx*) mit einem deutlich sichtbaren Kiefertaster (*Mxp*) und einer äusseren und einer inneren Lade (*Lobus externus* und *Lobus internus*, *Lob*), welche mit Fühlapparaten besetzt sind. Ganz vorn in der Mittellinie bemerkt man die eigentümliche, fischschwanzähnliche Unterlippe (*Lb*), die der Länge nach fein gestreift ist. Zu beiden Seiten der Mittellinie ist sie ausserdem mit 2 kleinen, je in ein langes Haar endenden Lippenpalpen (*Lbp*) versehen.

Die Vorderbrust ist grün und wohl entwickelt; die Mittelbrust hat auf der Seite einen milchweissen Streifen, welcher nach vorn hin in einen mehr sahnefarbigen übergeht. Der Vorderrand ist hier mit vielen Wärzchen bedeckt; er ist unten von rötlicher Farbe und hat in der Mittellinie einen grösseren, rötlichen Fleck. Auf der Seite des Prothorax ist zugleich ein sehr grosses und deutliches Atemloch und

oben auf der Brust eine charakteristische, olivfarbige Zeichnung, die an 2 nebeneinanderliegende Kommata erinnert, zu erkennen. Dies wird besonders deutlich auf einem Glyzerin-Gelatine-Präparat der Prothoraxhaut (Tafel VI, Abb. 26), auf dem sich die Zeichnung als eine bräunliche Verdickung des Chitins erweist. Ebenso wie im Larvenstadium IV, befindet sich oben auf dem Rücken (Tafel V, Abb. 23) ein grasgrünes, von 11 Paar grossen, grünen Rückenwarzen flankiertes Mittelfeld. In der Mittellinie des Feldes bemerkt man 11 weissliche, rhombische Flecke, die alle in der Mitte mit einem silbergrauen, quergelegenen Fleck versehen sind, von welchem, besonders nach unten hin, deutlich sichtbare Radiärstreifen ausgehen. Der erste Fleck in der Mitte ist klein und liegt am Vorderrande des 2. Rückenwarzenpaares, der 2. und 3. Mittelfleck sind grösser, und die Flecke 3—7 sind sehr gross; danach nehmen sie deutlich an Grösse wieder ab. Innerhalb eines jeden Rückenwarzenpaares sind 2 kleinere, querliegende, weissliche Flecke von mehr oder weniger dreieckiger Form. Die Rückenwarzen dominieren übrigens nicht so stark wie nach der vorigen Häutung, da es sich hier meist um flache Kegel handelt. Oben auf diesen sind 2 kuppelförmige Wärzchen zu sehen, die mit einem hellbraunen, etwa 344 μ langen, stachelförmigen, im äussersten Drittel schwarzen Haar ausgerüstet sind. Hierdurch wird der Eindruck erweckt, als seien die Rückenwarzen doppelt. Sie sind übrigens, ebenso wie die ganze Rückenseite des Tieres, mit vielen kleinen, dunkelgrünen Warzenbildungen übersät, und innerhalb jeder Rückenwarze beobachtet man eine kegelförmige Verlängerung des grossen, wellenförmigen, weisslich-grünen Streifens, der unten alle Rückenwarzen miteinander verbindet (Tafel VI, Abb. 24). Die Seitenteile des Tieres sind von hellerer grüner Farbe, und die grossen Seitenwarzen sind fast hellblaugrün. Es sind, wie gewöhnlich, 1 Paar Frontwarzen und 11 Paar Seitenwarzen vorhanden, die alle quergeriffelt und mit einem grossen, stachelförmigen Haar versehen sind. Unter dem Rückenstreifen bemerkt man 10 weissgelbe Fleckchen, danach eine Reihe grösserer, ovaler Flecke mit einem dunkelgrünen Mittelfleck. Unter dem Rückenwarzenpaar No. 2—9 gibt es im ganzen ausser einem kleineren, halbmondförmigen Fleck von hellerer Farbe zwischen dem 1. und 2. Warzenpaar 9 solche grosse, längliche Flecke. Unter den grossen Seitenflecken befindet sich eine neue Reihe Flecke, so ein kleiner Seitenfleck unter dem 2., unter dem 3. ein grösserer, auf jeder Seite des 4. ein kleiner, unter dem 5. ein kleiner, ein grösserer zwischen dem 6. und 7., ein kleiner unter dem 7., ein grösserer zwischen dem 7. und 8., ein kleiner unter dem 8., ein grösserer zwischen dem 8. und 9., ein kleiner unter dem 9. und ein grösserer nach dem 9; endlich eine Reihe gelber Flecke, von denen der erste am Grunde des 1. Seitenstachels liegt. Unter den Seitenwarzen sind auf jeder Seite 8 Atemlöcher zu bemerken, ausser — wie schon erwähnt — einem silberglänzenden auf dem Prothorax. Unter diesen beobachtet man wieder den bereits erwähnten milchartigen, auf einem hervorstehenden Seitenwall angebrachten Streifen.

Die Farbe des Bauches ist hellgrün; auf der Unterseite der Brust sieht man die 6 Brustfüsschen, die beinahe glasklar, am Ende jedoch mit einer bräunlichen Tarse versehen sind. Die abdominale Mittelfurche und die Seitenbuckeln sind ausserdem deutlicher als im Larvenstadium IV.

Das Larvenstadium Vb.

Wie schon erwähnt (S. 22) ist der Schluss des 5. Larvenstadiums einer selbständigen Häutung ähnlich. Dass eine solche jedoch nicht stattgefunden hat, ergibt sich sowohl aus Form und Grösse des Kopfes als aus der noch immer unveränderten Zeichnung der Vorderbrust. Die Farbe des Tieres hat sich dagegen nach gelblich-grün verändert, und die 2 dorsalen Längsstreifen sind weissgelb oder crèmefarbig geworden. Auch alle Rücken- und Seitenflecke sind viel gelblicher, und es zeigen sich jetzt, auf der Innenseite jeder Rückenwarze heidekrautfarbige, längslaufende Flecke. Die Mitte des Rückens ist gelblich-grün, die Seitenfelder sind grünlicher — weiterhin sogar von grünlich-bläulicher Schattierung. Das ganze Tier ist ovaler und plumper, und die Seitenwarzen sind nicht mehr so schlank, sondern breiter abgestumpft. Von der Seite gesehen sind die Rückenwarzen fast ganz verschwunden; es erscheinen nur einige sehr flache Kegel. Die gewöhnlichen, winzig kleinen, dunkelgrünen Tröpfchen sind überall auf dem Tiere zu sehen, und man hat den Eindruck, dass sich die Rückenhaut von der darunter liegenden, neugebildeten Haut abhebt. Der Seitenstreifen unter den Seitenwarzen ist milchig-weiss, weisser als anfänglich. Er geht nach vorn hin in einen sahnefarbigen Streifen über, der unten orangerot ist.

Der Prothorax ist grasgrün und oben mit einer mehr oder weniger verwischten Zeichnung versehen; auf dem Mesothorax scheint nach vorn hin in der Mittellinie ein schwacher rötlicher Fleck durch. Der Bauch ist hell-seegrün mit deutlichen Segmentgrenzen und einer Längsfurche in der Mitte; die 6 kleinen Thorakalbeine sind deutlich sichtbar.

Biologie.

Die Raupen sind nun fast immer aussen am Blattrande anzutreffen, wo grosse Einbuchtungen Zeugen ihrer Wirksamheit sind. Die Art des Nagens der Tiere ist ganz eigentümlich, soll aber erst unter Larvenstadium VI (s. S. 26–27) genauer beschrieben werden. Vor diesem hat die Raupe eine Länge von etwa 9 mm, eine Breite von etwa 6 mm und eine Höhe von etwa 3 mm. Wenn nach der vierten Häutung etwa 8 Tage vergangen sind, findet die fünfte statt.

6. Die Raupe nach der 5. Häutung.

(Larvenstadium VI).

Wenn die Raupe die 5. Häutung durchgemacht hat, ist sie etwa 10,71 mm lang, etwa 5,64 mm breit und etwa 4,21 mm hoch. Sie hat nun ihr Aussehen vollständig verändert, nachdem die grossen, stachelförmigen Haare ganz verschwunden sind[1]. Von oben gesehen (Tafel VII, Abb. 27) wirkt die Form eher oval. Betrachtet

[1] Eine Raupe, die unmittelbar vor der 5. Häutung, bei der Überführung zu neuem Futter, reichliche Flüssigkeitsmengen an die Blattoberfläche abgab, behielt einige stachelförmige Haare, obgleich in defektem Zustande. Sie machte später eine 6. Häutung durch, nach der jegliche Spur stachelförmiger Haare verschwunden war.

man das Tier dagegen von der Seite (Tafel VII, Abb. 28), erscheint es mehr gurkenförmig. Das junge Tier ist von gelb-grüner Farbe, während die etwas ältere Raupe schmutzig weisslich-grün ist. Wie gewöhnlich ist der Kopf von oben nicht zu sehen (Tafel VII, Abb. 27), dagegen ist etwas von ihm zu erkennen, wenn man die Raupe von der Seite (Tafel VII, Abb. 28) betrachtet. Er (Tafel VIII, Abb. 30) ist etwa 2,08 mm lang, etwa 1,70 mm breit, und oben von einem stärkeren Grün als an den Seiten. Die epikraniale Mittelfurche (*Epf*) ist sehr undeutlich; statt dessen ist ein keilförmiges Feld (*Fe*) vorhanden, welches fast die Hälfte der Länge des Kopfes einnimmt. Kranial stösst es zur Frons (*Fr*), die ungefähr dieselbe Form hat wie das Feld, deren Seiten aber durch 2 nach vorn hin divergierende, braune Linien (*S.l.*) scharf abgegrenzt sind. Vor der Frons liegt der bikonvexe Clypeus (*Cl*) und davor die beinahe viereckige, gelbbraune Oberlippe (*Lbr*). Unter ihr und lateral zu ihr fallen die grossen, mehrzähnigen, kastanienbraunen Mandibeln (*Md*) auf. Vor diesen bemerkt man zu beiden Seiten die 2 starken Unterkiefer (*Mx*) mit ihren gut entwickelten Kiefertastern (*Mxp*) samt der äusseren und inneren Lade (*Lob*); beide Laden sind mit Fühlhärchen und Fühlzäpfchen versehen. Weiter vorn in der Mittellinie sieht man die Unterlippe (*Lb*), welche nun nicht mehr wie ein Fischschwanz geformt, vielmehr mit einem umgekehrt herzförmigen Spinnzapfen (*Fusulus, Fu*) und 2 kleinen, lateral gestellten Lippenpalpen (*Lbp*) versehen ist. Lateral zu den Mandibeln befindet sich auf jeder Seite ein langes, bürstenförmiges Haar (*H*); über diesem springt eine gut entwickelte, 3-gliedrige Antenne (*An*) aus, die am Ende einige kurze Härchen und ein langes Haar trägt. Die Fühler sind unten weisslich und an der Spitze bräunlich; lateral zu ihrer Ausgangsstelle bemerkt man auf schwarzbraunem Hintergrund die 6 fast in einer Reihe stehenden Ozellen (*Oc*).

Der Prothorax ist gut entwickelt und von stark grüner Farbe; der Vorderrand des Mesothorax ist von einem gelblichen Streifen umrahmt. Ganz unten hat dieser jedoch eine orange-rötliche Farbe, welche in einem median-gerichteten grösseren Fleck samt in mehr oder weniger deutlichen Flecken auf beiden Seiten des grossen Flecks lokalisiert ist. Auf der Seite der Vorderbrust ist ein grosses, auffallendes Atemloch zu sehen, zu dem ein silberglänzender Trachéenstamm führt; oben bemerkt man 2 olivfarbige Fleckchen in geringem Abstand voneinander. Ein Glyzerin-Gelatine-Präparat der Prothoraxhaut zeigt unter starker Vergrösserung (Tafel VIII, Abb. 31), dass es sich um 2 braune, am ehesten rhombische Verdickungen von Chitin handelt. Kranial zu diesen befinden sich ausser einer schwach chitinisierten, schwanzförmigen Verdickung, die lateral von jedem dieser grossen Flecke ausgeht, 2 ringförmige Fleckchen.

Die etwas ältere Raupe ist zu beiden Seiten der Mittellinie, den Rücken entlang, mit einem gelben Streifen versehen, in dessen innerer Kante 9 kirschrote, langgestreckt-ovale Flecke (Tafel VII, Abb. 27) liegen. Innerhalb der ersten rötlichen Flecke befinden sich 2 gelblich-grüne, querstehende, ovale Flecke, ebenso, immer grösser werdend, innerhalb der folgenden roten Flecke; in der äussersten Spitze dieser Querflecke sieht man einen dunkelgrünen Fleck. Mitten zwischen

den beiden vordersten Paaren roter Flecke erkennt man einen gelblichen Mittelfleck, der weiter nach hinten auf dem Rücken grösser und mehr viereckig wird; der gelbe Mittelfleck umschliesst 2 dicht nebeneinanderliegende, dunkelgrüne Flecke auf jeder Seite. Hinter dem letzten der im ganzen 9 Mittelflecke, liegt noch ein gelblicher Fleck, ohne grüne Färbung. Unter dem gelben, gewellten Streifen sieht man 12 gelbliche Fleckchen, die vorn mit einem kleinen, grünlichen Fleck (Tafel VII, Abb. 28) versehen sind. Unter diesen Seitenflecken liegen wieder 12 sehr grosse, am ehesten tropfenförmige, grünliche Flecke mit dunklerer Mitte. Diese »Augenflecke« liegen in entsprechenden Vertiefungen. Unter diesen Flecken verläuft ein stark hervorstehender Seitenwall, dessen äusserer Umriss eine deutlich gewellte Linie (Tafel VII, Abb. 27) bildet, den Stellen entsprechend, wo bei der vorigen Häutung die Seitenwarzen gesessen haben. Auf dem Seitenwall findet man 3 Reihen Flecke untereinander, deren erste aus 8 grösseren, winkelförmigen und 8 kleineren, runden Flecken zwischen diesen besteht. Ganz unten, am Rande des Walles, sind 9 gelbliche Flecke, und zwischen ihnen 9 kleinere, weissliche Flecke vorhanden. Die grösseren, gelblichen liegen in den Zwischenräumen unter den winkelförmig gebogenen Flecken. Der Seitenwall ist, ebenso wie das ganze Tier, mit zahlreichen grünlichen, tropfenförmigen Fleckchen (Tafel VII, Abb. 27, 28 und 29) versehen. Unter dem Seitenwall befinden sich auf jeder Seite 8 deutliche Stigmen von weisslicher Farbe mit einem dunkelgrünen Ring. Unter den Stigmen sieht man wieder 10 lichtgrüne »Augenflecke« mit dunkelgrüner Mitte, und ganz unten bemerkt man einen weisslichen Streifen (Tafel VII, Abb. 28), der sich in den früher erwähnten, gelblichen Streifen längs dem Vorderrande des Mesothorax fortsetzt (s. auch Tafel VII, Abb. 29). Längs der Aussenseite des Tieres, besonders nach vorn hin und ausserdem oben, stehen vereinzelte Haare, von denen zwei nach hinten hin länger sind als die anderen.

Während die Oberseite des Tieres mehr weisslich-grün und die Seitenteile eher bläulich-grün sind, ist die Unterseite von hell-seegrüner Farbe. Durch die Mittellinie (Tafel VII, Abb. 29) zieht sich eine tiefe, deutliche Mittelfurche, und auf beiden Seiten sind 8 kräftige Buckeln hintereinander zu sehen. Diese dienen als eine Art Ersatzorgane für die fehlenden Warzenfüsse, was deutlich festgestellt werden kann, wenn das Tier auf einer Glasplatte kriecht. Vorn, auf der Unterseite des Thorax, bemerkt man die 6 kleinen, kegelförmigen, an der Spitze mit einer bräunlichen Kralle versehenen Brustfüsse. Am auffallendsten ist jedoch der starke, wallähnliche und hufförmige Prothoraxkragen, unter welchem sich die eingezogenen Mundteile und der Kopf verstecken. Unter den Mundteilen erscheinen besonders die Unterlippe mit dem Spinnzapfen und den Palpen und oben die Maxillen.

Biologie.

Im Gegensatz zu den früheren Larvenstadien, während deren die Nahrungsaufnahme meist innerhalb der Blattoberfläche geschah, findet sie nun gewöhnlich am Blattrande statt. Es war für die kleine Raupe charakteristisch, dass die Nahrungsauf-

nahme unten auf dem Boden des Areals vor sich ging, das das Tier im Blattfleisch ausgenagt hatte. Hier saugte es sich so fest, dass es nur mit Gewalt von der Unterlage losgemacht werden konnte. Die Nahrungsaufnahme selbst geschah unter Deckung des Prothorax, und den Kopf konnte man deshalb nicht von oben sehen. In den letzten Larvenstadien (s. S. 24) kommt die Raupe dagegen ungefähr parallel zum Blattrand zu sitzen, während sich der vordere Teil des Körpers so stark gedreht hat, dass er im Plan des Blattes liegt. Der Kopf ist nicht zu sehen, er ist unter dem mächtigen, hutförmigen Prothorax versteckt, dessen vorderer Rand reiterartig den Blattrand umfasst. Der Vorderteil des Tieres sitzt auf diese Art so fest, dass er nicht vom Blatt abzuschütteln ist, selbst wenn sich der übrige Teil des Körpers losmacht. Wenn man versucht, die Raupe mit einer Pinzette abzunehmen, muss man gewöhnlich recht kräftig zupacken, wobei fast immer eine Beschädigung mit damit verbundenem Bluten eintritt. In ausgestrecktem Zustand (vgl. den eingezogenen Zustand auf Tafel VII, Abb. 29) bildet der Prothorax einen so geräumigen Hohlraum, dass das Tier ohne Schwierigkeit mit den Mandibeln und den anderen Mundteilen darin arbeiten kann. Der Gedanke ist vielleicht naheliegend, dass diese eigentümliche Fresstellung auf eine biologische Zweckmässigkeit zurückzuführen ist. Die Raupe ist nämlich nicht nur fest am Blatt verankert, sondern die Nahrungsaufnahme kann ausserdem auch von eventuellen Feinden unbemerkt stattfinden.

III. Der Kokon und die Kokonbildung.

Wenn die Raupe im 6. Larvenstadium vollständig ausgewachsen ist, beträgt ihre Länge etwa 12,5 mm, ihre Breite etwa 7,5 mm und ihre Höhe etwa 4,5 mm. Sie hat nun eine typisch gelbliche Schattierung mit bleichen Farben angenommen und stellt die Nahrungsaufnahme ein. Von der Seite gesehen ist ihre Form hoch gewölbt (vgl. Tafel VII, Abb. 28) und erinnert etwas an die einer Landschildkröte. Die Raupe sucht einen passenden Ort auf, wo sie sich verpuppen kann, gewöhnlich zwischen zwei aneinanderliegenden Blättern oder in einem an der Spitze aufgerollten Blatt. Erst spinnt sie einige gröbere, breitere, gelbbraune Fäden von Blatt zu Blatt, wohl hauptsächlich, um die Blätter zu fixieren. Daraufhin umgibt sich das Tier mit einem sehr dichten Gespinst, wodurch ein regelmässiger, ovoider Kokon von etwa 7—8,5 mm Länge und etwa 5—6 mm Breite entsteht. Der Kokon, der, wenn die Imago herausschlüpft, mit einem Deckelchen geöffnet werden kann, ist anfänglich gelbbraun, am nächsten Tag aber schon rostfarbig, und später rotbraun. Wie bereits auf S. 5 erwähnt, fällt der Kokon mit den festgesponnenen Blättern auf die Erde, wenn das Laub abfällt, und die Überwinterung geschieht im Larvenstadium. Erst ein gutes Stück in das neue Jahr hinein verwandelt sich die Raupe zur Puppe, die gegen Ende Juni als Imago ausschlüpft.

Die Puppe.

Da ich in der Literatur weder eingehendere Beschreibungen noch befriedigende Abbildungen der Puppe habe finden können, will ich ihr Aussehen hier genauer besprechen.

Während, wie oben erwähnt (s. S. 27), die Überwinterung im Larvenstadium vor sich geht, findet die Verpuppung erst im späten Frühling statt. Schneidet man zu dieser Zeit vorsichtig mit einer spitzen Schere ein Loch in den Kokon, so dass ein länglicher, leicht zu entfernender Deckel entsteht, kann die Puppe herausgenommen werden. Man kann sie auf diese Weise jeden Tag nach stattgehabter Betrachtung wieder in ihr natürliches Gehäuse zurücklegen. Um ein Austrocknen des Kokons zu verhindern, muss er in einer Glasdose mit etwas feuchter Watte angebracht werden. Es bleibt aber auch dann noch schwer, die Puppe längere Zeit in lebendem Zustand zu erhalten, wenn sie schon einmal aus ihrem Kokon herausgenommen ist.

Die Puppe ist etwa 7,75 mm lang und etwa 4,48 mm breit; Bilder der Puppe, vom Rücken und Bauch samt der Seite gesehen, befinden sich auf Tafel IX, Abb. 32—34 (12×). Hieraus geht hervor, dass die Form des Tieres am ehesten ovoid ist. Eine Puppe, die am $^{22}/_{6}$ aus ihrem Kokon herausgenommen wurde, zeigte eine ganz helle, grünliche Farbe. Betrachtet man das Tier von der Bauchseite (Tafel IX, Abb. 32), bemerkt man die grossen, ovalen Augen, welche anfänglich bräunlich pigmentiert sind, später aber, im Laufe der Entwicklung, eine kohlschwarze Farbe annehmen; sie sind 0,77 mm lang und 0,69 mm breit. In dem 0,8 mm breiten Zwischenraum zwischen den Augen ist ein pyramidenförmiges, hervorstehendes Gebilde[1] zu sehen, das in eine schwach gebogene, braune und stark chitinisierte Spitze endet. Unter dem binokularen Mikroskop ist die Gesichtsfarbe übrigens hell-gelbbraun, wogegen die Mundteile etwas dunkler sind. In der darunterliegenden Mittellinie sieht man die fünfeckige Oberlippe (*Labrum*), die 0,4 mm breit und 0,23—0,29 mm hoch ist, während die fast viereckigen Maxillen-Anlagen auf jeder Seite 0,26 mm lang sind. Die gut entwickelten, trommelstockförmigen Labialpalpen in der Mittellinie haben eine Länge von 1,14 mm. Ausserhalb der Augen bemerkt man die sehr langen, reichgegliederten Fühler, welche längs dem Aussenrande des 2. Beinpaares liegen und allmählich gegen die Mittellinie des Tieres schwingen; sie sind 0,4 mm breit und von gelbweisser Farbe, während die Aussenseite mit einer feinen, dunkelbraunen Linie eingefasst ist. Zu beiden Seiten der Fühler bemerkt man starke Flügelanlagen, die in eine stumpfe Spitze auslaufen, welche sich in der Mitte des Stückes befindet, mit welchem das 3. Beinpaar frei hervorragt. Die quergehenden Flügelrippen in den Vorderflügeln hören dagegen schon am Ende des 2. Beinpaares und der Fühler auf. Das Mittelfeld in den Vorder- und Hinterflügeln ist am ehesten weisslich, wogegen die Kante gelblicher ist. Die starken Beine sind 0,34 mm breit, und ihr Ende ist von weissgelber Farbe; das gilt im besonderen für das frei hervorragende Glied des 3. Beinpaares. An den Beinen scheinen die bräunlichen Klauen deutlich durch. Unter den Flügelanlagen sind 3 deutliche, ovale, mit einem dunkelbraunen Chitinring umrahmte Atemlöcher zu bemerken; sie sind 0,14 mm breit und 0,11 mm lang.

[1] Vermutlich zum Öffnen des Kokons berechnet.

Wenn man die Puppe von der Rückenseite (Tafel IX, Abb. 33) betrachtet, sieht man, dass das Tier über dem Nacken mit einem grossen, zungenförmigen Schild, der die Spitze kaudal wendet, versehen ist. In der Nähe dieser Spitze sind 2 deutliche, ringförmige Figuren nebeneinander zu bemerken. Unten sieht man die starken Abdominalringe, von denen im ganzen 10 (vgl. auch Tafel IX, Abb. 34) vorhanden sind. Der erste Abdominalring, welcher der Spitze des Nackenschildes folgt, ist etwas schmäler als die nächsten. Alle Glieder sind in der Mitte breiter und nach den Seiten hin schmäler; sie sind mit einem 0,17—0,23 mm breiten Streifen von dornenartigen, dunkelbraunen Bürstchen versehen. Die Farbe der Abdominalsegmente ist gelblich, während der Nackenschild und die Flügel aussen auf den Seiten mehr weissgelblich sind. Längs des Rückens beobachtet man in der Mitte einen dunkleren, eher schwarzblauen Streifen, der nach hinten zu verschwindet; er ist vorn breiter, und zwar 0,86 mm, während er weiter nach hinten nur 0,67 mm breit ist.

Schon 3 Tage nach der 1. Herausnahme aus dem Kokon ($^{25}/_{6}$) ist die Farbe der Puppe auf der Bauchseite (Tafel IX, Abb. 32) mehr schwarzbraun geworden. Der Stirnwulst, die Stirn und die Maxillen sind jetzt braun, ebenso auch die Fühler, während die Augen grauschwarz sind. Die Flügelscheiden sind hauptsächlich mit grossen, schwarzen Flecken versehen; es kommen jedoch auch im Vorder- und Hinterrande braune vor. Die Beine sind unten gelblich-weiss, oben aber mehr weisslich-grün; die Behaarung scheint deutlich durch, und die Flügel längs den Fühlern sind ebenfalls braun. An der Spitze der Beine bemerkt man die Krallen, die nun eine schwarze Farbe angenommen haben. Auf der Rückenseite (Tafel IX, Abb. 33) sind der Nackenschild und die Flügelanlagen schiefergrün geworden, während der Mittelkiel des Nackenschildes von einem helleren Grün ist. Pro-, Meso- und Metathorax sind grau; der längsgefurchte Metathorax ist jedoch vorn von gelbgrauer Farbe. Die Abdominalsegmente sind gelblich, unten auf den Seiten jedoch stärker gelb. Oben auf den Abdominalringen befinden sich die früher erwähnten rostfarbigen Chitindörnchen, deren Spitze nach hinten gerichtet ist; die Segmenträndер sind dagegen hinten grau.

5 Tage nach der 1. Herausnahme des Kokons ($^{27}/_{6}$) ist die Chitinisierung weiter fortgeschritten: die Oberlippe und die Unterkiefer sind graubraun, während die Labialpalpen und der Stirnwulst von brauner Farbe sind. Die Augen sind schiefergrün, die Fühler jedoch braun, an der Spitze aber mehr weissgelb. Die Flügelanlagen sind nun schwärzer, mit braunen Flecken in einem in der Mitte befindlichen Gürtel. Die Beine sind grau, das distale Stück aber heller, am ehesten gelblich-grün. Der Nackenschild und die Flügelscheiden sind nach aussen, zur Seite hin, von der Rückenseite des Tieres aus gesehen (Tafel IX, Abb. 33) grau, mit einer grünlichen Schattierung. Die Abdominalringe sind dagegen braun, nach hinten hin grau; das letzte Segment ist ebenfalls grau.

7 Tage nach der 1. Herausnahme des Kokons ($^{29}/_{6}$) — und wahrscheinlich kurze Zeit vor dem Erscheinen der Imago — sind nunmehr die Augen ausgesprochen grau

geworden, mit einem dünnen, längslaufenden schwarzen Streifen. Die Oberlippe und die Maxillen haben eine tiefer graubraune Farbe, während die Labialpalpen noch immer braun sind. Die Fühler sind auch braun, der letzte Teil ist aber bedeutend heller, nämlich von derselben Farbe wie der periphere Teil der Beine. Die Flügelscheiden sind schwarz mit brauner Schattierung, besonders in der Mitte. Die Hinterkörperringe sind schwarzgrau mit breitem, schwarzem Unterrand und durch gelblich-weisse Gelenkhäute voneinander getrennt. Oben sind die Abdominalsegmente einschliesslich 2—8 mit einer rostfarbigen Oberkante versehen, während die mittlere Partie der Ringe mehr gelblich-braun ist.

Die Beobachtungen mussten hier leider eingestellt werden, weil die Puppe starb; ich kann sie aber durch die Beschreibung einer anderen Puppe, die am 13. Juni eines anderen Jahres, einen Tag vor dem Schlüpfen zum Schmetterling, aus ihrem Kokon herausgenommen wurde, ergänzen: Die Puppe hat eine matte, bräunliche Farbe und ist, wie gewöhnlich, dadurch charakterisiert, dass die Fühler, die Flügelanlagen und die Gliedmassen ziemlich frei auf der äusseren Seite des Tieres liegen. Der Stirnauswuchs zwischen den gelblich-braunen Augen ist bräunlich und mit 2 schwarzen Flecken versehen. Die Augen sind in der Mitte mit einem runden, dunklen Fleck und einem der Länge nach laufenden, bräunlichen Streifen versehen. Die Beine, Fühler und Labialpalpen sind hellbraun; letztere haben eine weissliche Spitze; Oberlippe und Unterkiefer sind dagegen mehr braun. Die Flügelscheiden sind dunkelbraun, und die vorderen Flügel haben 2 schwarze, linienförmige Querbänder, von welchen das eine (distale) abgebrochen ist. In der äussersten Kante des Flügels erscheint dagegen ein breites, schwarzes Querband. Die Farbe der Hinterflügel ebenso wie der Ring, von welchem sie ausgehen, ist mehr gräulich; unter der Insertionsstelle kann man zugleich auf jeder Seite einen dunkleren Fleck beobachten. Der Nackenschild ist hellbraun, während die Hinterkörperringe, besonders in den lateralen Partien, gelblich sind. In ihrem oberen Teile wirken sie dagegen, infolge der zahlreichen, dichtstehenden Dörnchen, am ehesten rotbraun, während der untere Teil mit schwarzen, nadelförmigen Zeichnungen versehen ist; das letzte Hinterkörpersegment ist von gelblicher Farbe. Lateral auf den Abdominalringen sind mehrere Atemlöcher zu sehen, die mit einem bräunlichen Ring umgeben sind. Wenn man das Tier von der Dorsalseite betrachtet, kann man deutlich beobachten, wie sich das in der Mitte gelegene, hellgelbe und saitenförmige Herz rhythmisch kontrahiert.

Die abgeworfene Puppenhaut ist weisslich-gelb und mit bräunlichen Mundteilen und bräunlichem Stirnauswuchs versehen; die obere Hälfte der Abdominalsegmente ist stark braun.

In der Literatur sind so viele gute Beschreibungen und Abbildungen der Imago zu finden, dass ich mich nicht veranlasst fühle, diese in der vorliegenden Abhandlung eingehender zu besprechen.

F. Übersicht.

Cochlidion limacodes Hufn. ist ein kleiner (die Flügellänge ist ca. 1 cm), ockergelber Nachtschmetterling, der hauptsächlich in den südlichen Teilen von Dänemark vorkommt. Seine Raupen sind sehr eigentümlich: sie erinnern an nackte Schnekken. Da die Literatur eine genaue Beschreibung des Aussehens und der Biologie der Raupe in den verschiedenen Larvenstadien sowie der Anzahl der Häutungen vermissen lässt, ist es das Hauptziel der vorliegenden Untersuchung, einiges hierüber mitzuteilen. Zu diesem Zwecke war es nötig, Züchtungen von Raupen aus Eiern vorzunehmen und gleichzeitig das Einsammeln von Raupen und Imagines zu betreiben.

In der Natur legt das Weibchen etwa 100—200 Eier einzeln z. B. auf Eichenblätter, im Laboratorium aber setzt es seine Eier willig auf der Innenseite der Glasdosen, in denen es eingesperrt gehalten wird, ab. Die Eier, welche bevorzugt in der Nacht abgelegt werden, sind etwa 0,90 mm lang und etwa 0,65 mm breit; sie sind oval und bilden eine flache Kuppel. Das frisch abgelegte Ei ist gelblich-weiss; die Eierschale hat auf der Aussenseite das Muster eines Stahldrahtnetzes. Im spitzen Ende befindet sich oft das Mikropylfeld, welches etwa 6—8 feine, zum Durchgang der Spermien bestimmte Mikropylkanäle hat. Die Schlüpfungszeit ist, der Temperatur entsprechend, 8—10 Tage im Juni und im Juli.

Die frisch ausgeschlüpften Raupen sind 0,88—1,02 mm lang und 0,40 mm breit; ihre Form ist flachgedrückt walzenförmig, ihre Farbe hellgrün mit einem dunkleren, grünlichen Streifen in der Mittellinie des Rückens. Auf dem Rücken befindet sich zu beiden Seiten der Mitte je eine Reihe lampenkuppelförmiger Warzen, die oben mit einem kleinen, dunkeln Ring versehen sind; an den Seiten des Tieres und auf der Vorderbrust sind lange Haare angebracht. Der Kopf ist braun, etwa 0,31 mm lang und etwa 0,23 mm breit; er kann gewöhnlich von oben nicht gesehen werden, weil er unter den Prothorax eingezogen ist; dieser ist oben mit einer charakteristischen, olivfarbigen Zeichnung versehen, die an ein Andreaskreuz erinnert. Kurze Zeit nach dem Schlüpfen werden die jungen Raupen mit sehr langen, beweglichen Haaren versehen (»Igelraupen«), die mit einer kleinen »Seitenzacke« ausgerüstet sind. Die Haare »wachsen« anfänglich stark, indem sie sich von den früher erwähnten Warzen aus durch eine Art Ausstülpungsprozess entwickeln, der augenscheinlich dadurch entsteht, dass sich die Härchen allmählich mit Blut füllen.

Nach einer Larvenzeit von 7—8 Tagen findet die Häutung statt, und es kommt eine grünliche, sehr merkwürdige Raupe zum Vorschein. Das Tier, welches von oben gesehen langgestreckt-oval und von der Seite gesehen flach konvex ist, hat nun eine Länge von etwa 1,88 mm, eine Breite von etwa 0,83 mm und eine Höhe von 0,78 mm. In der Mitte längs des Rückens befinden sich 11 Paar quergeriffelte Warzen und ein Paar grössere »Frontwarzen«, die alle mit zahlreichen grünlichen Dörnchen versehen sind. Auf jeder Seite sind fernerhin 11 ebenfalls quergefurchte, mit keulenförmigen, weisslichen Härchen ausgerüstete Seitenwarzen zu sehen. Von den Rücken-

warzen gehen 2 Härchen, von den Seitenwarzen dagegen nur 1 pfriemenförmiges, unverzweigtes, an der Spitze gebräuntes Haar aus. In einem grünlichen Streifen in der Mittellinie des Rückens kann man 8 weissliche Flecke bemerken, die von einem weniger deutlichen Seitenfleck flankiert sind. Unter den grossen Rückenwarzen befindet sich ein deutlicher, weisslicher, unter den Seitenwarzen ein unbestimmterer Streifen. Das bräunliche, etwa 0,44 mm lange und etwa 0,31 mm breite Köpfchen ist oft unter den Prothorax eingezogen, welcher oben eine aus einem grösseren und einem kleineren Fleck bestehende Zeichnung trägt.

Etwa 7 Tage nach der 1. Häutung findet die nächste (2.) statt. Von oben gesehen, ist die Form der Raupe nun am ehesten eiförmig; sie ist etwa 2,66 mm lang, etwa 1,78 mm breit und etwa 1,44 mm hoch. Oben ist die grünliche Raupe mit 11 Paar Rückenwarzen und 1 Paar Frontwarzen versehen. Die Rückenwarzen sind mit 2 kräftigen, pfriemenförmigen Haaren ausgerüstet, während die Front- und Seitenwarzen nur ein solches Haar tragen. Sowohl die Rücken- als die Seitenwarzen sind unten mit einem weisslichen Streifen verbunden, und in der Mitte, den Rücken entlang, liegen 10 auffallende, weissliche Flecke. Das bräunliche, etwa 0,58 mm lange und etwa 0,51 mm breite Köpfchen ist gewöhnlich unter den grünlichen Prothorax eingezogen; der Mesothorax ist mit einem weisslichen Vorderrand versehen. Oben auf dem Prothorax sind ein grösserer V-förmiger und ein kleinerer Fleck zu sehen.

Etwa 8 Tage nach der 2. Häutung findet die nächste (3.) statt. Die Form der Raupe ist ellipsoidartig; sie hat eine Länge von 3,81 mm, eine Breite von 2,31 mm und eine Höhe von 1,66 mm. Sie ist der Raupe nach der 2. Häutung sehr ähnlich, doch ist die Farbe zwischen den Rückenwarzen eher grasgrün. Es sind, wie gewöhnlich, 11 Paar Rückenwarzen vorhanden, die auch in diesem Stadium oben doppelt sind. Aus jeder der kleinen Warzen entspringt ein kräftiges, pfriemenförmiges, im äussersten Viertel schwarzes Haar. Im graugrünen Mittelfelde des Rückens befinden sich im ganzen 9 rautenförmige Flecke; auf den Seiten des Tieres sind die kräftigen Seitenwarzen samt 9 weisslich-grünen Löchern und andere kleinere Flecke nahe bei und gegenüber den Rückenflecken zu sehen. Das hellgrüne, etwa 1,49 mm lange und etwa 1,21 mm breite Köpfchen ist gewöhnlich unter den grasgrünen Prothorax eingezogen; der Mesothorax ist mit einem sahnefarbigen Vorderrand und einem orangeroten Frontstreifen versehen. Oben auf dem Prothorax ist eine W-ähnliche Zeichnung zu sehen.

Etwa 7 Tage nach der 3. Häutung findet die nächste (4.) statt; von oben gesehen, ist die Form der Raupe nun eiförmig; ihre Grundfarbe ist grünlich. Die Länge beträgt etwa 6,21 mm, die Breite etwa 3,57 mm und die Höhe etwa 2,43 mm; oben ist ein grasgrünes, von 11 Paar grossen, grünen Rückenwarzen flankiertes Mittelfeld. In der Mittellinie sind 11 weissliche, rhombische Flecke zu sehen, und innerhalb jedes Rückenwarzenpaares trifft man auf 2 kleinere, weissliche, am ehesten dreieckige Flecke. Die flachen Rückenwarzen sind mit 2 kuppelförmigen, kleinen Warzen versehen, die je ein langes, pfriemenförmiges, an der Spitze schwarzes Haar

tragen. Die deutlichen, mit Dornen versehenen und quergeriffelten Front- und Seitenwarzen haben dagegen nur 1 pfriemenförmiges Haar. Alle Rückenwarzen sind unten mit einem weisslichen Streifen verbunden, und an der Seite des Tieres findet sich ein ähnlicher, jedoch mehr milchartiger Streifen. Unter jedem Rückenstreifen sind 10 kleine, weissliche Flecke, danach eine Reihe grösserer, ovaler Flecke mit einem dunkelgrünen Mittelfleck zu sehen; endlich eine neue Reihe weisslicher Flecke unter 9 grossen Seitenflecken, neben einer Reihe gelblicher Flecke in der Nähe der blaugrünen Seitenwarzen. Schliesslich sind noch 8 kleine Atemlöcher zu bemerken, nebst einem besonders grossen, silbergrauen auf dem grünlichen Prothorax. Der Kopf ist hellgrün und etwa 1,72 mm lang und etwa 1,38 mm breit; der Mesothorax ist vorn mit einem sahnefarbigen Streifen mit einem in der Mitte liegenden rötlichen Fleck versehen. Oben auf dem Prothorax kann man ausserdem 2 kommaähnliche Zeichnungen beobachten.

Etwa 8—10 Tage nach der 4. Häutung findet die nächste (5.) statt; von oben betrachtet ist das Tier oval, von der Seite dagegen mehr gurkenförmig. Die Länge der gelbgrünen Raupe beträgt nun etwa 10,71 mm, die Breite etwa 5,64 mm und ihre Höhe etwa 4,21 mm. Die etwas ältere, weisslich-grüne Raupe ist zu beiden Seiten der Mittellinie längs des Rückens mit einem gelblichen Streifen versehen, in dessen innerer Kante 9 kirschfarbige Flecke von länglich-ovaler Form beobachtet werden können. In der Mittellinie sind im ganzen 9 gelbliche, viereckige Flecke, die nach hinten zu an Grösse zunehmen. Unter dem gelblichen Rückenstreifen sieht man zuerst 12 gelbliche Fleckchen, danach 12 sehr grosse tropfenförmige, grünliche Flecke. Auf dem Seitenwulst trifft man 2—3 Reihen gelblicher und weisslicher Flecke verschiedener Grösse an. Unter dem Seitenwulst kann man 8 mit einem dunkelgrünen Ring umgebene Atemlöcher von weisslicher Farbe beobachten, und auf dem stark grünen, kragenförmigen Prothorax ist ein besonders grosses Atemloch zu sehen. Danach folgen 12 lichtgrüne Augenflecke mit dunkelgrüner Mitte samt einem weisslichen Streifen, der sich auf den Mesothorax fortsetzt. Der Mesothorax ist längs dem Vorderrande gelb mit einem orangeroten Mittelfleck, und der Prothorax hat oben 2 braune, rhombische Zeichnungen. Der grünliche, etwa 2,08 mm lange und etwa 1,70 mm breite Raupenkopf ist mit kräftigen, kastanienbraunen Oberkiefern versehen. Auch die Unterkiefer sind gut entwickelt und mit je einer Kieferpalpe samt einer äusseren und einer inneren Lade versehen, die mit Fühlhärchen und Fühlzäpfchen besetzt sind. Vorn in der Mittellinie findet man die Unterlippe, die in früheren Larvenstadien einem Fischschwanz ähnlich war, aber nunmehr mit einem umgekehrt herzförmigen Spinnzapfen samt 2 kleinen Lippenpalpen versehen ist. Lateral auf dem Kopf kann man 6 Ozellen und einen 3-gliedrigen Fühler bemerken. Übrigens ist der Raupenkopf — mit Ausnahme der Unterlippe — samt der Bauchseite des Tieres prinzipiell in allen Larvenstadien gleich gebaut, und eine Beschreibung wird deshalb nur hier beim letzten Stadium gegeben. — Auf der seegrünen Unterseite sind 3 Paar kleine, kegelförmige Beine zu sehen, die an der Spitze mit einer bräunlichen Klaue versehen sind; als Ersatz für die fehlenden »Warzenfüsse« sind ausserdem auf jeder Seite der Mittellinie 8 kräftige Buckeln zu bemerken.

Die jungen *Cochlidion*-Raupen beschaffen sich ihr Futter auf Eichenblättern durch Wegnagen der Epidermis und des darunterliegenden Blattfleisches; dagegen bleiben die Oberhaut auf der entgegengesetzten Seite und alle gröberen Blattrippen verschont. Hierdurch entstehen etwa 1—2 mm lange, kommaähnliche Fresspuren, auf deren Boden die Raupen mit der Unterseite festgesaugt sitzen. Wenn sich die Häutung vollziehen soll, stellt die Raupe die Nahrungsaufnahme ein, und unter grossen, konvulsivischen Zusammenziehungen kriecht sie aus der alten Haut heraus. Gleich nach der 1. Häutung ist sie gefrässiger, und die Fresspuren zeigen sich nun als grössere Flecke; nach der 2. Häutung entstehen sogar Löcher quer durch das Blattfleisch, die nach der 3. und 4. Häutung noch grösser werden. Nach der 4. und 5. Häutung trifft man die Raupe gewöhnlich am Blattrande, wo sich nach ihrer Nagearbeit grosse Einbuchtungen im Blattrande zeigen. Hier nimmt das Tier eine charakteristische Fresstellung ein, indem es sich mit dem Hauptteil des Körpers parallel zum Blattrande anbringt. Der vorderste Teil der Raupe windet sich dagegen so stark herunter, dass der Prothorax in Reiterstellung auf dem Blattrande sitzt. Im letzten Larvenstadium ist die Vorderbrust in eine mächtige, kragenförmige Partie umgewandelt, die einen geräumigen Tunnel bildet, in welchem die Nahrungsaufnahme vor sich gehen kann, ohne dass der Kopf von aussen überhaupt zu sehen ist.

Wenn die Raupe eine Länge von etwa 12,5 mm, eine Breite von etwa 7,5 mm und eine Höhe von etwa 4,5 mm erreicht hat, stellt sie die Nahrungsaufnahme ein. Die gelbliche, an eine Schildkröte erinnernde Raupe sucht nun einen passenden Ort auf, wo die Verpuppung vor sich gehen kann; sie geschieht in der Regel zwischen zwei dicht aneinanderliegenden Blattflächen, die durch gelbbraune Fäden zusammengesponnen werden. Der ovoide, etwa 8,5 mm lange und etwa 5,5 mm breite Kokon ist zuerst gelbbraun, später rotbraun. Im Herbst fällt der Kokon zusammen mit den Blättern auf die Erde, und die Überwinterung findet im Larvenstadium statt; die ovoide, etwa 7,75 mm lange und etwa 4,68 mm breite Puppe erscheint erst nach einiger Zeit im neuen Jahre. Zuerst ist sie hell-grünlich, später wird die Farbe gräulich-gelb. Die Mundteile sind dunkelbraun, und zwischen den schwarzen Augen befindet sich eine pyramidenförmige Spitze, die wahrscheinlich zum Öffnen des Kokons bestimmt ist. Die Fühler sind vielgliedrig, kräftig und von bräunlicher Farbe; die Beine sind dagegen am ehesten grau, ebenso die Flügelanlagen und der zungenförmige Nackenschild, an dessen Hinterkante sich 2 kleine, ringförmige Figuren befinden. Die Abdominalsegmente sind bräunlich und mit einem Rand versehen, der oben aus rostfarbigen, bürstenförmigen Dörnchen besteht.

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TAFELERKLÄRUNG

Sämtliche Zeichnungen der Tafeln I—IX sind mit dem Abbeschen Zeichenapparat und dem Zeichentisch von Zeiss hergestellt, und zwar in der Regel in Objekttischhöhe. Die Mikrophotographien habe ich mit dem Edingerschen Projektionsapparat aufgenommen; zu den Aufnahmen wurden ausschliesslich feinkörnige »Silbereosin-Platten« von Perutz verwendet. Die angegebenen Vergrösserungen beziehen sich immer auf die Vergrösserungen nach der Reproduktion.

Für alle Abbildungen gültige Bezeichnungen:

ad.Scl.	adfrontales Sklerit
An	Fühler, Antenne
Ch	Choriontextur
Cl	Clypeus
Ep	Epicranium
Epf	epikraniale Mittelfurche
Fe	hinteres Mittelfeld
Fr	Frons
Fu	Spinnzapfen, Fusulus
H	Haar
Lb	Unterlippe, Labium
Lbp	Lippenpalpe, Palpus labialis
Lbr	Oberlippe, Labrum
Lob	innere und äussere Lade, Lobus internus und externus
Md	Oberkiefer, Mandibula
Mi	Mikropyle
Mx	Unterkiefer, Maxilla
Mxp	Unterkieferpalpe, Palpus maxillaris
Oc	Ozel
S.l.	Seitenlinie, Skleritlinie
U	Farbige Ausbreitung des Epicranium

TAFELN

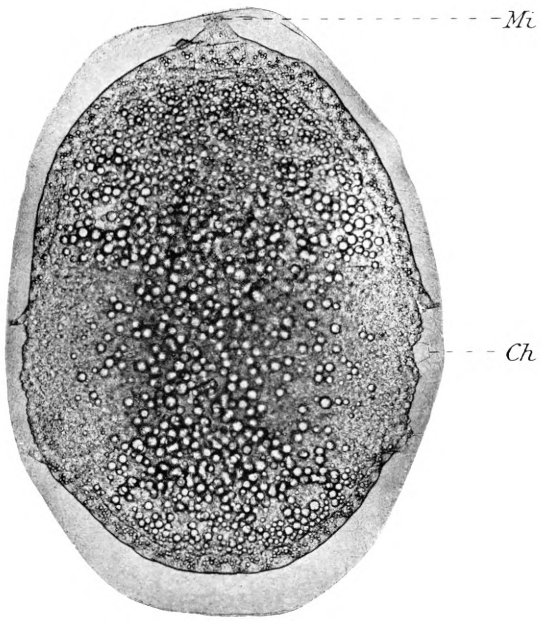
Tafel I.

Abb. 1. Mikrophotographie eines etwa $^1/_2$ Tag alten, lebenden Eies von *Cochlidion limacodes* HUFN. Vergr. 70 ×. Man bemerkt sowohl die Chorionstruktur (Ch) als den Mikropylapparat (Mi).

Abb. 2. Mikrophotographie eines etwa 7 Tage alten, lebenden Eies von *Cochlidion limacodes* HUFN. Vergr. 70 ×. Das Deutoplasma auf der Rückenseite des Tieres ist zum grössten Teil von der Raupe verzehrt worden.

Abb. 3. Die frisch ausgeschlüpfte Raupe von *Cochlidion limacodes* HUFN. Vergr. 64 ×. Man sieht deutlich die paarweise angeordneten, grossen Rückenwarzen und die Seitenwarzen.

Abb. 4. Kopf einer frisch ausgeschlüpften Raupe, von oben gesehen. Vergr. 176 ×.



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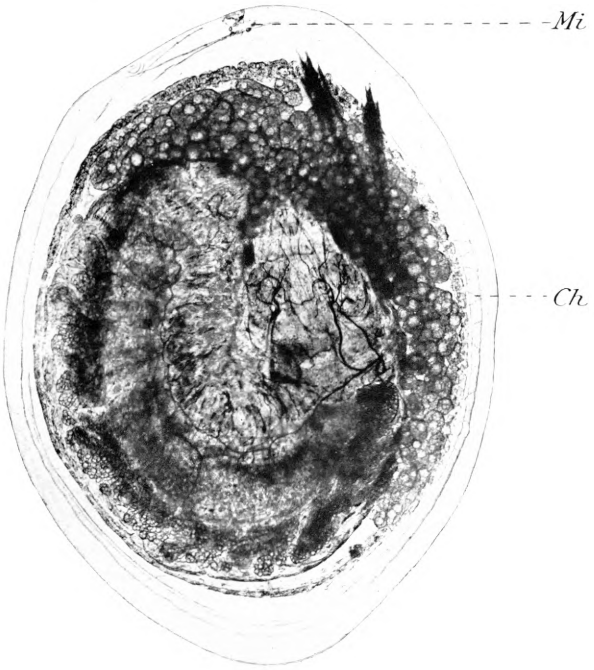

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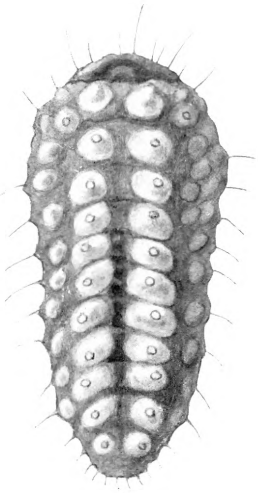

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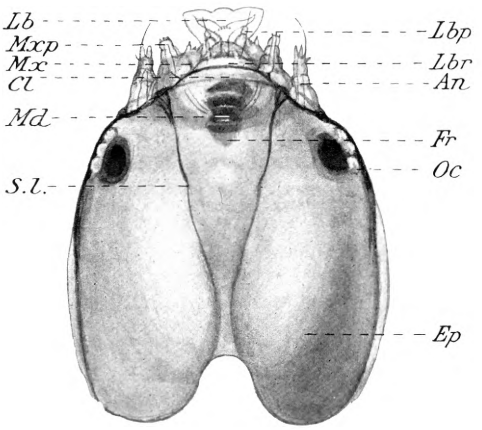

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Tafel II.

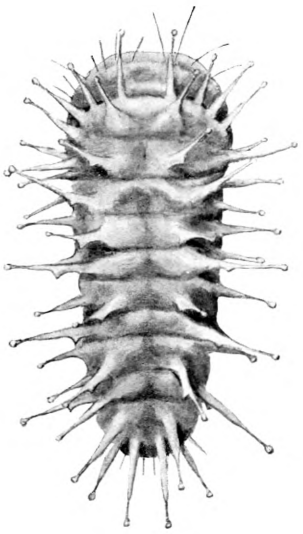
Abb. 5. Die charakteristische Rückenzeichnung der Prothoraxhaut einer frisch ausgeschlüpften Raupe. Vergr. 85 ×.

Abb. 6. Die junge Raupe (»Igelraupe«), von der Seite gesehen. Man bemerkt die sehr langen, stecknadelähnlichen Rücken- und Seitenhaare. Vergr. 64 ×.

Abb. 7. Die junge Raupe (»Igelraupe«) von *Cochlidion limacodes* Hufn., von oben gesehen. Vergr. 64 ×.

Abb. 8. Die junge Raupe (»ältere Igelraupe«) von *Cochlidion limacodes* Hufn., von oben gesehen. Vergr. 64 ×.

Abb. 9. Die Raupe von *Cochlidion limacodes* Hufn. nach der 1. Häutung, von oben gesehen. Vergr. 48 ×. Die Form der Rücken- und Seitenhaare hat sich nun vollständig verändert: die Seitenzacken sind verschwunden.



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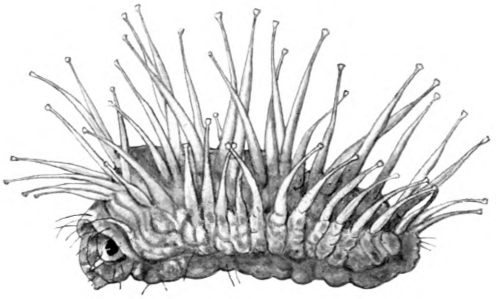

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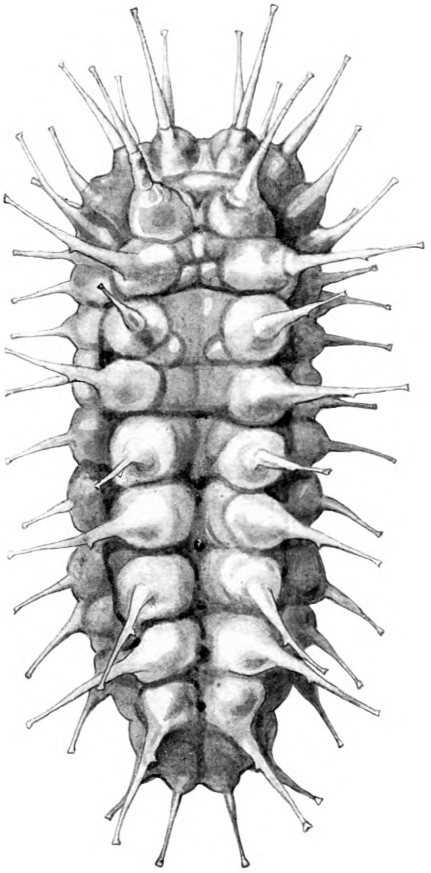

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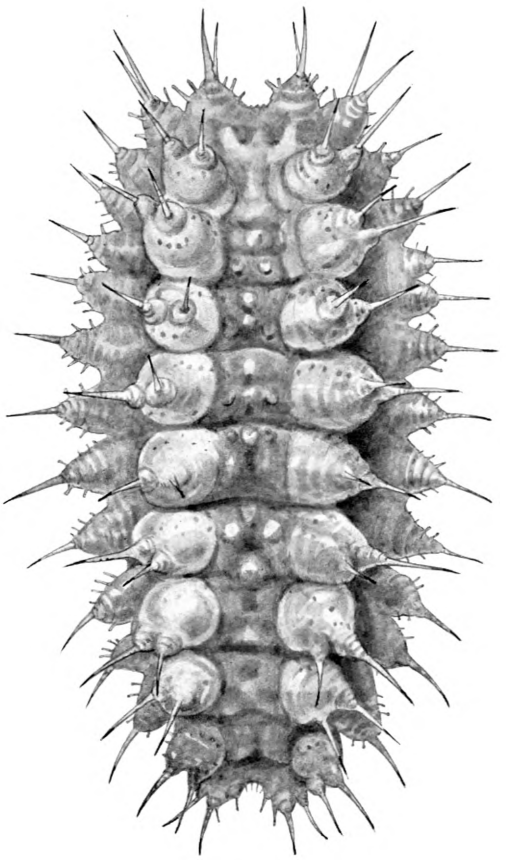

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Tafel III.

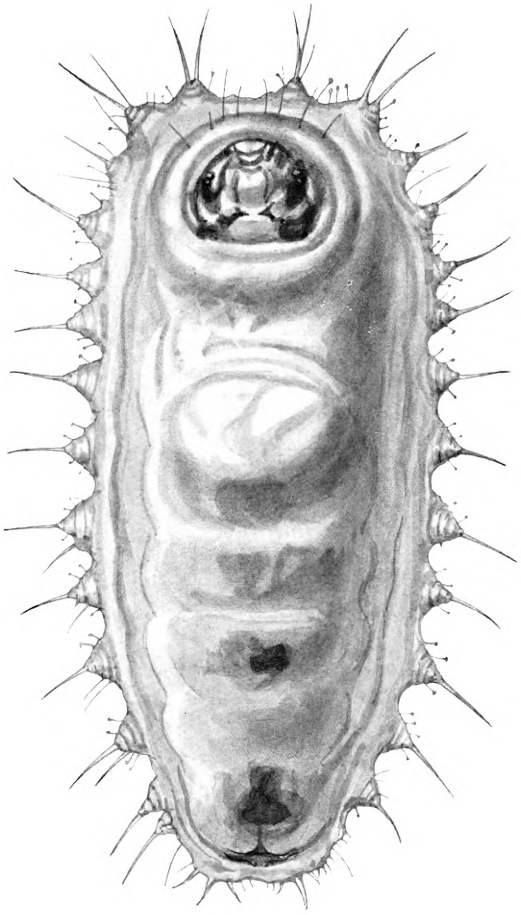
Abb. 10. Die Raupe von *Cochlidion limacodes* HUFN. nach der 1. Häutung, von der Seite gesehen. Vergr. 48 ×. Vorn und nach unten sieht man nur einen kleinen Teil des Kopfes.

Abb. 11. Die Raupe von *Cochlidion limacodes* HUFN., von der Unterseite gesehen. Vergr. 48 ×. Der Kopf ist tief in einen kräftigen Prothoraxkragen eingezogen. Die keulenförmigen Haare sind deutlich auf den Seitenwarzen zu sehen.

Abb. 12. Kopf der Raupe von *Cochlidion limacodes* HUFN. nach der 1. Häutung, von oben gesehen. Vergr. 176 ×. Man sieht deutlich die Ozellen, die Antennen, die Maxillen und die fischschwanzähnliche Unterlippe.

Abb. 13. Prothoraxzeichnung einer Raupe von *Cochlidion limacodes* HUFN. nach der 1. Häutung. Vergr. 85 ×. Glyzerin-Gelatine-Präparat.

Abb. 14. Fresspuren der jungen Raupen auf einem Eichenblatt. Vergr. 10 ×. Die Epidermis der anderen Seite scheint in den Gruben hindurch.



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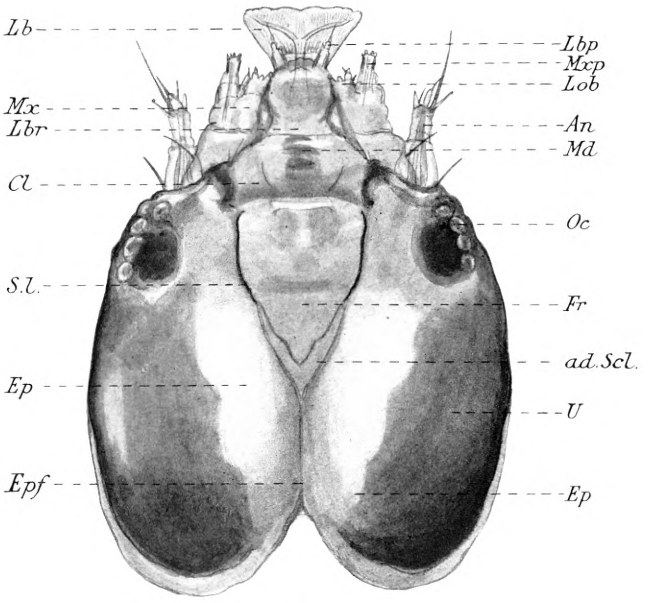

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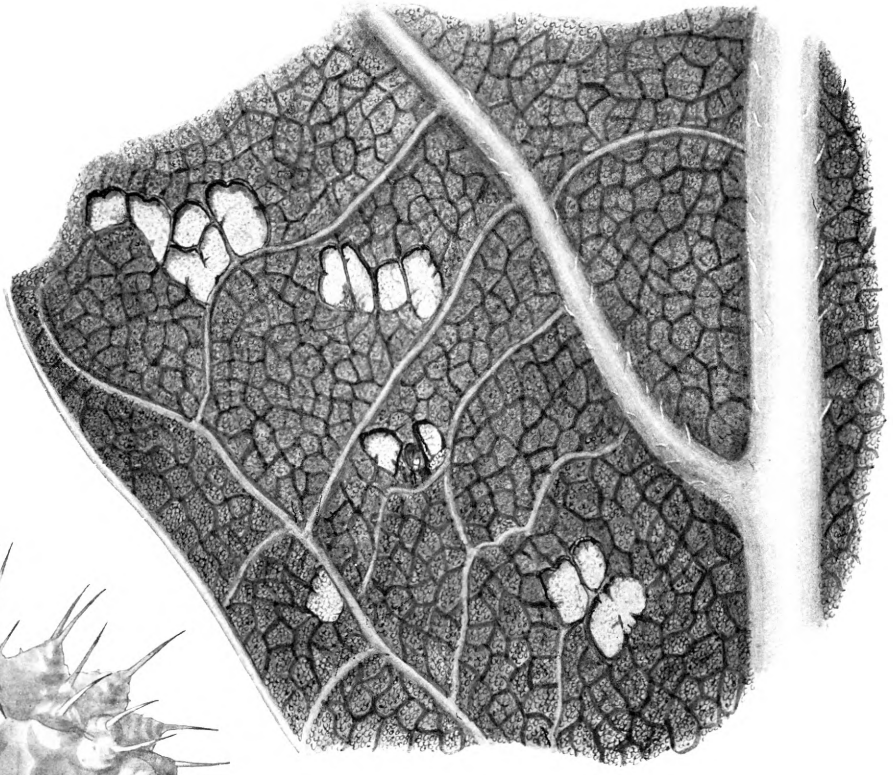

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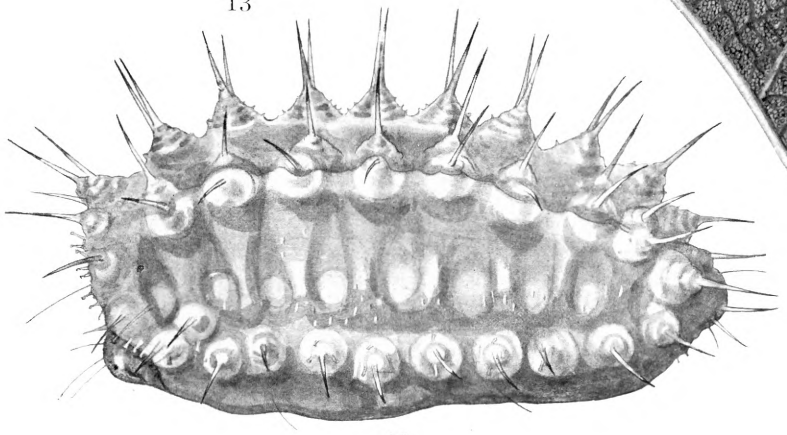

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Tafel IV.

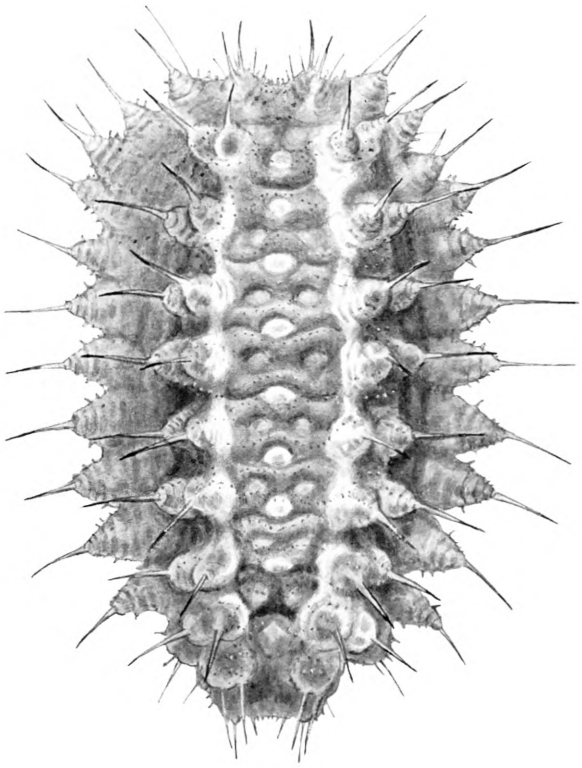
Abb. 15. Die Raupe von *Cochlidion limacodes* Hufn. nach der 2. Häutung, von oben gesehen. Vergr. 32 ×. Man sieht in der Mittellinie des Rückens die charakteristischen Zeichnungen. Auf den Seitenwarzen bemerkt man die keulenförmigen Haare.

Abb. 16. Die Raupe von *Cochlidion limacodes* Hufn. nach der 2. Häutung, von der Seite gesehen. Vergr. 32 ×. Die kegelförmigen, weisslichen Verlängerungen in die Rückenwarzen hinauf sieht man deutlich. Nur ein kleiner Teil des Kopfes wird vorn unten sichtbar.

Abb. 17. Kopf einer Raupe von *Cochlidion limacodes* Hufn. nach der 2. Häutung, von oben gesehen. Vergr. 98 ×. Die verschiedenen Mundteile sind mehr oder weniger eingezogen. Auf den Seiten der Kopfkapsel bemerkt man die recht umfangreichen, olivgrünen Ausbreitungen (U).

Abb. 18. Prothoraxzeichnung einer Raupe von *Cochlidion limacodes* Hufn. nach der 2. Häutung. Vergr. 85 ×. Glyzerin-Gelatine-Präparat.

Abb. 19. Die Raupe von *Cochlidion limacodes* Hufn. nach der 3. Häutung, von oben gesehen. Vergr. 24 ×. Das charakteristische Mittelfeld der Raupe und die doppelten Rückenwarzen sind deutlich zu sehen. Die zahlreichen, keulenförmigen Haare der Seitenwarzen sind auch zu erkennen.



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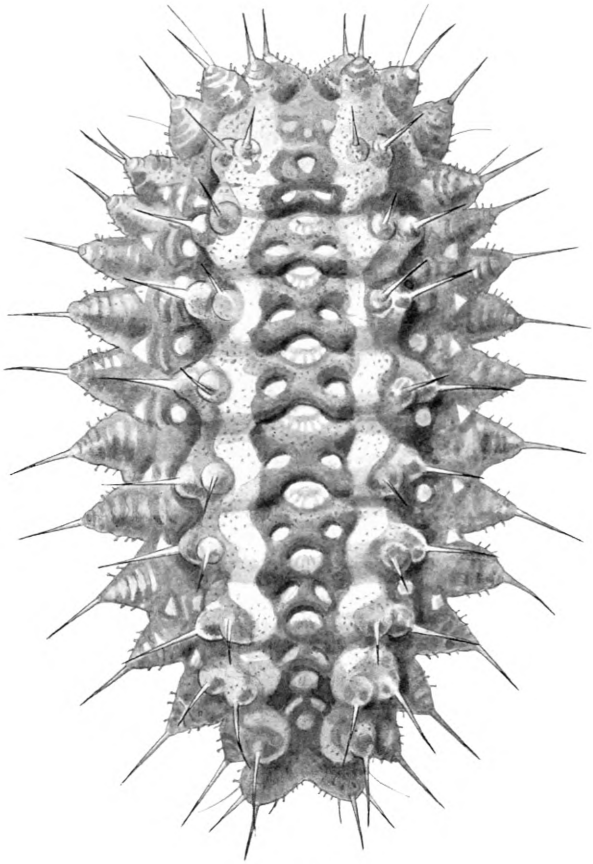

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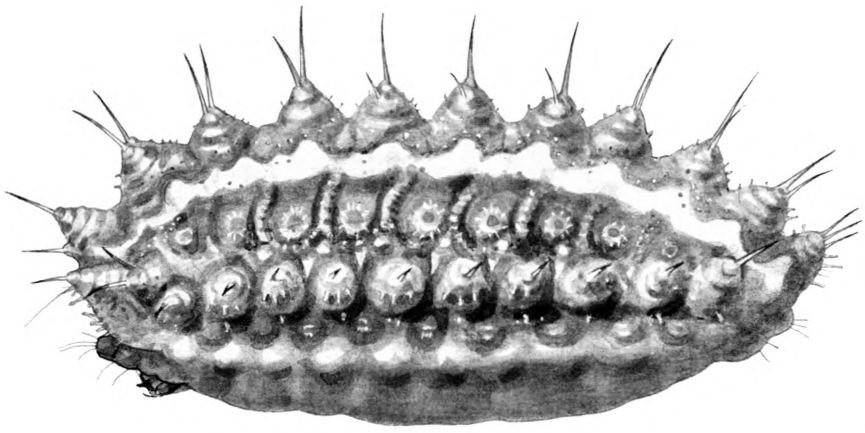

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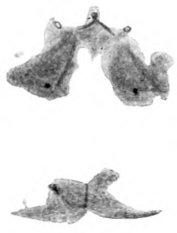

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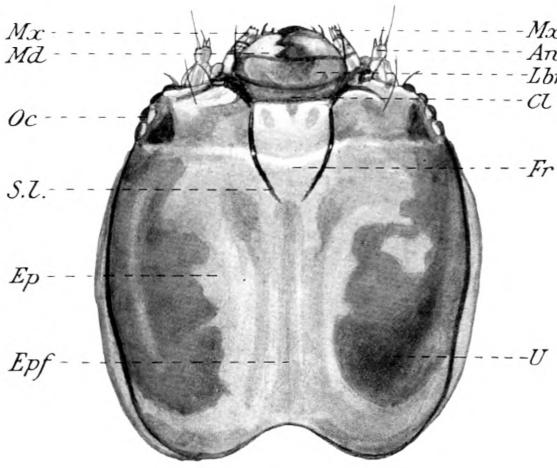

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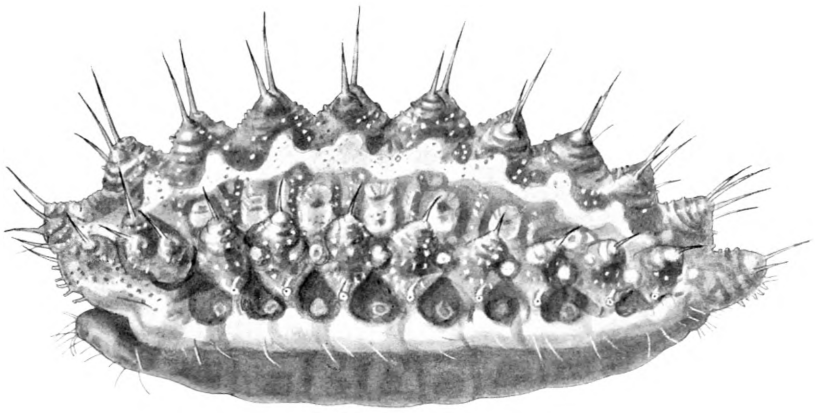
Tafel V.

Abb. 20. Die Raupe von *Cochlidion limacodes* Hufn. nach der 3. Häutung, von der Seite gesehen. Vergr. 24 ×. Der Kopf ist unter den Prothoraxkragen eingezogen.

Abb. 21. Kopf einer Raupe von *Cochlidion limacodes* Hufn. nach der 3. Häutung, von oben gesehen. Vergr. 47 ×. Die verschiedenen Mundteile sind deutlich zu sehen, da sie vollkommen ausgestreckt sind.

Abb. 22. Prothoraxzeichnung einer Raupe von *Cochlidion limacodes* Hufn. nach der 3. Häutung. Vergr. 85 ×. Glyzerin-Gelatine-Präparat.

Abb. 23. Die Raupe von *Cochlidion limacodes* Hufn. nach der 4. Häutung, von oben gesehen. Vergr. 21,3 ×. Man bemerkt sowohl das charakteristische Mittelfeld und die kräftigen, behaarten Seitenwarzen als auch die doppelten Rückenwarzen.



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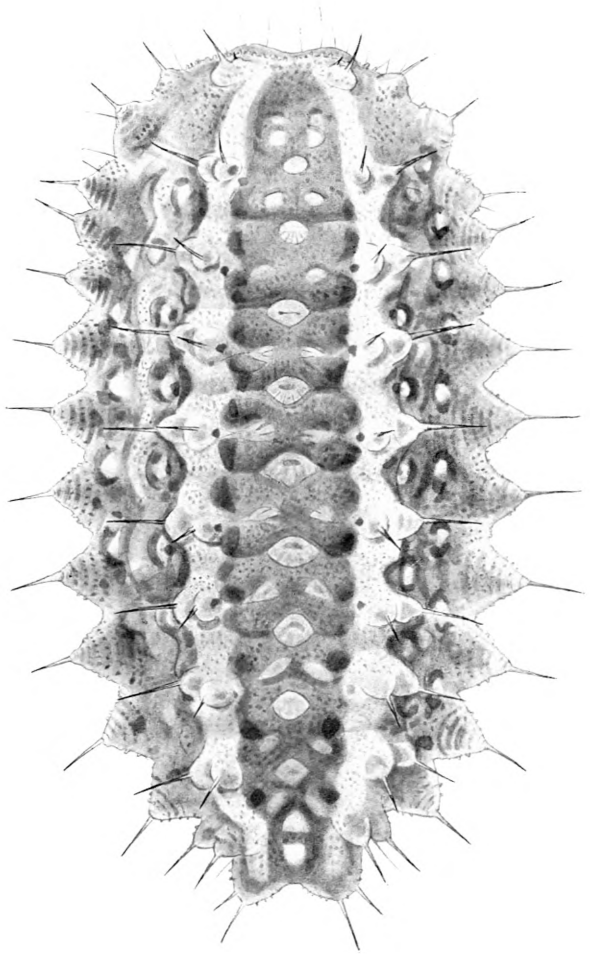

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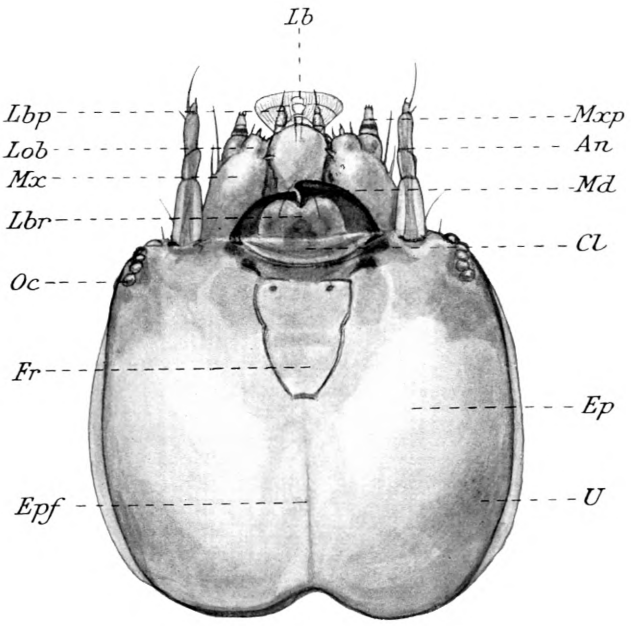

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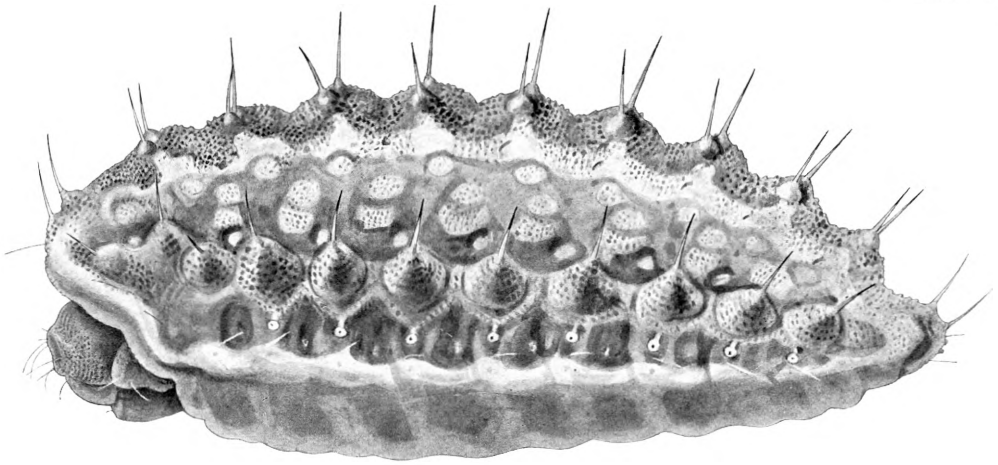
Tafel VI.

Abb. 24. Die Raupe von *Cochlidion limacodes* Hufn. nach der 4. Häutung, von der Seite gesehen. Vergr. 21,3 ×. Auf den Seiten der Raupe sieht man deutlich 8 Atemlöcher über der hellen Seitenlinie. Nur ein kleiner Teil des Kopfes ist vorn unten zu sehen.

Abb. 25. Kopf einer Raupe von *Cochlidion limacodes* Hufn. nach der 4. Häutung, von oben gesehen. Vergr. 47 ×. Die verschiedenen Mundteile sieht man deutlich in ausgestrecktem Zustande.

Abb. 26. Prothoraxzeichnung einer Raupe von *Cochlidion limacodes* Hufn. nach der 4. Häutung. Vergr. 85 ×. Glyzerin-Gelatine-Präparat.



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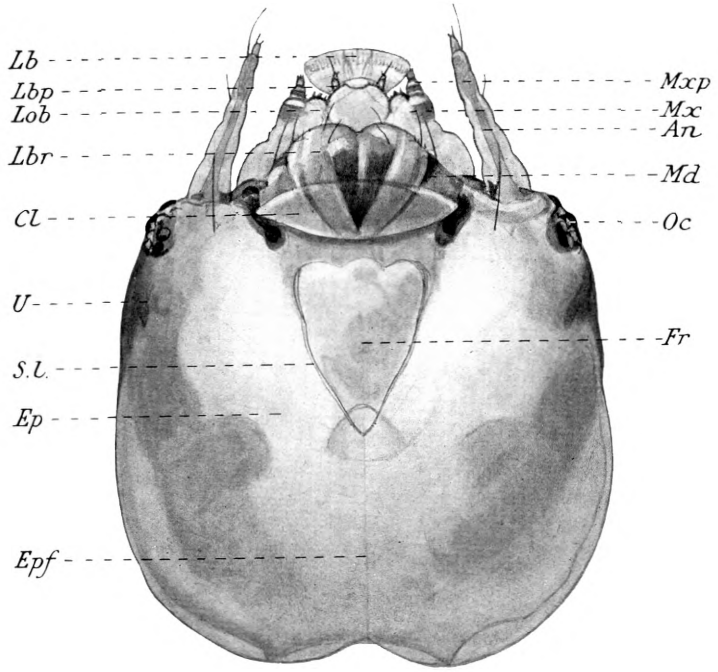

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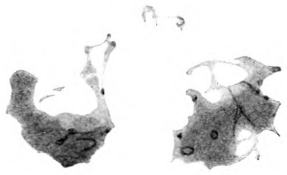

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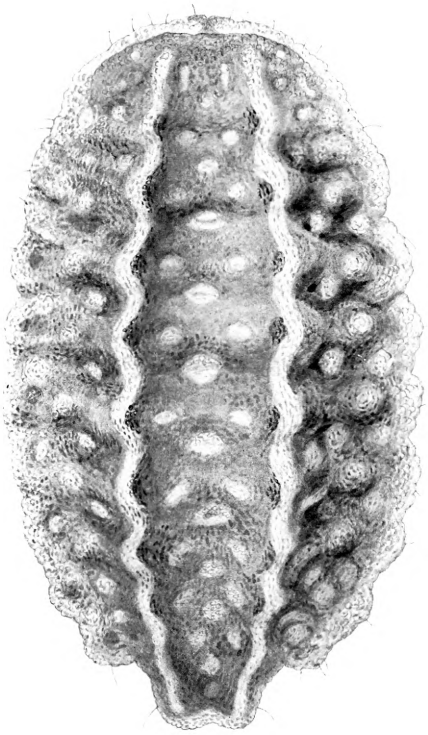
Tafel VII.

Abb. 27. Die Raupe von *Cochlidion limacodes* Hufn. nach der 5. Häutung, von oben gesehen. Vergr. 12 ×. Auf der Innenseite der zwei gewellten Rückenlinien bemerkt man die früher erwähnten 9 kirschroten, ovalen Flecke. Die Rücken- und Seitenwarzen sind nun vollständig verschwunden, und nur wenige Haare sind übriggeblieben.

Abb. 28. Die Raupe von *Cochlidion limacodes* Hufn. nach der 5. Häutung, von der Seite gesehen. Vergr. 12 ×. Sowohl die eine Rückenlinie als die Seitenlinie sind deutlich zu sehen. Vorn unten wird nur ein kleiner Teil des Kopfes sichtbar. Darüber, auf dem Prothoraxkragen, sieht man deutlich ein prothorakales Atemloch, und über der Seitenlinie die 8 abdominalen Atemlöcher.

Abb. 29. Die Raupe von *Cochlidion limacodes* Hufn. nach der 5. Häutung, von der Unterseite gesehen. Vergr. 12 ×. Ausserhalb der kräftigen Seitenlinien sieht man auf jeder Seite die 8 Atemlöcher; ferner, in der Mitte der Bauchseite, die Mittelfurche und die 16 Buckeln. Vorn sieht man die 3 Paar kleinen Thorakalbeine, und unter dem mächtigen Prothoraxkragen bemerkt man die eingezogenen Mundteile.



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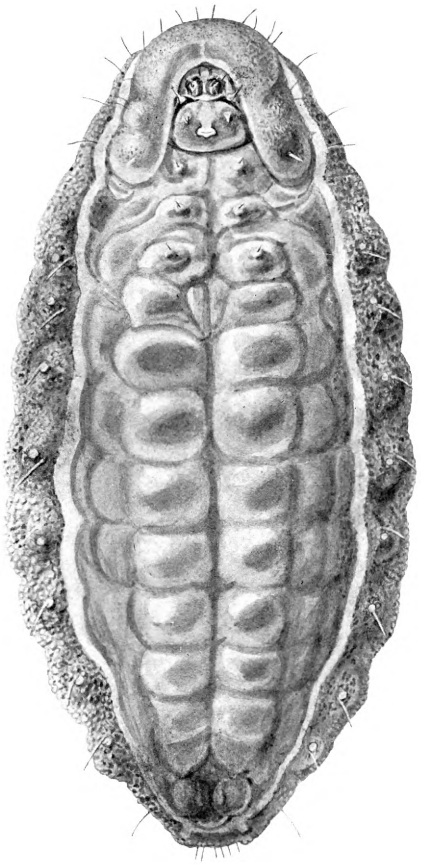

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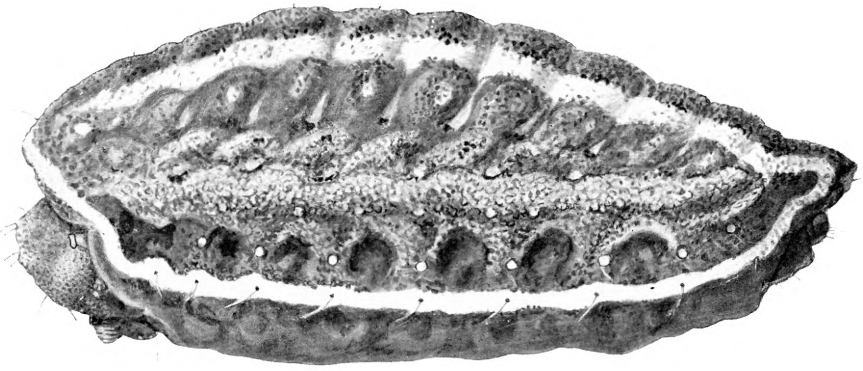

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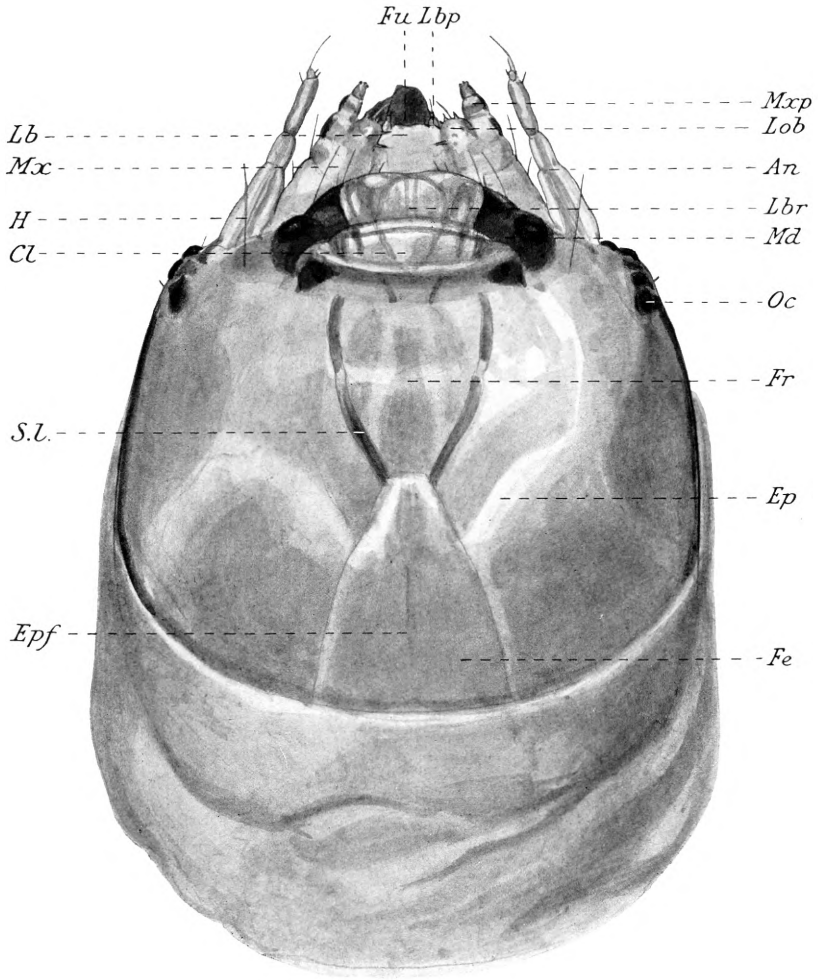
Tafel VIII.

Abb. 30. Kopf der Raupe von *Cochlidion limacodes* Hufn. nach der 5. Häutung, von oben gesehen. Vergr. 47 ×. Man bemerkt deutlich die ausgestreckten Mundteile. Die Unterlippe ist nun konisch und nicht mehr fischschwanzähnlich.

Abb. 31. Prothoraxzeichnung einer Raupe von *Cochlidion limacodes* Hufn. nach der 5. Häutung. Vergr. 85 ×. Glyzerin-Gelatine-Präparat.



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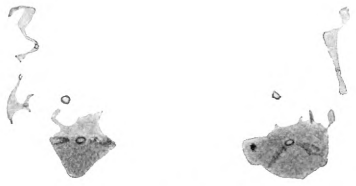


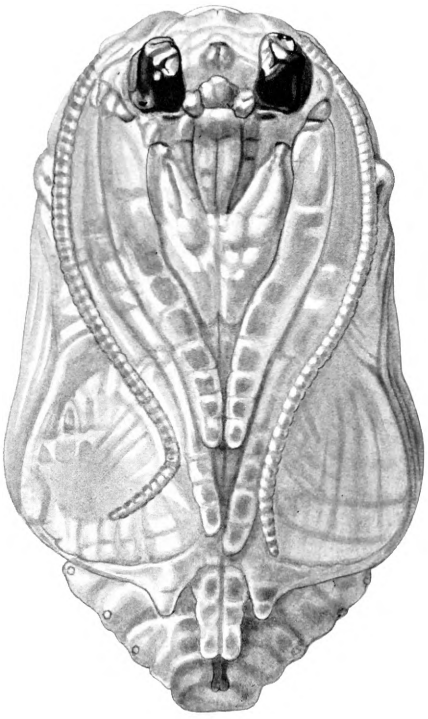
31

Tafel IX.

Abb. 32. Die Puppe von *Cochlidion limacodes* HUFN., von der Bauchseite gesehen. Vergr. 12 ×. Die grossen Augen und Fühler und die kräftigen Flügelscheiden fallen sofort auf.

Abb. 33. Die Puppe von *Cochlidion limacodes* HUFN., von der Rückenseite gesehen. Vergr. 12 ×. Der kräftige Nackenschild und die mit Dörnchen besetzten Abdominalringe werden deutlich sichtbar.

Abb. 34. Die Puppe von *Cochlidion limacodes* HUFN., von der Seite gesehen. Vergr. 12 ×. Sowohl die Abdominalsegmente als der freie Teil des letzten Beinpaares werden nun deutlich sichtbar.



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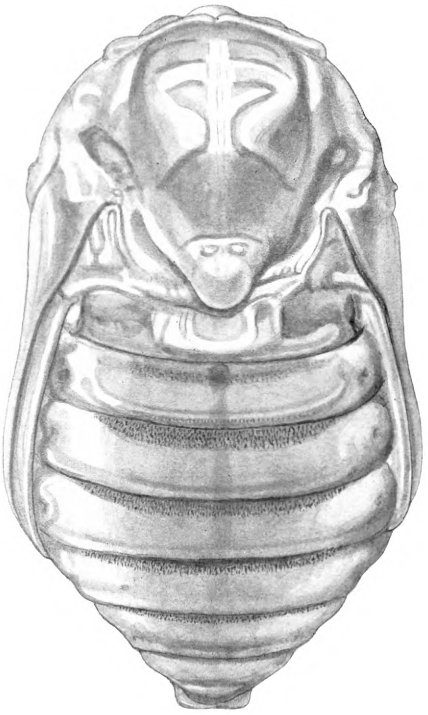

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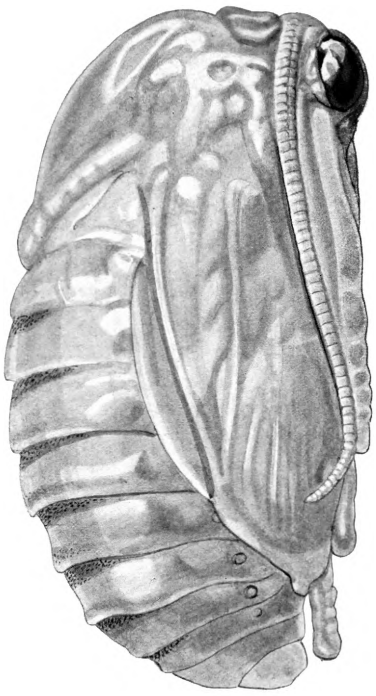

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DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB

BIOLOGISKE SKRIFTER

BIND II (KR. 61.00):

		kr. ø.
1.	BÖCHER, TYGE W.: Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. I. Über die Flechtenheiden und Dünen der Insel Läsö. 1941	4.00
2.	SØRENSEN, THORVALD: Untersuchungen über die Therophytengesellschaften auf den isländischen Lehmflächen (»*Flags*«). 1942	3.00
3.	ORLA-JENSEN, S.: The Lactic Acid Bacteria. Die echten Milchsäurebakterien. Ergänzungsband. 1943	18.00
4.	WESTERGAARD, M.: Cyto-Taxonomical Studies on *Calamagrostis Epigeios* (L.) Roth, *Ammophila Arenaria* (L.) Link, and their Hybrids (*Ammophila Baltica* (Flügge) Link). 1943	8.00
5.	NIELSEN, K. BRÜNNICH: The Asteroids of the Senonian and Danian Deposits of Denmark. *Opus posthumum* edited by TH. MORTENSEN and ALFRED ROSENKRANTZ. 1943	9.50
6.	ROSENVINGE, L. KOLDERUP, and LUND, SØREN: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. II. Corynophlaeaceæ, Chordariaceæ, Acrothrichaceæ, Spermatochnaceæ, Sporochnaceæ, Desmarestiaceæ, Arthrocladiaceæ. With supplementary Comments on Elachistaceæ. 1943	6.00
7.	BÖCHER, TYGE W.: Studies on the Plant Geography of the North-Atlantic Heath Formation. II. Danish Dwarf Shrub Communities in Relation to those of Northern Europe. 1943	12.50

BIND III (KR. 60.50):

1.	OLSEN, SIGURD: Danish Charophyta. Chorological, Ecological and Biological Investigations. 1944	22.00
2.	JESSEN, KNUD, and HELBÆK, HANS: Cereals in Great Britain and Ireland in Prehistoric and Early Historic Times. 1944	8.50
3.	GRAM, K., JØRGENSEN, C. A., og KØIE, M.: De jydske Egekrat og deres Flora. 1944	26.00
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BY

KJELD LADEFOGED

SECOND EDITION

København 1958
i kommission hos Ejnar Munksgaard

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I. Introduction.

Knowledge of the growth periodicity of the various species of trees is of importance for the understanding of their nature and growth reaction to different external conditions.

In Denmark the time of foliation, flowering, and defoliation is known from observations made in the field as well as from phenologic investigations carried out by LANGE (1873, 1879, and 1884) and BRUUN (1889 and 1919). The time of the extension growth of the roots has been investigated by O. G. PETERSEN (1898 and 1903) and LADEFOGED (1939).

On the other hand we have no certain knowledge of the periodicity of wood formation in this country. From observations of the rising of the sap and when the bark 'slips' we know in practice the approximate time of the beginning of wood formation in spring and its termination in autumn. But beyond this our knowledge of its periodicity and dependence on external conditions is pretty insufficient.

If we want to form an opinion in this direction it may be done on the basis of the many, and often very valuable, investigations carried out abroad, chiefly in Central Europe, England, and U.S.A.

Owing to the often considerable climatic differences the results of these investigations cannot directly be transferred to conditions in Denmark. To this comes that the results frequently differ to a certain extent, and chiefly apply to species of trees of a rather peripheric interest to Danish forestry.

From the desire to obtain a more satisfactory basis for the determination of the periodicity of wood formation in our forest trees I have from the time from March 1944 till November 1945 watched cambial activity and wood formation in the following species of trees:

Conifers:

Pinus silvestris L. Scotch pine.
Larix decidua MILL. Larch.
Picea abies L. KARST. Norway spruce.
Picea sitchensis (BONG.) CARR. Sitka spruce.
Abies alba MILL. European silver fir.
Pseudotsuga taxifolia (PORR.) Britt. Douglas fir.

Hardwoods:

Betula pendula ROTH. Birch.
Alnus glutinosa (L.) GAERT. Alder.
Corylus avellana L. Hazel.
Carpinus betulus L. Hornbeam.
Fagus silvatica L. Beech.
Quercus robur L. Common oak.
Ulmus glabra HUDS. Elm.
Tilia cordata MILL. Lime.
Aesculus hippocastanum L. Horse-chestnut.
Acer pseudoplatanus L. Maple.
Prunus avium (L.) MOENCH. Wild cherry.
Sorbus aucuparia L. Mountain ash.
Fraxinus excelsior L. Ash.

Through our examinations it has in the first line been our aim to throw light on:

1. The time of the beginning and termination of cambial activity in branches, stem, and roots.
2. The process of wood formation in the most important species of trees.
3. The time of the beginning of summer wood formation, and the difference between spring and summer wood.

Further, investigations have been carried out concerning the duration of the shoot extension period and water transportation at breast height.

II. Literature.

Some of the first investigations of the periodicity of wood formation were undertaken by TH. HARTIG (1857 and 1863a). In Germany he i.a. watched the wood formation in 16-year-old *Pinus silvestris, Larix decidua, Quercus robur* and *Acer pseudoplatanus* all through a summer.

He found that cambial activity began first in the young branches, then it started in the stem, and last in the roots. Between the time it began in the branches and in the roots a period of $1\frac{1}{2}$ to $2\frac{1}{2}$ months elapsed.

In *Pinus silvestris* and *Quercus robur* cambial activity began in the branches as well as in the stem before May 5th. He did not notice the same growth condition till June 7th in *Larix decidua* and *Acer pseudoplatanus.*

In autumn cambial activity terminated in the same succession as it began in spring, 2 to 3 weeks later in the roots than in the stem.

SCHRÖDER (1879) in Russia measured the thickness of the stem at a week's interval in young ($3\frac{1}{2}$—$4\frac{1}{2}$ m high) *Quercus robur, Populus tremoluides* and *Picea abies* var. *sibirica.*

In *Picea abies* the wood formation was liveliest in May; in the *Quercus robur* and *Populus* in the middle of June. In all three trees it ceased in the middle of August.

Russow (1884) found in contradistinction to Th. Hartig that only a few days elapsed between the beginning of cambial activity in the stem and in the roots.

Gulbe (1888a and b) has in Russia examined the periodicity of wood formation in seventeen different species of hardwoods and conifers. In conformity with Th. Hartig and Russow he found that cambial activity started in the branches, while it began later in stem and roots. Between the time of its inception in the young branches and roots a period of 4 to 5 weeks elapsed.

In autumn it ceased in the same succession—two months later in the roots than in the branches.

Christison (1889) through eight years at short intervals measured the increase in circumference in nineteen different species of trees in a botanical garden at Edinburgh.

In *Quercus robur* and evergreen conifers the growth in thickness began earlier —in the other species of trees[1] not until some time after bud break.

In May and June wood formation was livelier in conifers than in hardwoods. Averagely 54 % of the new annual ring was formed by July 1st in conifers against 35 % only in hardwoods.

Mischke (1890) examined in Germany the process of wood formation in *Pinus silvestris* and *Picea abies* by cutting sections from the stem nine times in the course of a summer and counting how many new cells had formed radially.

In *Pinus silvestris* wood formation began in May. It progressed slowly till the end of June when it completely ceased—probably owing to drought. In August it started again, and for a short time it was very lively.

In *Picea abies* wood formation began at the end of April. It was most lively during the time from the middle of May till the middle of June as well as in August.

R. Hartig (1882b and 1891, pp. 161—164) has in various places in Germany examined the inception of cambial activity in trees in different growth localities.

He found that it started earlier in spring in sun-exposed than in shaded stems.

The branches are more quickly warmed up in spring than the stem and roots. Therefore cambial activity starts first in the branches.

Mer (1892a) found under investigations of the time for the inception of cambial activity in *Quercus, Fagus, Carpinus, Tilia, Populus* and *Picea* that 10 to 15 days passed between its inception in the stem and the roots.

Jost (1892) through a period of two years regularly measured the increase of the circumference of the stem with a steel band in 16 different species of trees at the botanical garden in Strassburg. In 10 species of trees he further watched the growth in thickness by measuring their diameters with a "Fuhlhebel".

The growth in thickness began in May and reached maximum in June or July. Hereafter it quickly decreased and ceased in September or October.

[1] Of ring porous trees only Quercus robur was measured.

The growth in thickness in the branches all the time preceded that in the stem.

He found a still lively cambial activity at the base of one- and two-year-old branches after the leaves and buds were fully developed. From this he concludes that there is no connection between the development of the leaves and the growth in thickness of the branches.

REUSS (1893) constructed a dendrograph by means of which he through a period of two years followed the growth in thickness of the stem of a 15-year-old open-grown *Tilia*.

The growth in thickness began in May after foliation.

The first year it already ceased at the beginning of July, the second year not until the end of August.

FRIEDRICH (1897) constructed a "Zuwachs-Autograph" which might be placed on the stem and automatically recorded the changes in its circumference. With a series of such instruments he through a period of 5 years watched the growth in thickness from day to day at breast height in i. a., older *Fagus silvatica, Acer pseudoplatanus, Tilia cordata, Picea abies* and *Pinus silvestris* at the botanical garden at Mariabrunn.

The growth in thickness on the whole began simultaneously with foliation. It did not, however, really gather speed till after the leaves were completely developed. In several of the species of trees there were two annual maxima: one at the end of May, and another towards the middle of July.

The growth in thickness ceased within the period between the middle of August and the beginning of October.

REICHE (1897) found that in Chile the growth in thickness began after bud break.

WALTER (1898) all through a summer watched the wood formation in the stems of four 100—200-year-old *Fagus silvatica* standards in the neighbourhood of Giessen. At intervals he extracted cores with a borer from 1.5 m height, and under the microscope he then counted how may new cells had formed radially.

The opening of the buds began slowly on April 21st. Wood formation in the stem did not begin till a month had passed and lasted till August 18th.

WIELER (1898) applied the same method to examine the periodicity of wood formation in amongst other trees, *Pinus silvestris, Picea abies, Abies alba, Quercus robur* and *Fagus silvatica* in various parts of Germany. The variation in the individual trees and species of trees between the dates for the inception and termination of wood formation was very great.

O. G. PETERSEN (1898) found in 1896 beginning wood formation on May 20th in the stems of 2—5-year-old *Fraxinus excelsior, Betula pendula, Fagus silvatica, Quercus robur, Acer pseudoplatanus, Picea abies* and *Pinus Mugo*. In *Alnus glutinosa* it could only be ascertained on June 11th.

BUCKHOUT (1907) watched the periodicity of the growth in thickness from 1897—1900 in two old *Larix decidua* MILL. and *Pinus strobus* L. in Pennsylvania. Like JOST he measured at intervals how much the stem had increased in circumference.

The growth in thickness began simultaneously with bud break at the end of

April. In *Larix decidua* it ceased already in July; in *Pinus strobus* not until mid-September. The reason of this great difference he seeks in the fact, that the growth of *Larix decidua* is adapted to Alpine climates, whereas that of *Pinus strobus* is adapted to a milder climate.

The rainfall and temperature of the various years exercised no influence on the time for the beginning of the growth in thickness.

AMILON (1910) found under investigations of 20—22-year-old *Larix sibirica* LEDEBOUR in Bjurfors Kronopark North of Ystad, in Sweden, that cambial activity started earlier in spring in the upper than in the lower part of the stem.

He thinks that the reason of this is that the upper part of the stem is more thin-barked and therefore more quickly gets warmed up than its lower part. In this connection he draws attention to the fact that no thin-barked trees, by nature, grow in Sweden.

BROWN (1912) by cutting sections from the stem has through two years watched the formation of wood in 22-year-old and 100-year-old *Pinus rigida* MILL. in Ithaca in North America.

Contrary to the abovenamed investigators he found that wood formation began in the stem at some distance from the top shoot; not until 19 days later did it reach up into the latter.

The time for the beginning of wood formation in the lower part of the stem was dependent upon the insolation, thickness of the bark, etc.

The extension growth of the roots preceded the growth in thickness.

By applying the same methods BROWN (1915) examined the periodicity of wood formation in *Pinus strobus* L. The trees were of all ages and grew in different parts of North America.

He found that the growth in thickness might be divided into a) growth in thickness without division into cells and b) growth in thickness by division into cells.

a) It started in March and was due to an extension radially of the cambium cells and the youngest sieve tissue cells.
b) It started a few days before bud break at the end of April.

As in *Pinus rigida* MILL. wood formation began in the stem at some distance from the top shoot.

Wood formation continued in branches, stem and roots as long as temperature conditions permitted it.

The formation of summer wood started in the middle of August, and first in the branches.

The formation of sieve tissue continued longer into the autumn than wood formation.

KNUDSON (1913) in 1909 watched the formation of wood in the stem of four 13-year-old *Larix laricina* KOCH in a nursery in Ithaca in North America. At intervals he cut out 1 cm deep sections from the stem under each circle of branches from top to root and measured the width of the fresh-formed wood ring.

He found, like BROWN, that the cambium cells extended radially before the beginning of the division into cells.

In contrast to BUCKHOUT he found, that wood formation did not begin till a month after bud break.

During the period from May 25th till June 3rd over one third of the new annual ring was formed. By July 6th wood formation was almost completely finished in the whole stem.

New investigations (1911) showed that wood formation in the stem by far preceded wood formation in the branches.

KNUDSON supports his opinion on not named works and arrives at the conclusion, that wood formation can only begin after the young needles are so far developed that they yield a sufficiently large assimilation surplus.

MACDOUGAL (1921 and 1924) constructed a dendograph which in similarity with FRIEDRICH's "Zuwachs-Autograph" may be placed round the stem and which carefully records the changes in its circumference. With a series of such instruments he through several years followed the course of the growth in thickness in many various species of trees in North America.

In *Fraxinus excelsior* and *Pseudotsuga taxifolia* the growth in thickness preceded bud break. In most of the other species of trees—amongst others *Quercus robur*—it began from a few days and up to 10—12 weeks after bud break.

The growth in thickness in the roots often lasted few weeks only, and it started later than in the stem.

The width of the annual ring increased with the duration of the growth period.

"Ringed" stems did not grow in thickness under the ringing place.

KORSTIAN (1921) followed with the same dendrograph the growth in thickness from April till June in an *Acer negundo* L. and a *Picea pungens* ENGEL in Big Cottonwood Canyon, 25 miles southeast of Salt Lake City, Utah.

From this examination, which covered a short period, he arrived at the conclusion that the growth in thickness in evergreen conifers begins simultaneously with the opening of the buds. In deciduous trees it can on the other hand only begin when the foliage is so far developed, that it produces a sufficiently large assimilation surplus.

PEARSON (1924) also followed the course of the growth in thickness with a dendrograph in two young *Pinus scopulorum* ENGELM. in Arizona.

In one tree the growth in thickness of the stem started in May and ceased on September 10th. In the other tree it began on June 1st and terminated already on August 27th.

ROMELL (1925) in connection with investigations of the periodicity of shoot extension also—through three years—followed the course of the growth in thickness in the stem of *Pinus silvestris*. During the first two years he followed it by making measurements on cores extracted at certain intervals in time. The last year he measured at intervals how much the stem had increased in circumference.

The investigations were carried out in Central Sweden and comprised 20 trees evenly spread over the following four plantations:

a) thinned
b) non-thinned } plantation on a south slope.
c) thinned
d) non-thinned } plantation at a flat area.

The two first years the growth in thickness started a few days later than the shoot extension; the last year not until 18 days later.

There was no conspicuous difference between the time of the beginning of the growth in thickness in the unevenly treated and exposed plantations. On the other hand wood formation proceeded relatively more quickly in early spring in the thinned than in the non-thinned plantations.

In comparison with the shoot extension the period of growth in thickness varied much from year to year. In 1923 it was 27 days shorter than in 1922. ROMELL concludes from this, that the shoot extension and the growth in thickness are caused by widely differing factors.

In contradistinction to SCHWARZ (1899), LAITAKARI (1922) and MACDOUGAL (1921 and 1924) ROMELL found that the width of the annual ring did not increase with the length of the growth period.

MORIKAWA (1927) found by investigations in Japan that in *Pinus densiflora* SIEBOLD and ZUCCARINI and *P. Thunbergii* PARLATORE wood formation began in the two-year-old branches coincident with bud break.

CHALK (1927 and 1930) has in the neighbourhood of Oxford investigated the periodicity of wood formation in *Fraxinus excelsior* L., *F. oxycarpa* WILLD. as well as *Pseudotsuga taxifolia* BRITT. He followed the growth in thickness by means of MacDougal's dendrograph and by measurements on sections.

In *Fraxinus excelsior* wood formation started three weeks before foliation, and first in the stem. By May 26th the leaves were completely expanded, and about one third of the new annual ring was formed by then.

In *Pseudotsuga taxifolia* the growth in thickness in the stem began about 12 days before bud break.

The winter buds were fully developed by July 21st. By this time 90 % of the new annual ring had been formed in *Fraxinus excelsior*, and in *Pseudotsuga taxifolia* 73 %.

In *Fraxinus excelsior* wood formation ceased at the middle of August; in the *Pseudotsuga taxifolia* about the middle of September.

COSTER (1927) has through four years carried out comprehensive investigations concerning the periodicity of wood formation in a large number of species of trees within the dry monsoon area in East Java (Toeban) and the more rainy West Java (Tjibodas and Buitenzorg).

In the periodically deciduous species of trees wood formation began simultaneously with foliation. That also applied to ring porous trees (among others *Quercus robur*) introduced from Europe.

Wood formation was most active as long as the foliage was young. It ceased at leaf fall.

The lignification of the newly formed wood elements continued into the leafless period.

In tree species where the growth of the branches was not synchronous, wood formation in the branches closely followed the growth rhythm of the branches themselves. In these trees there were therefore at the same time branches with a beginning cambial activity, branches that were in the midst of the period of wood formation, and branches in which the cambium was at rest. The ring porous *Castanea sativa* MILL. introduced from South Europe belonged to these trees.

In the evergreen trees (naturally occurring *Quercus* species, *Castanea argenta* BL. and others) wood formation took place all the year round, if there was sufficient precipitation. If longer periods of drought occurred (East Java) wood formation generally ceased during the latter.

LODEWICK (1925 and 1928) in North America followed the periodicity of wood- and sieve-tissue formation in, among others *Fraxinus americana* L., *Quercus borealis* MICH., *Betula lutea* MICH., *Acer saccharum* MARCH., *Liriodendron tulipifera* L. and *Thuja occidentalis* L. The investigations were carried out partly by application of MacDougal's dendrograph and partly by measurements on sections.

In the ring porous trees wood formation started in the stem just before or simultaneously with bud break. In the diffuse porous it only began two to three weeks after bud break, when the leaves were from a quarter to completely expanded.

In *Fraxinus excelsior* in open stands wood formation began first in the stem just under the crown. In other cases it began at the surface of the ground and spread from there up through the stem. In the thin roots of *Fraxinus excelsior* it began a week later than in the stem.

Sieve tissue formation started simultaneously with wood formation.

In the ring porous trees summer wood formation began as soon as the foliage was fully developed.

A few years later LODEWICK (1930) found by investigations of *Pinus palustris* MILL. in West Florida that the width of the annual ring here increases with the rate of rainfall during the summer months.

SWARBRICK (1927 a) has examined cambial activity in fruit trees. He found, like KNUDSON and BROWN, that about a fortnight before the beginning of division into cells the cambial cells extended radially. At the same time the cambium was "... translucent, and it was much more turgid than during the winter" (p. 151).

Wood formation began in the branches and spread from here in basipetal direction.

In the course of summer the cambium cells increased somewhat in size.

In the same year SWARBRICK (1927 b) published the result of investigations on the effect of ringing in the stems of fruit trees.

Wood formation began first in the stem above the ring.

Between the rings of double-ringed stems no wood formation took place, even though there still were branches in this place. The cambium in stead entered into a vaecuolate condition. SWARBRICK concludes from this that the connection between

wood- and sieve-tissue is of great importance for the coordinated and continuous physiological activity in the stem.

REES (1929) in 1926 and 1927 examined the periodicity of wood formation in nine 150—300-year-old *Picea rubra* LINK in different growth localities in the neighbourhood of Wanakena in the State of New York. He was content to determine the growth condition on sections taken at certain intervals from branches, stem, and roots.

Wood formation started c. a fortnight before bud break. In well drained grounds it began at the end of May; in wet and cold soil on the other hand not until the middle of June.

COCKERHAM (1930) at Leeds in England at intervals of four to five weeks in the course of a year felled in all thirty sycamores and each time carefully investigated the cambial activity from top to root.

The cambium began to swell at the end of March. Immediately afterwards the formation of sieve tubes started.

Wood formation began simultaneously with bud break at the end of April.

The differentiation of the sieve tubes was most active just before bud break and after the termination of wood formation in autumn.

PRIESTLEY (1930) in a way reviews the hitherto obtained results concerning the periodicity of wood formation.

PRIESTLEY, SCOTT and MALINS (1933) at Leeds in England investigated the time for the beginning of cambial activity in thirty six hardwood- and conifer-species.

For the investigations a special method was used, the so-called "strip" method. The bark is loosened from the stem, and the new-formed wood is scraped off with a knife. In this way we get long strips of it which float out in water and are excellent objects for microscopic study. The process has been described by DETLEV MÜLLER (1943).

Of conifers only young trees were examined at a newly planted area. In these young vigorous trees cambial activity started in the stem a few days after it had begun at bud base. In the *Pinus*-, *Picea*- and *Abies*-species it began before but break. In *Larix decidua* it only began after the needles on the dwarf shoots were fully developed.

The hardwoods are divided into the following three groups:

1) *Fraxinus excelsior*, *Quercus robur* group. To this also *Aesculus hippocastanum* and *Ulmus glabra* belong, so that all "English-grown timber" trees with ring porous wood belong to this group.

In these trees wood formation started on the young branches before bud break and rapidly spread in basipetal direction, so that it reached stem base before the buds were well open.

2) *Alnus glutinosa*, *Fagus silvatica* group. Here wood formation started on the one-year-old branches after bud break only. When shoot extension began wood formation quickly increased, and it soon reached down to stem base.

3) A large and varied group comprising i. a. *Rosaceae*, *Acer*, *Salix*, and *Populus*. Cambial activity began in the latter "at various stages relative to the opening of the buds" (p. 372), and comparatively long time passed before it reached stem base.

Investigators seek the reason why wood formation in the ring porous trees begins before, and in the diffuse porous not till after bud break, in the difference between the annual ring formation of the two groups.

WIGHT (1933) five miles from Leeds in England each month through a period of a year—except in the summer months—felled a 20-year-old *Pinus silvestris*. From each tree he took sections from top to root and examined wood formation and starch content. Like many of the abovementioned workers he found that wood formation began at bud base and from there spread in basipetal direction. In the stem it began c about bud break time.

IWANOV (1934) in Russia through a period of three years followed the growth in thickness in *Picea abies* and *Pinus silvestris*.

He found that as a consequence of lower temperature wood formation was not so lively in the lower, shaded parts of the stem as in the upper, sunny ones.

The summer wood percentage was greatest in the lower part of the stems.

He draws the conclusion from the investigations that as a consequence of the effect of the shade on the stems of the dominant trees the undergrowth in the forests reduce the production of stem wood.

KIENHOLZ (1934) in connection with measurements of the growth of the top shoot and the needles in a series of North American species of trees also followed the course of growth in thickness in two *Pinus resinosa* AITON by means of MacDougal's dendrograph.

The growth in thickness began between May fifth and May twelfth and terminated in October.

There was a certain correlation between the growth in the various organs. The extension growth of the roots and the top shoot and the most active growth in thickness thus took place simultaneously at the beginning of July.

ELLIOTT (1935) has examined the time of the sieve-tube formation in *Acer pseudoplatanus*.

He found that as long as wood is formed, no sieve tubes are formed. When wood formation ceases in the autumn, sieve tube formation begins and continues until the fall of the leaves.

The last formed sieve tissue cells winter in incomplete condition. Before the cambium begins to divide in the spring, these sieve tissue cells grow and form a special type of sieve tissue, which he calls the spring type of sieve tubes.

SIGMOND (1935) has through a period of three years investigated when cambial activity at breast height ceases in *Picea abies*, *Abies alba*, and *Pinus silvestris* in the heights around the Lunzer Lake in Niederösterreich. In all the trees the division of the cambium ceased at the beginning of September. The walls of the summer wood cells on the other hand continued to grow in thickness into late October.

BROWN (1935) examined on sections the cambial activity in *Populus tremuloides* MICHW. and *P. balsamifera* L. at Alberta in Canada.

Wood formation began at bud base in the second week of May; ten to twenty days later it started in the roots. It took shortest time in the youngest trees.

In root shoots wood formation began simultaneously with that in the branches of the mother tree. From the root shoots wood formation spread to the older roots.

GÄUMANN (1935, pp. 227—229) has on sections followed the course of wood formation in *Fagus silvatica*. Wood formation began in the middle of May and ceased in the middle of September.

ABELL (see DETLEV MÜLLER (1943, p. 163)) found that cambial activity in *Fagus silvatica* in Geel Forest in Denmark began c. eight days after foliation.

III. Technique, Locality and Climate.

Technique.

The investigations are carried out on sections taken in the course of 1944 and 1945 from branches, stem, and roots. The sections were as a rule cut with a sharp knife. Some times also cores were taken with an increment borer.

Of the sections or the cores there was by means of a razor blade made a micron section which after being stained with haematoxylin (after DELAFIELD) was examined under the microscope while still wet[1].

All measurements on the sections were made with a Zeiss Zeichnenapparat. The sections were projected down on the table in 50 to 200 times magnifications. Then the measurements were taken with compasses and read on a transversal plotting scale.

A more detailed description of the technique used will be found in the introductions to the separate parts of the investigations.

Locality.

The investigations concerning the time of the beginning of wood formation have chiefly been carried out in Geel Forest, Rude Forest and Store Dyrehave at Hillerød as well as in Bogø Forest.

The investigations concerning the course of wood formation within the growth period have all been carried out in Bogø.

Climate.

Climatic conditions in the various months of 1944 and 1945 for Bogø and Geel Forest (Lyngby) appear from Table I.

With exception of May and June 1944 the vegetation period in both years was considerably warmer than normal. Particularly August 1944 was extremely hot.

In Bogø July and August 1944 were very poor in rain.

[1] As the young unlignified wood elements shrink on drying it is of the greatest importance that all observations and measurements are carried out before the sections become dry.

TABLE I.

The Monthly Mean Temperature and Rainfall in 1944 and 1945 and Averagely for the Years from 1886—1925 Measured at Bogø and Lyngby Meteorologic Station.

Month	Mean Temperature C°						Rainfall mm.					
	Bogø			Lyngby			Bogø			Lyngby		
	1886–1925	1944	1945	1886–1925	1944	1945	1886–1925	1944	1945	1886–1925	1944	1945
January	0.1	3.2	–0.9	–0.5	3.0	–1.5	40	45	57	39	66	58
February	0.0	1.4	2.3	–0.7	0.9	1.7	33	14	60	30	20	59
March	2.0	1.5	5.2	1.3	1.3	4.9	38	30	18	37	35	13
April	5.8	6.2	7.7	5.5	5.9	7.5	36	37	45	42	21	40
May	10.8	9.9	11.6	10.9	9.9	11.2	41	73	18	39	53	36
June	14.5	13.6	15.3	14.5	13.9	14.8	47	67	80	52	50	111
July	16.4	17.4	18.0	16.3	17.9	17.4	71	34	45	63	55	74
August	15.9	19.1	17.3	15.4	19.0	17.1	67	19	58	82	33	112
September	13.0	13.3	13.9	12.3	12.9	13.4	47	59	16	53	116	59
October	8.7	9.7	10.4	7.9	9.4	9.9	57	54	46	56	41	63
November	4.4	4.9	..	3.6	4.4	..	45	92	..	47	91	..
December	1.7	1.5	..	1.0	1.8	..	50	41	..	53	39	..
The year...	7.8	8.5	..	7.3	8.4	..	573	565	..	592	620	..

IV. The Cambium during the Rest Period.

The appearance of the cambium during the rest period has been examined on sections taken in the course of winter from new-felled trees.

During the rest period the secondary cambium is usually four to eight cells wide. The number is greatest in those parts of the branches, that grow most in thickness, smallest in older branches and roots with slight growth in thickness. It is on the whole wider in conifers than in hardwoods.

After BROWN (1915) the cambium in *Pinus strobus* L. is two to four cells wide in the two-year-old branches, and seven to ten cells wide in the stem. After HANSON and BRENKE (1926) it is in *Fraxinus campestris* BRITT. four to six, and in *Acer Saccharinum* L. three to four cells wide. SWARBRICK (1927 a) states that in the branches of fruit trees it is seven cells wide.

The cambium cells consist of an initial cell and young not yet differentiated protoplasm-filled wood- and sieve-tissue cells formed at the end of the preceding growth period, cf. COCKERHAM (1930, Fig. 1) and ELLIOT (1935).

The young wood- and sieve-tissue cells are distributed round the initial cell in the following way:

Secondary bark:

The cambium { two to five undifferentiated sieve tissue cells.
the initial cell.
one to three undifferentiated wood cells.

Secondary wood:

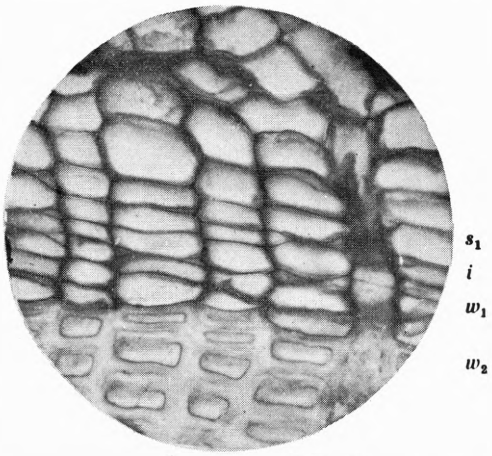
During the resting stage the cell walls of the cambium generally stand out sharply and distinctly under the microscope. The form of the cell is most often rectangular, see Fig. 1.

V. The Preliminary Change of the Cambium.

When the temperature begins to rise in spring and the buds begin to swell the appearance of the cambium alters as described by SWARBRICK (1927 a).

The cell walls become semi-transparent and appear more slurred under the microscope than in the resting period (comp. Figs. 1 and 2). The protoplasm simultaneously passes from a gel-like into a sol-like condition.

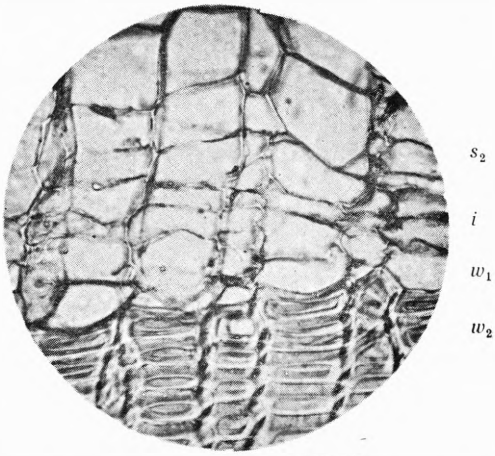
At the same time the radial cell walls of the cambium begin to extend, and the cambium as a whole increases in width: comp. KNUDSON (1913), BROWN (1915),



(480 ×).

Fig. 1. The cambium of a *Larix decidua* during the resting period. Transverse section taken at breast height in 15-year-old *Larix decidua* at the beginning of February, 1945.

s_1 Young, undifferentiated sieve tissue cells formed at the end of preceding growth period.
i The initial cell.
w_1 Undifferentiated wood cells formed at the end of preceding growth period.
w_2 Summer wood from preceding year.



(480 ×).

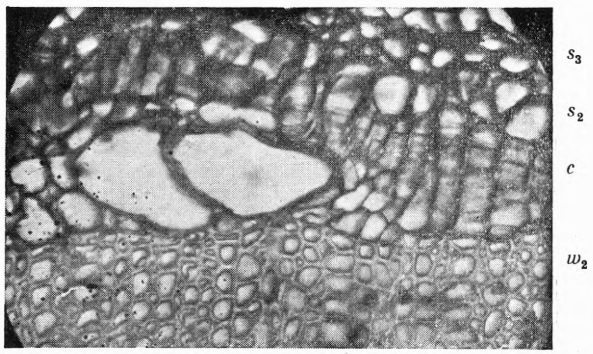
Fig. 2. The cambium of the *Larix decidua* at the preliminary change. Transverse section taken at the middle of April 1945 at breast height of the same *Larix decidua* as the section in Fig. 1.

s_2 Spring sieve tissue.
i The initial cell.
w_1 Young wood cells under differentiation (see w_1, Fig. 1).
w_2 Summer wood from preceding year.

SWARBRICK (1927 a), REES (1929), COCKERHAM (1930), PRIESTLEY, SCOTT and MALINS (1933) and WIGHT (1933). Often the width of the cambium is almost doubled before the beginning of the division into cells[1].

The sieve tissue cells (s_1, Fig. 1) are differentiated in the course of short time into spring sieve tissue (s_2, Fig. 2) as described by ELLIOTT (1935).

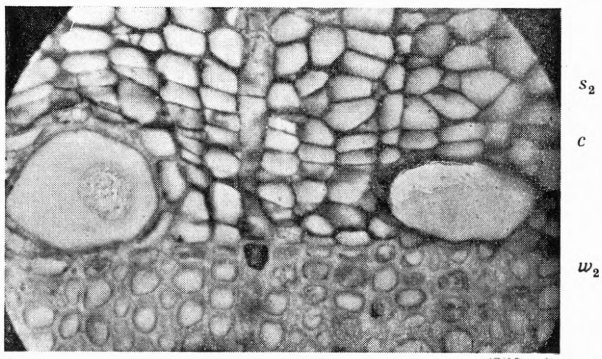
In broad leaved trees a few of the young wood cells (w_1, Figs. 1 and 2) increase much more in size than the others and press the neighbouring cells strongly together



(340 ×).

Fig. 3. Transverse section through the cambium in an older *Ulmus glabra* a few days after the beginning of cell division. Two large vessels are almost completely differentiated. The cambium appears as a slurred belt winding round the vessels. In the wedges to the right and left of the vessels fully differentiated parenchyma cells are seen.

s_3 Collapsed sieve tissue.
s_2 Spring sieve tissue.
c Cambium at division stage.
w_2 Last year's summer wood.



(340 ×).

Fig. 4. Transverse section in same *Ulmus glabra* as in Fig. 3. The section was taken c. one week after the beginning of cell division. To the left is seen a fully formed and lignified[2] vessel. To the right a vessel under differentiation.

s_2 Spring sieve tissue.
c Cambium at division stage.
w_2 Last year's summer wood.

and the cambium outwards (see Figs. 3 and 4). These particularly quick growing cells develop into the first spring vessels, which do not, however, succeed in becoming completely differentiated before the beginning of cell division.

This change in the cambium in the spring, which may be called the preliminary change, begins first in the one-year-old branches, whereafter it spreads in basipetal direction. Same observation is made by WIGHT (1933) in *Pinus silvestris* L.

After my own observations the lignification of the cell walls of the vessels proceeds considerably quicker in the ring porous than in the diffuse porous trees.

In Figs. 5 and 6 is stated the approximate time of the beginning of the preliminary change in the springs of 1944 and 1945.

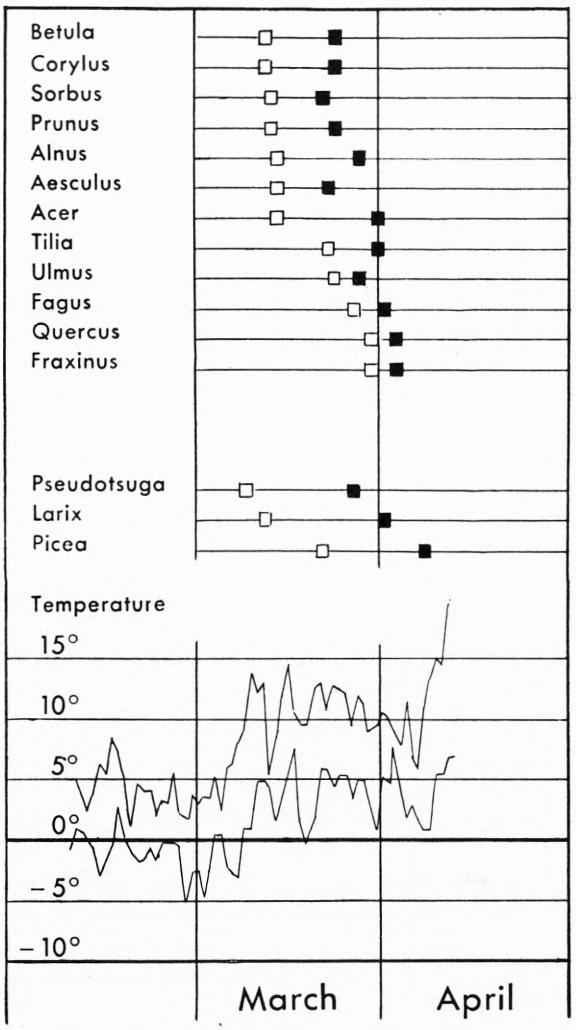
[1] BROWN (1915) found that the cambium in *Pinus strobus* L. was 70 % wider, and REES (1929) that in *Picea rubra* LINK it was over 100 % wider.

[2] SWARBRICK (1927a, p. 151) writes about the lignification of the cell walls of the vessels in fruit trees: "After becoming empty the lignification of the vessel walls did not take place for at least ten days".

Fig. 5. The approximate time of the transition of the cambium from the resting stage to the preliminary change in the spring of 1944:

□ in 1-year-old top branches.
■ at 1.3 m height in the stem.

The dates apply to the older trees in close stands.
Entered the maximum and minimum temperatures measured at the Meteorological Station at Lyngby.



Pseudotsuga taxifolia and *Picea sitchensis*: In 1945 the preliminary change in the branch cambium might already be observed in the middle of March. The mean temperature was at this time about 4°—5° C. The maximum temperature had not exceeded 12° C.

Pinus silvestris, Larix decidua, Picea abies, Betula pendula, Alnus glutinosa, Corylus avellana, Carpinus betulus, Ulmus glabra, Tilia cordata, Aesculus hippocastanum, Acer pseudoplatanus, Prunus avium, and *Sorbus aucuparia*: In these species the preliminary change could not be observed in the branch cambium till the end of March (1945) or the beginning of April (1944) after some warm spring days with a maximum temperature above 12° C.

Fagus silvatica, Quercus robur, and *Fraxinus excelsior*: In these species the pre-

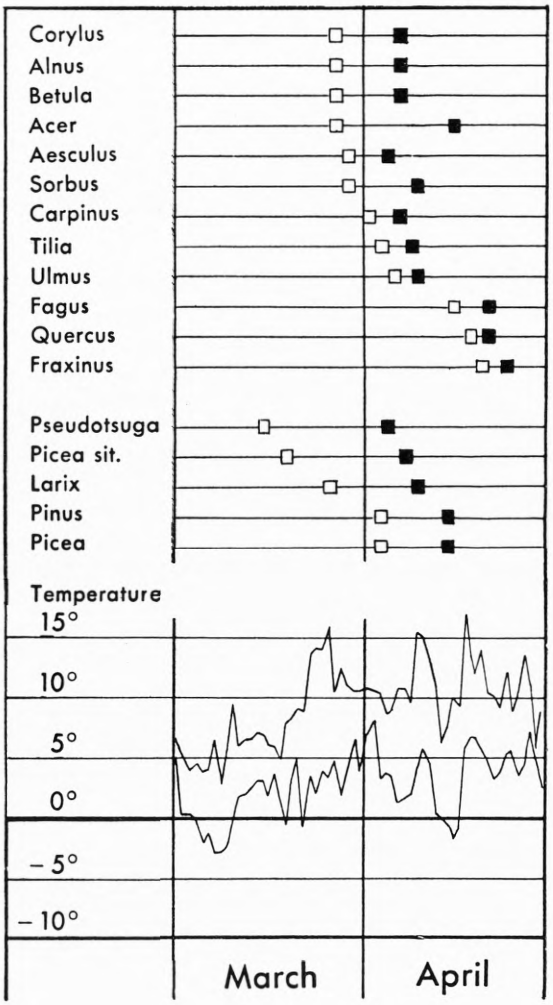


Fig. 6. The approximate time of the transition of the cambium from the resting stage to the preliminary change in the spring 1945:

□ in 1-year-old top branches.
■ at 1.3 m height in the stem.

The dates apply to the older trees in close stands.
Entered the maximum and minimum temperatures measured at the Meteorological Station at Lyngby.

liminary change in the branch cambium only occurred towards the end of April. The time seems to be more autonomously determined than in other species of trees.

In young trees in sheltered and warm localities the change in the cambium began some days earlier than shown in Figs. 5 and 6.

The condition of the soil was apparently of subordinate importance.

The change in the cambium spread more quickly from the young branches and down to stem base in the hardwoods than in the conifers. And it took shorter time in hardwoods in the ring porous than in the diffuse porous trees (see Figs. 5 and 6).

When the cambium is at the stage of change it is sensitive towards frost. On March 20th 1945 I laid a packing with a cold mixture round vigorous 3-year-old branches of a young *Pseudotsuga taxifolia* and a *Picea sitchensis*. In both branches the change in the cambium was already quite distinct. The packing was placed by

means of the same process as I had previously used in a similar experiment, see BORNEBUSCH and LADEFOGED (1940). The temperature reached down to — 8° and — 10° C.

In July both branches were cut off. In the cold-affected places frost ring formations appeared similar to those found by me in the same species of wood after the spring frost in 1938, see LADEFOGED (1938).

VI. The Time of the Inception of Cell Division.

The transition between the preliminary change of the cambium and the stage of division occurs gradually. It has therefore only been possible to determine the time of the inception of cell division (the wood formation) with an exactitude of about 3 to 5 days.

Methods, Material, and Elaboration.

For each species of tree is determined:

a) The date of the inception of cell division in the branches and the other part of the stem in relation to bud break.

The determinations have been made by a comparison of bud development and cambial activity in young and older new-felled trees. The summer felling in 1945 was of great value for the said investigations.

b) The date of the inception of cell division at breast height and in the roots in relation to bud break.

These determinations are made by following the development of buds and cambial activity at breast height and in the roots of the following trees:

	Number		Age Years
	1944	1945	
a) Trees over 10 Years:			
Conifers:			
Pinus silvestris	—	5	25—30
Larix decidua	6	7	25—100
Picea abies	8	8	25—35
Picea sitchensis	—	6	18—25
Abies alba	—	5	35—40
Pseudotsuga taxifolia	5	8	14—20
Hardwoods:			
Betula pendula	6	6	35—60
Alnus glutinosa	8	8	15—35
Corylus avellana	6	8	c. 10
Carpinus betulus	—	5	c. 30
Fagus silvatica	6	8	35—100
Quercus robur	8	8	25—40
Ulmus glabra	9	6	15—60
Tilia cordata	6	4	20—60
Aesculus hippocastanum	3	2	c. 100
Acer pseudoplatanus	6	6	30—100
Prunus avium	6	—	10—35
Sorbus aucuparia	7	6	10—25
Fraxinus excelsior	7	7	35—45
b) Trees under 10 Years:			
Conifers:			
Picea abies	5	—	7
Hardwoods:			
Betula pendula	6	6	2—8
Alnus glutinosa	8	8	3—8
Fagus silvatica	6	5	7—9
Quercus robur	6	6	7—8
Ulmus glabra	4	6	2—7
Acer pseudoplatanus	6	6	2—9
Fraxinus excelsior	6	5	2—7

TABLE II. Number of Days between the Inception of Cell Division at Breast Height and Bud

Species of Tree	Number of Trees		Age	Bud Break	
	1944	1945		1944	1945
Hardwoods					
Ring porous:					
Fraxinus excelsior	7	7	35—45	$^{23}/_{5} \pm 1.3$	$^{19}/_{5} \pm 2.3$
Quercus robur	8	8	25—40	$^{19}/_{5} \pm 2.5$	$^{15}/_{5} \pm 2.4$
Ulmus glabra with flowers	4	3	20—60	$^{7}/_{5} \pm 3.1$	$^{13}/_{4} \pm 0.3$
— without flowers	5	3	15—25	$^{29}/_{4} \pm 2.0$	$^{9}/_{4} \pm 1.1$
Diffuse porous:					
Carpinus betulus	—	5	c. 30	—	$^{15}/_{4} \pm 1.9$
Tilia cordata	6	4	20—60	$^{15}/_{5} \pm 1.3$	$^{20}/_{4} \pm 1.9$
Sorbus aucuparia	7	6	10—25	$^{3}/_{5} \pm 2.7$	$^{16}/_{4} \pm 1.7$
Prunus avium	6	—	10—35	$^{4}/_{5} \pm 1.9$	—
Fagus silvatica	6	8	35—100	$^{9}/_{5} \pm 1.5$	$^{5}/_{5} \pm 1.7$
Aesculus hippocastanum	3	2	c. 100	$^{5}/_{5} \pm 2.1$	$^{12}/_{4} \pm$
Acer pseudoplatanus	6	6	30—100	$^{4}/_{5} \pm 2.8$	$^{21}/_{4} \pm 3.7$
Corylus avellana	6	8	c. 10	$^{29}/_{4} \pm 0.9$	$^{8}/_{4} \pm 1.1$
Betula pendula	6	6	25—60	$^{26}/_{4} \pm 3.1$	$^{9}/_{4} \pm 1.5$
Alnus glutinosa	8	8	15—35	$^{7}/_{5} \pm 1.9$	$^{7}/_{4} \pm 0.3$
Conifers					
Picea abies	8	8	25—35	$^{25}/_{5} \pm 1.7$	$^{11}/_{5} \pm 3.2$
Pseudotsuga taxifolia	5	8	14—20	$^{2}/_{5} \pm 2.7$	$^{4}/_{5} \pm 1.8$
Picea sitchensis	—	6	18—25	—	$^{3}/_{5} \pm 2.6$
Abies alba	—	5	35—40	—	$^{27}/_{4} \pm 2.7$
Pinus silvestris	—	5	25—30	—	$^{30}/_{4} \pm 1.3$
Larix decidua	6	7	25—100	$^{27}/_{4} \pm 2.2$	$^{2}/_{4} \pm 1.9$

The results appear from Tables II and III.

Different trees were used each year.

The forest trees grew in close stands. The *Tilia cordata* were open-grown. The *Corylus avellana, Sorbus aucuparia* and most of the *Prunus avium* grew as undergrowth under older hardwoods and conifers. The young trees stod in open culture areas or as natural reproduction under older hardwoods.

The trees were all growing well.

The bud break was determined by examinations from day to day.

The sections from the stem were taken at 2 to 4, from the roots at 8 to 10 days intervals.

The examinations were supplemented with a number of sections taken from newly felled trees.

Break in 1944 and 1945 in Trees over 10 Years, and of the Inception of Growth in the Roots.

Cell Division at 1.3 m. Height in the Stem. Began the Following Number of Days				Extension Growth in the Roots Began		Cell Division in the Roots Began	
Before Bud Break		After Bud Break					
1944	1945	1944	1945	1944	1945	1944	1945
8 ± 0.9	9 ± 0.9		..	$^{29}/_{5}$	$^{20}/_{5}$	$^{12}/_{6}$	$^{22}/_{5}$
5 ± 0.7	8 ± 1.0	..	..	$^{16}/_{5}$	$^{27}/_{4}$	$^{24}/_{6}$	$^{8}/_{6}$
4 ± 1.2	3 ± 0.7	..	..	$^{15}/_{5}$	$^{28}/_{4}$	$^{27}/_{6}$	$^{10}/_{6}$
..	..	1 ± 0.4	1 ± 0.8	..	..	..	..
..	..	—	7 ± 2.1	—	$^{3}/_{5}$	—	$^{7}/_{6}$
..	..	8 ± 1.6	4 ± 0.1	$^{25}/_{5}$	$^{27}/_{4}$	$^{25}/_{6}$	$^{11}/_{6}$
..	..	10 ± 1.0	13 ± 4.0	$^{25}/_{5}$	$^{10}/_{5}$	$^{25}/_{6}$	$^{15}/_{6}$
..	..	15 ± 3.7	..	$^{25}/_{5}$	—	$^{25}/_{6}$	—
..	..	13 ± 3.1	15 ± 1.8	$^{14}/_{5}$	$^{14}/_{4}$	$^{26}/_{6}$	$^{13}/_{6}$
..	..	15 ± 2.1	30	$^{25}/_{5}$	$^{5}/_{5}$	$^{18}/_{6}$	$^{29}/_{5}$
..	..	18 ± 3.4	29 ± 3.2	$^{17}/_{5}$	$^{28}/_{4}$	$^{25}/_{6}$	$^{12}/_{6}$
..	..	20 ± 1.6	33 ± 2.4	$^{28}/_{5}$	$^{25}/_{5}$	$^{25}/_{6}$	$^{11}/_{6}$
..	..	24 ± 2.2	39 ± 2.3	$^{14}/_{5}$	$^{14}/_{5}$	$^{25}/_{6}$	$^{27}/_{5}$
..	..	27 ± 2.6	43 ± 1.8	$^{14}/_{5}$	$^{3}/_{5}$	$^{25}/_{6}$	$^{16}/_{6}$
4 ± 0.7	6 ± 1.7	..	..	$^{5}/_{5}$	$^{20}/_{4}$	$^{3}/_{6}$	$^{21}/_{5}$
2 ± 0.2	6 ± 0.7	..	..	$^{11}/_{5}$	$^{30}/_{4}$	$^{25}/_{5}$	$^{22}/_{5}$
—	5 ± 3.1	..	..	—	$^{24}/_{4}$	—	$^{24}/_{5}$
..	..	—	2 ± 3.3	—	$^{27}/_{4}$	—	$^{26}/_{5}$
..	..	—	3 ± 1.1	—	$^{28}/_{4}$	—	$^{14}/_{6}$
..	..	26 ± 2.6	46 ± 3.3	$^{18}/_{4}$	$^{8}/_{4}$	$^{3}/_{6}$	$^{25}/_{5}$

The successive Order of the Inception of Cell Division.

Division of cells begins at bud base. From here it spreads in basipetal direction through the branches, the stem, and finally stretches down into the roots; cf. TH. HARTIG (1857), GULBE (1888a and b), STRASBURGER (1891), JOST (1892), SWARBRICK (1927a), COCKERHAM (1930), PRIESTLEY, SCOTT, and MALINS (1933), WIGHT (1933) and BROWN (1935).

RUSSOW (1884), KNUDSON (1913), BROWN (1912 and 1915) and CHALK (1927) found in contradistinction to this that division of cells begins first in the stem. TH. HARTIG (1857), LODEWICK (1925, 1928 and 1930) found that in some cases it may begin at stem base.

PRIESTLEY (1930) has gone through the lastmentioned results critically. His view is that they rest on insufficient investigations.

TABLE III.

Number of Days between the Inception of Cell Division at Bases of Stem and Bud Break in 1944 and 1945 in Trees under 10 Years.

Species	Number of Trees		Age	Bud Break		The Division at Stem Base Began on the Following Number of Days			
						Before Bud Break		After Bud Break	
	1944	1945		1944	1945	1944	1945	1944	1945
Hardwoods									
Ring porous:									
Quercus robur	6	6	7—8	$^{20}/_{5} \pm 1.7$	$^{15}/_{5} \pm 2.4$	5 ± 0.9	8 ± 1.0	..	..
Fraxinus excelsior..	6	5	2—7	$^{18}/_{5} \pm 0.9$	$^{15}/_{5} \pm 2.1$	4 ± 0.2	1 ± 0.7	..	..
Ulmus glabra.....	4	6	2—7	$^{26}/_{4} \pm 1.3$	$^{10}/_{4} \pm 1.9$	at bud break	3 ± 0.9	..	..
Diffuse porous:								..	..
Fagus silvatica	6	5	7—9	$^{8}/_{5} \pm 0.1$	$^{8}/_{5} \pm 2.0$	..	..	18 ± 2.2	9 ± 1.8
Acer pseudoplatanus	6	6	2—9	$^{24}/_{4} \pm 1.9$	$^{13}/_{4} \pm 4.9$	..	..	12 ± 5.5	$22 \pm 3,3$
Betula pendula	6	6	2—8	$^{22}/_{4} \pm 1.9$	$^{8}/_{4} \pm 1.1$	..	..	12 ± 1.0	32 ± 4.4
Alnus glutinosa....	8	8	3—8	$^{7}/_{5} \pm 1.9$	$^{7}/_{4} \pm 0.3$	..	..	13 ± 1.9	17 ± 2.1
Conifers									
Picea abies.....	5	—	7	$^{1}/_{6} \pm 1.7$	—	4 ± 0.7	..	..	..

The Time of the Inception of Cell Division in Relation to Bud Break.

1. At Bud Base.

The division of cells at bud base begins some days before or simultaneously with bud break except in *Larix decidua* (see Figs. 7, 8, 9 and 10).

Among the tree species there are the following general differences:

a) Hardwoods.

α) The diffuse porous

In the diffuse porous the time of the inception of cell division in relation to bud break depends on how much the buds extend before bursting.

In *Betula pendula, Alnus glutinosa, Corylus avellana, Fagus silvatica* and *Tilia cordata* where bud extension as a rule is comparatively slight the division of cells begins simultaneously with or at the earliest two days before bud break.

In *Sorbus aucuparia, Acer pseudoplatanus, Aesculus hippocastanum* and *Prunus avium*, where the shoot extension is often fairly considerable, cell division begins up to one week before bud break.

β) The ring porous

In *Quercus robur, Fraxinus excelsior* and flower-bearing *Ulmus glabra* cell division begins 1 to 9 days before bud break. The same applies to cases where the bud extension is very slight only (*Fraxinus excelsior*).

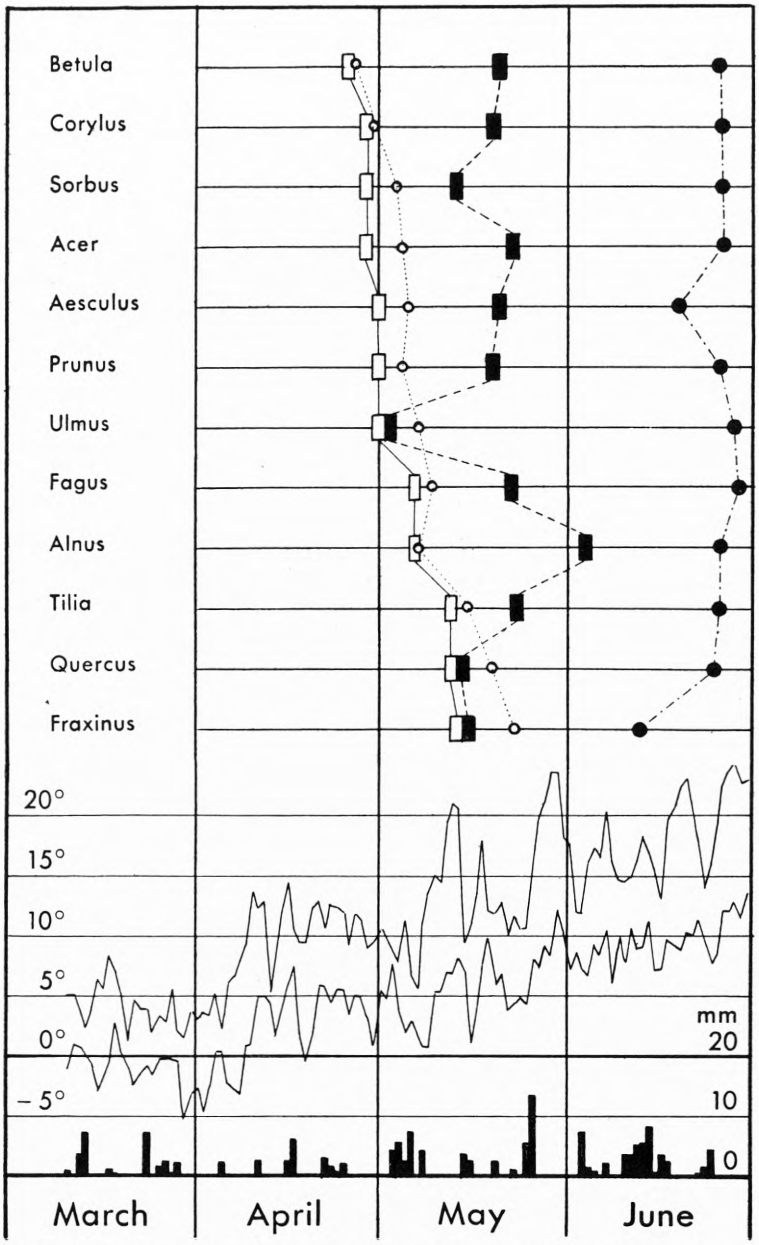


Fig. 7. Mean time for the inception of cell division (wood formation) in 1944 in hardwoods over ten years:

□ At bud base.
■ At 1.3 m height in the stem.
● In the roots at ten cms depth and c. 1.5 m from stem base.
o Time of bud break.

Rainfall and maximum and minimum temperatures recorded as measured at the Meteorological Station at Lyngby.

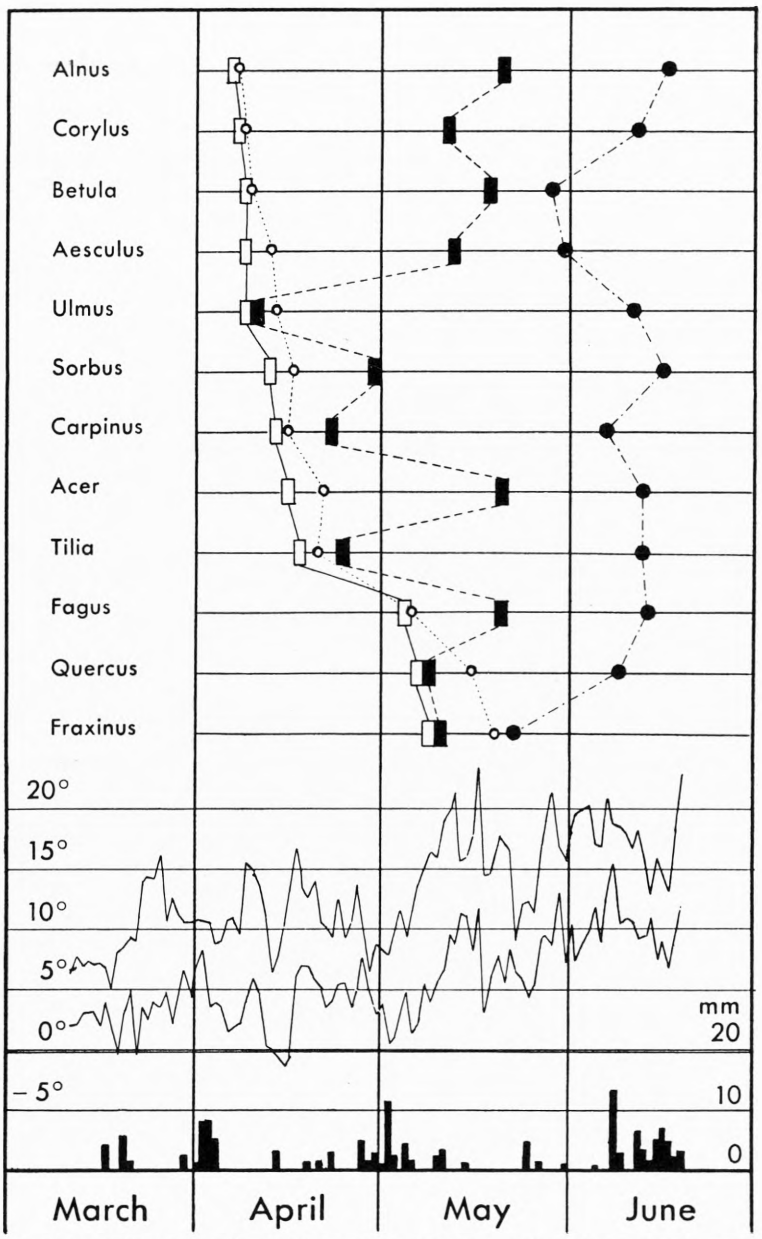


Fig. 8. Mean time of inception of cell division (wood formation) in 1945 in hardwoods over ten years:

□ At bud base.
■ At 1.3 m height in stem.
● In roots at 10 cms depth and 1.5 m from stem base.
o Time of bud break.

Rainfall and maximum and minimum temperatures recorded as measured at the Meteorological Station at Lyngby.

In *Ulmus glabra* without flowers cell division on the other hand in many cases only begins simultaneously with bud break[1], cp. Russow (1884).

b) *Conifers.*

In *Pinus silvestris, Picea abies, Picea sitchensis, Abies alba* and *Pseudotsuga taxifolia* cell division generally begins 5 to 15 days before bud break.

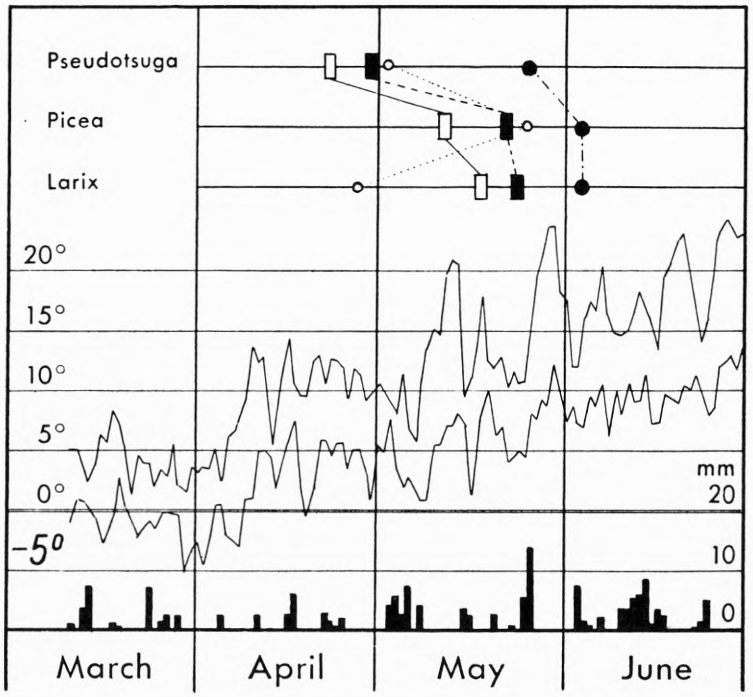


Fig. 9. Mean time of the inception of cell division (wood formation) in 1944 in conifers over ten years:

□ At bud base.
■ At 1.3 m height in the stem.
● In the roots at 10 cms depth and 1.5 m from stem base.
o Time of bud break.

Rainfall and maximum and minimum temperatures recorded as measured at the Meteorological Station at Lyngby.

In *Larix decidua* where little shoot extension takes place only in connection with bud break of the dwarf shoots, cell division does not begin till shortly before, or simultaneously with, the bursting of the long shoots.

[1] Chalk (1927) found that in *Fraxinus excelsior* cambial activity begins one week before the flower buds burst. Coster noticed the same thing in *Prunus puddum* Roxb. and *Magnolia obovata* Thunb. which also flower before foliation.

After Gill (1933) there is, however, no beginning cambial activity in connection with the growth and development of catkins.

Literature only gives one piece of information of the time of the inception of cell division at bud base in relation to bud break. After BROWN (1935) it here begins after bud break only in *Populus tremuloides* Michw. and *P. balsamifera* L.

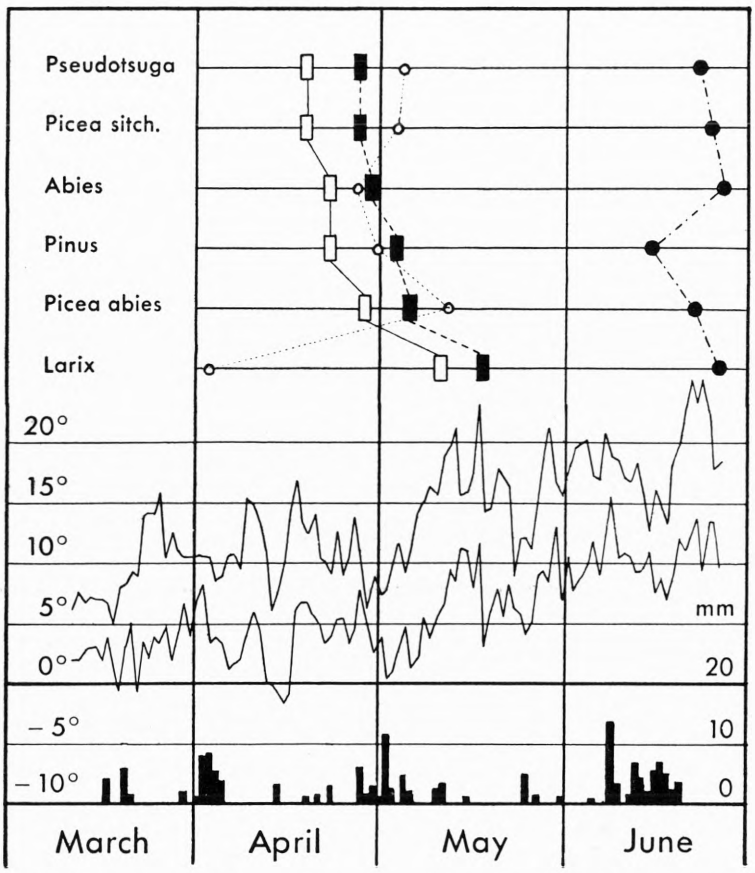


Fig. 10. Mean time for the inception of cell division (wood formation) in 1945 in conifers over ten years:

□ At bud base.
■ At 1.3 m height in the stem.
● In the roots at 10 cms depth and 1.5 m from stem base.
o Time of bud break.

Rainfall and maximum and minimum temperatures recorded as measured at the Meteorological Station at Lyngby.

There is on the other hand more information about the time of its inception in the young branches.

After R. HARTIG (1891) it here begins before or simultaneously with bud break in *Pinus silvestris*, *Picea abies*, and *Fagus silvatica*. ANTEVS (1917) after own investigations states that cambial activity in the young branches only begins after the foliage more or less has developed. NYDAM (see COSTER, 1927, pp. 77—78) found new-formed vessels in young *Fraxinus excelsior*- and *Quercus robur*-branches before the buds had begun to swell. COCKERHAM (1930) thinks that cambial activity begins in the young branches in *Acer pseudoplatanus* about the time

of bud break. PRIESTLEY, SCOTT and MALINS (1933) found, as mentioned above (pp. 371—372), that wood formation in ring porous species began before bud break; in the diffuse porous on the other hand "at various stages relative to the opening of the buds". In *Pinus*, *Picea*, and *Abies* wood formation begins "within a short time of any signs of movement in the uppermost buds". In the branches of *Larix decidua* it only begins after the needles of the dwarf shoots are fully developed.

In the diffuse porous species cell division most often begins in the branches in the lower parts of the crown. The reason of this is probably that the shaded buds burst before the sunny ones[1].

In 45-year-old *Acer pseudoplatanus* in 1945 up to 11 days and in 120-year-old *Fagus silvatica* up to 9 days elapsed between bud break in the lower and upper parts of the crown.

In the ring porous trees and in conifers the buds almost burst simultaneously all over the crown, and in conformity with this cell division begins practically simultaneously in all branches.

2. At Breast Height (1.3 m.) in the Stem.

Cell division takes place at a quicker rate in basipetal direction in the ring porous than in the diffuse porous trees and conifers (comp. Figs. 7, 8, 9 and 10).

In the ring porous and in evergreen conifers cell division begins in the lower part of the stem a few days before or at the latest simultaneously with bud break. In the diffuse porous and in *Larix decidua* it does not on the other hand begin till after the foliage (the needles of the shoots in *Larix decidua*) are partly or completely expanded (see Tables II and III).

This is conformity with most statements found in literature. At variance with this MACDOUGAL (1921 and 1924) found that in *Quercus robur* the growth in thickness in the stem began after bud break only.

HUBER (1935) connects the generally late foliation in the ring porous species with the fact that they must have formed some fresh spring wood before foliation, because the rising of the sap (in contradistinction to the diffuse porous species) mainly takes place in the new spring vessels (mentioned by DETLEV MÜLLER 1943, p. 163 and CARL MAR: MØLLER (1945), pp. 281 and 282).

The relation between bud break and the inception of cell division in the stem varies on the whole somewhat with α) age, β) exposure to light and γ) the size of the crown.

[1] ENGLER (1913) thinks that the reason of this is that the sunny buds have greater difficulty in bursting than the shaded ones on account of more and thicker raments.

HUBER (1931) gives quite a different explanation. According to him the sunny buds always possess a larger "Treibwilligkeit" than the shaded ones. When the latter nevertheless are the first to burst it is due to the fact that—as a consequence of their being placed within the crown—they may sooner benefit by the rising water flow than the sunny buds.

MÜNCH (1936) after experimental investigations arrives at the result, that ENGLER's explanation must be considered the most probable one.

α) Age.

In the diffuse porous species a shorter time elapses between bud break and the inception of cell division at stem base in the young (low) trees than in the older (high) ones (comp. Tables II and III).

The difference is undoubtedly due to the fact, that the distance between crown and stem base is shorter in the young than in the older trees.

β) Exposure to Light.

In sun exposed c. 30-year-old *Picea abies, Pseudotsuga taxifolia* and *Pinus silvestris*-stems cell division began in the lower parts of the stems in 1945 up to two weeks before bud break and, approximately estimated, one week earlier than in shaded stems within close-grown stands.

The reason must be sought in the fact that the sun-exposed stems are more quickly warmed up in spring than the shaded ones, comp. R. HARTIG (1891), AMILON (1910) and IWANOV (1934).

In conformity with MER (1892), BROWN (1912), CHALK (1927), and LODEWICK (1928) I have not observed that cell division begins earlier in the sun-exposed side of the stem than in their shaded side as stated by WALTER (1898) and SCHUITMAKER (see COSTER, 1927, pp. 79 and 80).

γ) The Size of the Crown:

In the diffuse porous species a shorter time elapses between the inception of cell division at bud- and stem-base when the trees have large crowns than when they have small ones (see Table IV). In trees with very small crowns, poor in leaf, (whips) wood formation may completely fail to appear in the lower part of the trunk, comp. R. HARTIG (1869), O. G. PETERSEN (1904, p. 180), RUBNER (1910, pp. 246—250) and PRIESTLEY (1930, p. 335).

The explanation must be sought in difference in stuff production, possibly also in difference in growth hormone production (see pp. 34 to 36).

TABLE IV.

The Number of Days by which Cell Division at Breast Height Started after Bud Break in 1944 and 1945 in *Fagus silvatica, Betula pendula* and *Acer pseudoplatanus* With Large and Medium Sized Crowns Respectively. The Figures were Arrived at by Dividing the Trees in Table II after Crown Breadth.

Species	Trees with:			
	Large Crowns		Medium Sized Crowns	
	1944	1945	1944	1945
Fagus silvatica	5 ± 0.7	13 ± 2.6	18 ± 2.2	19 ± 0.3
Acer pseudoplatanus	11 ± 1.5	35 ± 0.7	25 ± 1.8	41 ± 3.0
Betula pendula	21 ± 3.0	23 ± 2.0	27 ± 2.7	35 ± 3.7

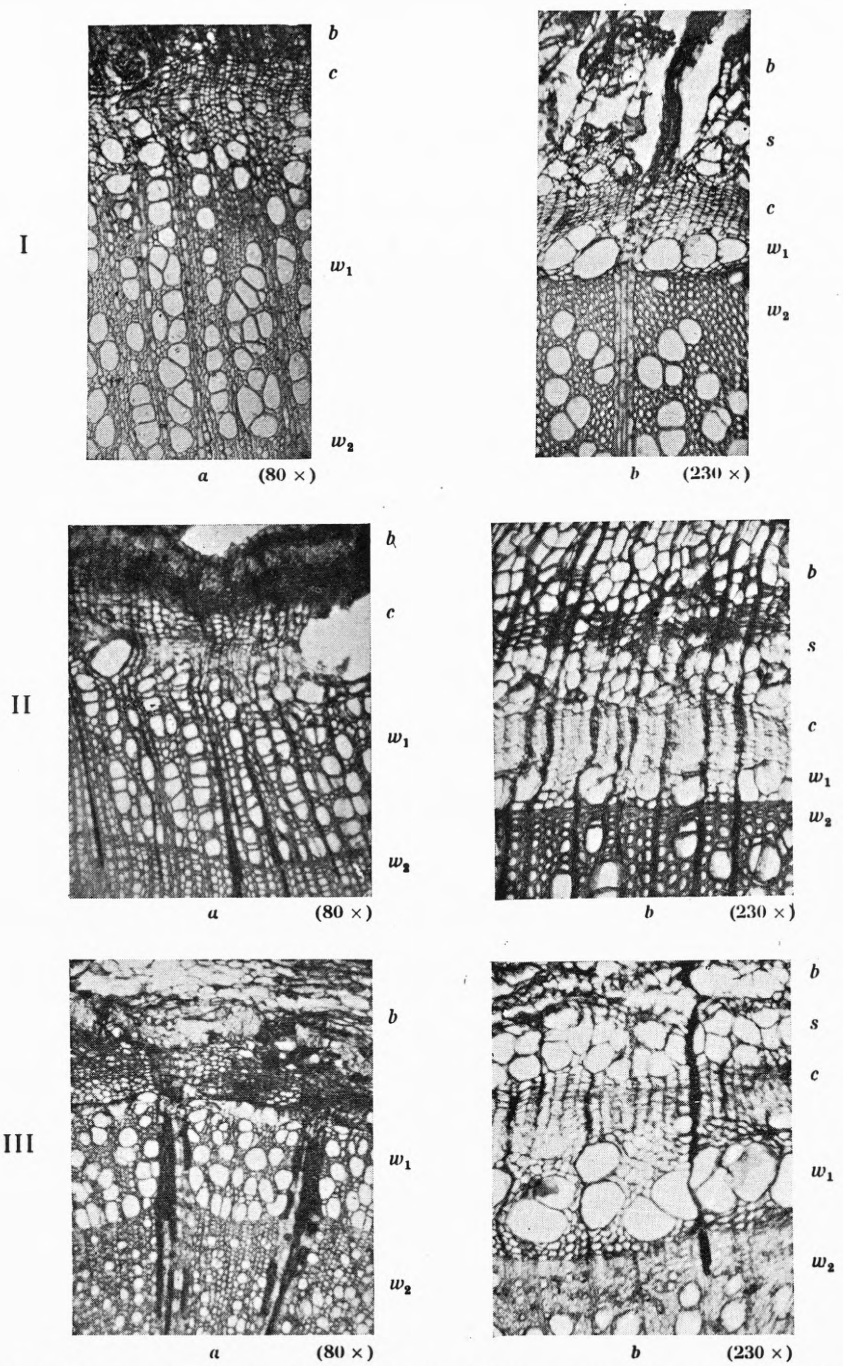


Fig. 11. The difference in wood formation per June 1, 1945 in a one-year-old, vigorous top branch (*a*) and at 1.3 m height in the stem (*b*) in

I: A 35-year-old *Prunus avium*.
II: A 35-year-old *Alnus glutinosa*.
III: A 120-year-old *Fagus silvatica*.

b = bark, *s* = sieve tissue, *c* = cambium, w_1 = new-formed wood and w_2 = summer wood, from last year.

As a consequence of the relatively long period that elapses between the beginning of cell division at bud- and stem-base in the diffuse porous trees and the conifers a relatively great part of the annual ring has already formed in the young branches in the said species at the time, when wood formation is to begin in the lower part of the stem (see Fig. 11).

In the ring porous trees there is on the contrary little difference between the wood formation in the young branches and in the lower part of the stem as long as the differentiation of the large spring vessels is taking place.

3. In the Roots.

Cell division in the roots only begins when the ground temperature has reached 10° to 13° C.

On May 15th, 1945 cell division had started in branches and stem in young *Fraxinus excelsior* and *Acer pseudoplatanus* that stood in the shade under older *Fagus silvatica*, *Fraxinus excelsior* and *Acer pseudoplatanus* in Geel forest. In the roots the cambium was on the other hand still in the resting period.

On the same day I placed a maximum and a minimum thermometer (model "Six") at 5 cms depth in the ground among the young trees. I then read the temperature at 2 to 3 days' interval. Simultaneously I followed the cambial activity in the roots.

The cell division started within a time when the ground temperature ranged between 10° and 12° C.

Thereafter I moved the thermometer out into some swamp-like, pretty watery and cold soil under a mixed stand of uneven-aged *Betula pendula*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Alnus glutinosa*, *Fagus silvatica*, *Prunus avium*, *Ulmus glabra* and *Sorbus aucuparia*, all of different ages.

In this place cell division in the roots began within a period when the temperature of the ground ranged between 10° and 13° C.

Cell division starts first in the roots in the uppermost layer of the ground, which is most quickly warmed up. If a root grows so near the surface of the ground, that part of its surface is bare from stem basis and a piece outward, cell division begins in this part of the root either simultaneously with or a few days after cell division has begun in the lower part of the stem.

In older *Fagus silvatica* and *Quercus robur* in clayey lands from 4 to 6 weeks may pass between the beginning of cell division in the surface roots and the deepest roots[1].

In well drained shaded forest lands cell division begins in the roots at 10 cms depth two to eleven weeks after bud break, and two to eight weeks after it has begun at breast height (see Table II and Figs. 7, 8, 9 and 10). The variation in individuals as well as in species is very considerable. The times stated in the tables must therefore not be taken too rigoristically.

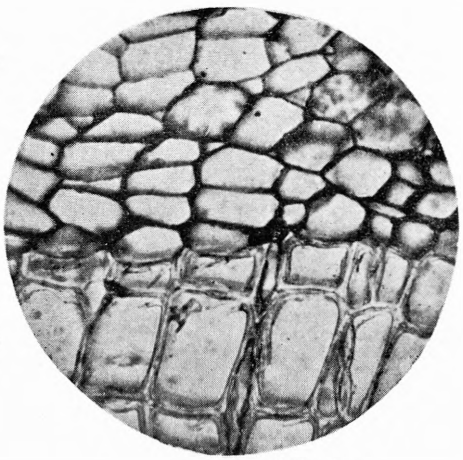
[1] In 1944 I observed this condition in c. 120-year-old *Fagus silvatica* and *Quercus robur* that grow just above the slope to the Baltic in Fanefjord forest. By digging into the slope I easily reached the deepest roots.

Existing literature also gives us the impression that there is much variation. The various investigators record the following intervals between the beginning of cell division in stem and roots:

TH. HARTIG (1857): 1 month in *Larix decidua* and *Pinus silvestris*, 2½ months in *Quercus robur*, and 14 days in *Acer pseudoplatanus*.

RUSSOW (1884): A few days in *Quercus robur*, *Fraxinus excelsior*, *Pinus silvestris* and *Larix decidua*. In *Tilia cordata* cell division begins in the roots earlier than in the stem.

GULBE (1888a and b): Averagely 14 days.



(480 ×)

Fig. 12. Transverse section through the cambium in an 1-year-old *Picea abies* root 14 days after the beginning of extension growth. The cambium is still at the rest stage.

b Secondary bark.
c Cambium.
w_2 Summer wood from last year.

MER (1892a): 10 to 15 days in *Fagus silvatica*, *Quercus robur*, *Carpinus betulus*, *Tilia cordata* and *Picea abies*.

BROWN (1915): Over 1 month in *Pinus strobus* L.

LODEWICK (1928): 1 week between stem base and the thick roots in *Fraxinus americana* L.

COCKERHAM (1930) found that in thin roots in *Acer pseudoplatanus* cambial activity may continue all through winter.

In the main roots in older trees O. G. PETERSEN (1898) found beginning wood formation on 2nd to 5th June in *Fraxinus excelsior* and *Sorbus aucuparia*; from 7th to 9th July in *Acer pseudoplatanus*, *Betula pendula*, *Populus*, *Tilia cordata*, *Larix decidua*, *Picea abies* and *Pinus silvestris*; and from 24th to 26th August in *Quercus robur*.

None of the said investigators give any information about soil, insolation or root depth.

There is not the same state of interpendence between the growth in length and thickness in the roots as between that of the branches. In spring one often sees fresh new-formed root tips in young roots in which the secondary cambium is not yet in the rest stage (see Fig. 12).

VII. The Reason why Cambial Activity Begins at Bud Base.

Investigations in the years 1934—41 have shown why cambial activity begins at bud base and from here spreads in basipetal direction. When the buds of the trees begin to swell in spring, new growth hormones are formed within them. From the buds the growth hormones proceed down through the cambium of branches, stem and root and cause it to resume growth.

α) Earlier Assumptions.

Already JOST (1893, p. 192) draws attention to the fact "... dass nicht immer und nicht allein die Zufuhr von Baustoffen die Cambialtätigkeit bedingt ...".

He arrived at this result partly from his observation that cambial activity begins first at bud base, and partly through a series of experiments.

He thus found, that if the buds are removed from a branch at some time before bud break, it does not grow in thickness, comp. TH. HARTIG (1858 and 1862), LUTZ (1895) and WIELER (1897). He showed that the reason was not due to failing assimilation by letting intact branches shoot in the dark. Even if the leaves under such conditions are unable to assimilate wood formation nevertheless takes place in the branches at the cost of the stored nutrient materials, comp. WIELER (1897).

He further found, that if we at some time before bud break remove all buds on the branches of fir, they do not grow in thickness even though the old assimilative needles still are left on the branches. On the other hand they grow in thickness if all the old needles are removed, but the buds are left to develop into new shoots. Even in darkness such branches grow in thickness.

He also found that if the stems or branches of the trees are "ringed" little or no wood formation takes place under the ringing belt. But above it wood formation is lively, compare i. a. TH. HARTIG (1862), STRASBURGER (1891), MER (1892a) and SWARBRICK (1927b).

COSTER (1927) after similar observations and experiments as JOST advances the assumption that some hormone issues from buds and leaves which somehow influences the growth in thickness. He writes among other things (p. 77): "Durch die vielen Versuche ist vorerst unzweideutig bewiesen, dass der Anfang des neuen Dickenwachstums bei periodisch kahlstehenden Laubhölzern von einem Reiz abhängig ist, der von den sich entfaltenden Knospen oder anderen auswachsenden Organen ausgeht".

MÜNCH (1932) and SNOW (1933) take a similar view.

β) The Presence of Growth Substances.

The presence of growth substances has been shown by CZAJA (1934), ZIMMERMANN (1936—37), SÖDING (1936, 1937, and 1940—41), AVERY, BURKHOLDER and CREIGHTON (1937) and BENNET and SKOOG (1938). These investigators have come to the following results:

a) During the rest stage buds and cambium contain no—or very small—quantities of active growth hormones.

b) Swelling buds, leaves, and flowers that are growing contain and produce considerable quantities of active growth hormones.

c) The growth hormone proceeds from the said organs down through the cambium[1] in branches, stem and roots and is followed by beginning cell division.

d) As long as the cambium is growing it contains larger and smaller quantities of growth hormones. When growth ceases in autumn the growth hormone content declines and becomes very small.

SÖDING (1937 and 1940—41), MÜNCH (1938) and JOST (1940) think, by the way, that the cambium is itself able to produce growth hormones after a first supply is received from the young shoot organs that are developing.

γ) The Effect of Growth Hormones.

That the growth hormones are able to make the cambium in trees resume growth is shown by experiments by SÖDING (1936 and 1940—41), GOUWENTAK (1936 and 1941) and GOUWENTAK and MAAS (1940). By means of auxin preparations or extractions from swelling buds these investigators have produced wood formation in different species of trees.

The experiments have chiefly been carried out by decapitating branches or young stems and thereafter applying a paste with the growth hormone onto the cut surface. In these branches or young stems wood formation began long before it started in untreated control-branches or -stems placed under completely similar external conditions.

After GOUWENTAK and MAAS (1940) and GOUWENTAK (1941) the periodicity of cambial activity cannot, however, directly be explained by a difference in the growth hormone production, as the cambium is not always equally susceptible to the influence of growth hormones. They found that it had an "independent", presumably material-physiologically determined, resting period which may be divided into a preliminary, middle and subsequent resting period. Under the middle resting period there cannot by means of experiments be produced any wood formation by growth substance influence, except after a preceding rest-breaking treatment.

δ) Various Reflections.

There is reason to assume that the change in the cambium (its preliminary change) preceding the beginning division into cells (see p. 16) is due to the beginning spread of growth hormones downwards from the swelling buds[2].

The growth hormones possibly proceed downwards through the cell walls of

[1] After HUBER, SCHMIDT and JAHNEL (1937) the transport of the growth hormone also takes place in the sieve tissue, comp. KASTENS (1924).

SÖDING (1940—41) has made a close study of this and found that the sieve tissue may contain growth materials.

BOYSEN JENSEN (1943, p. 330) writes: "In leaves the growth hormone transport seems to take place in the leaf traces, presumably in their sieve part".

After HELLINGA (1937) the growth hormone transport may only take place in a direction leading away from buds and leaves.

[2] SÖDING (1937 and 1940—41) found fairly large quantities of growth substances in the cambium some time before the inception of wood formation.

the cambium, cf. WEIJ 1932. The change in the appearance of the latter seems to indicate that this is so (comp. Figs. 1 and 2).

The formation of growth hormones in flower buds under expansion offer an explanation of the reason why cell division in the young branches begins simultaneously with flowering when this occurs before bud break (*Ulmus glabra*, see also footnote p. 24).

The downward progression of growth hormones from the swelling buds of the root shoots and young leaves explains why wood formation begins locally in roots with root shoots, compare BROWN (1935).

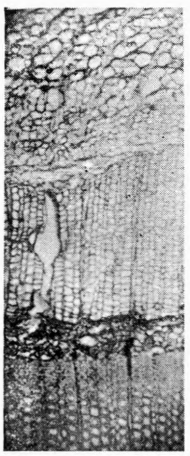


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Fig. 13. Cross section through the new formed wood under a callus growth at the end surface of a *Larix decidua* billet cut at the end of February 1945. The section was taken on August 1, same year, $2^1/_2$ cms from the cut surface of the billet.

b Bark.
c Cambium.
w_1 New formed wood.
w_2 Last year's summer wood.

Beginning wood formation is not absolutely dependent of any connection with shoot organs under development.

In forests it is often seen that callus growths form between bark and wood at bruises on stumps or on clean boled stems.

If we examine such stumps or stems a new formation of wood from the callus tissue will often be found 2 to 10 cms inside the stem or the stump (see Fig. 13). The new-formed wood ring is widest just under the callus growth and narrows inwards like a wedge. In stems it proceeds in acropetal as well as in basipetal direction.

It is to be supposed that this wood formation is due either to the wound effect from the cut surface[1], growth hormones formed in the callus tissue, or wintered growth hormones (see MÜNCH, 1938, p. 621).

The wood formed is just as ineffectually differentiated as the wood which SÖDING (1937), GOUWENTAK and MAAS (1940) and GOUWENTAK (1941) succeeded in producing experimentally by external supplies of growth hormones. On cross sections the width of the tracheids is less than in normally built wood. The cell walls are thin and give the impression of incomplete lignification. The wood is very crisp when cut with a knife.

[1] After GOUWENTAK and MAAS (1940) the wound effect is able to produce a much limited wood formation.

VIII. The Course of Wood Formation and the Time of its Termination.

Methods.

1. A Survey of Applicable Methods.

The process of wood formation may be determined by two different processes:

a) By measurements on the outside of the stem of its diameter or circumference.

By this method the process of wood formation may only be determined with approximate exactness; as established diameter- or circumference-changes are due not only to growth in the wood, but also to the growth in the bark and the ± changes in the circumference of the stem that is due to difference in the sap tension.

In the night when the transpiration is reduced the stem "swells". Reversely its volume decreases in daytime when the transpiration increases, compare KAISER (1879), FRIEDRICH (1897), and KORSTIAN (1921), MACDOUGAL (1921 and 1924), PEARSON (1924) and CHALK (1927).

During rainy periods the stem is for the same reason relatively thicker than during periods of drought, see HAASIS (1932).

In cold periods its volume decreases, see FRIEDRICH (1907).

β) By measuring the width of the new formed wood ring in sections or increment cores.

We get an approximate determination by this method only, as the width of the new formed wood ring may vary considerably even within rather narrow areas of a stem, i. a. as a consequence of eccentric growth.

2. The Method Applied.

The present examinations are carried out after the latter method (β)[1].

In order to some extent to avoid the uncertainty due to local variations in the width of the annual ring the width of the new formed wood ring at the various dates in the summer is stated in percentage of the width of the preceding year's annual ring. This method has previously been used by CHALK (1927) and gives a fairly safe determination of the process of wood formation.

Measurements which during the winter 1945 I have made on a great number of cut stems have shown that if one sticks to the same side of the stem there proves to be a fairly constant relation between the width of the two adjoining annual rings, comp. CHALK (1930, p. 10). For trees with a diameter of over 10 cms one may usually calculate with a correlation coefficient of 80 to 90. An absolute condition is, however, that the stem is well formed in the place in question. There must be no gnarls, furrows or other irregularities.

[1] Circumference measurements with sensitive, selfrecording measuring instruments had to be abandoned in advance as they were too expensive to buy.

In 1944 circumference measurements were tried till mid-June with a steel band with Vernier scale. The variations in the records were so large from one measurement to the next that this method was abandoned.

In order more easily to compare the process of wood formation in the various trees the per cents found are calculated in relation to 100 at the time of the termination of wood formation.

Material.

The examinations comprise the following species of trees:

1944	Age	1945	Age
Conifers:			
Picea abies	15—35	*Larix decidua*	13—45
Hardwoods:		*Picea abies*	10—35
Betula pendula	15—35	*Betula pendula*	10—26
Alnus glutinosa	10—45	*Alnus glutinosa*	14—55
Fagus silvatica	20—120	*Fagus silvatica*	14—70
Quercus robur	20—35	*Quercus robur*	14—70
Ulmus glabra	15—60	*Acer pseudoplatanus*	20—35
Acer pseudoplatanus	12—40	*Fraxinus excelsior*	20—59
Fraxinus excelsior	15—30		

The trees for which the process of wood formation is stated separately in Tables and Figures are described in Tables V—XIII.

The other trees were dominant or co-dominant trees in closed well nursed stands. The *Acer pseudoplatanus* on the whole were found as undergrowth under older *Fagus silvatica, Acer pseudoplatanus* and *Fraxinus excelsior.*

The growth conditions may no doubt be counted among the very best in Denmark.

The soil was in most cases deep, very mouldy and had a suitable content of clay.

The ground flora chiefly consisted of such herbs that characterize a soil rich in nutrients in good biological condition.

Taking of Sections.

In 1944 sections were taken 3 to 5 times during the summer from 20—25 trees within each species. With the exception of a few trees (see Tables V—XIII) new trees were used every time. The sections were taken at breast height (1.3 m) and from 1.5 to 2 cms thick, leafy branches in the uppermost half of the tree.

In the spring of 1945 4 to 10 trees were chosen within each species. From these trees 8 sections were taken from the stem during summer from the middle of the crown, and at breast height. The first place corresponds to $^2/_3$ to $^3/_4$ of the full height of the trees[1].

The sections were each time extracted at the same side of the stem and at the same height over the ground (see Fig. 14). The method mentioned p. 15 was applied.

[1] As the sections are to be taken in places free of adjoining branches, callus growths etc. it has been impossible to extract them at the same relative height in all trees.
In trees with very deep crowns they were taken somewhat above the midst of the crown.

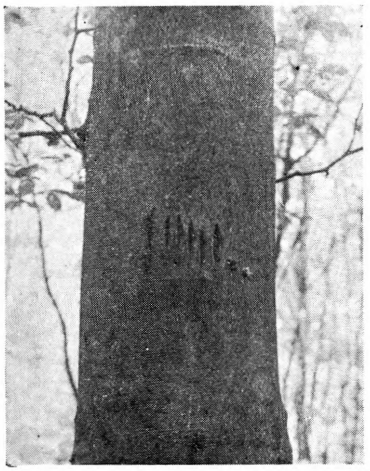

Fig. 14. Scar at breast height after 6 sections and 2 increment cores extracted in the course of the summer 1945. Photograph taken in October 1945, from the stem of *Acer pseudoplatanus* No. 2. (See Table VIII).

Tables and Figures.

The process of wood formation in the various species of trees is shown by curves in Figs. 15—30.

In the Figures are entered precipitation and mean temperature measured at the Meteorological Station at Bogø.

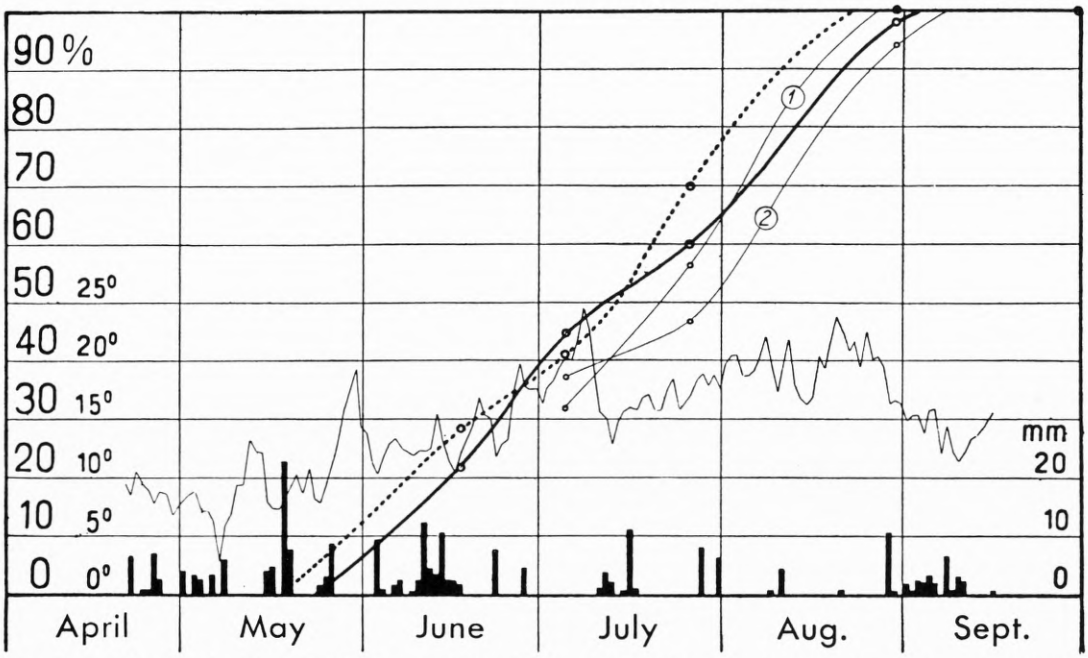

Fig. 15. *Betula pendula*. The relative process of wood formation in 1944. The thin curves show wood formation in the two trees described in Table V. The thick curves show the mean for medium sized to large crowns and in close stands in sandy and clayey ground and well drained swamp soil:
..... In 1.5 to 2 cms thick, leafy branches in the upper half of the crown. —— At 1.3 m height in the stem.

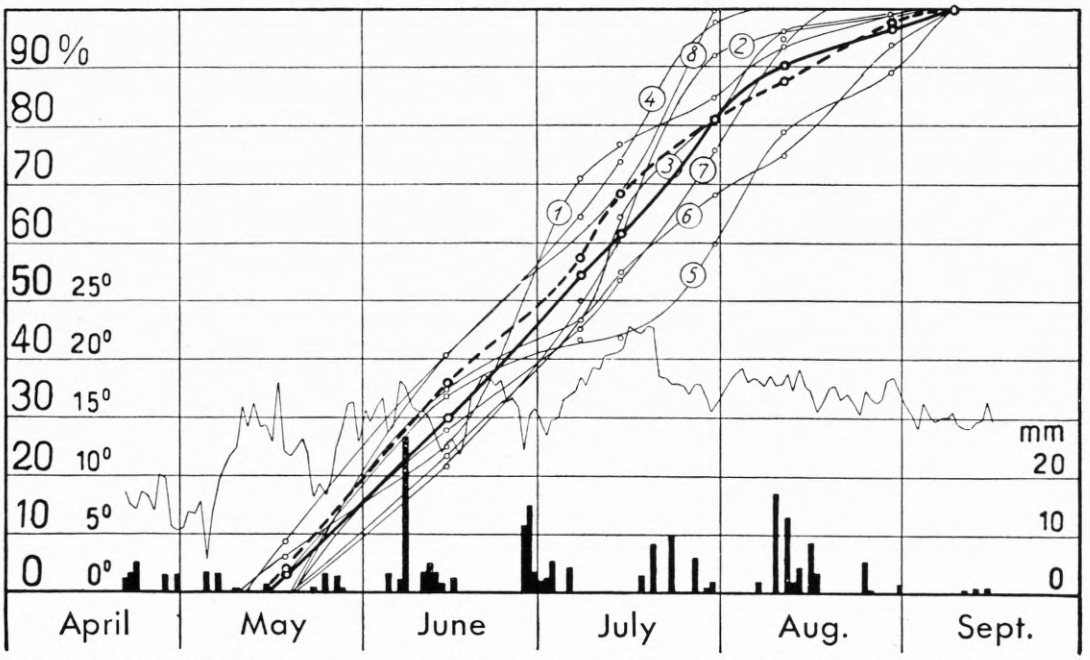

Fig. 16. *Betula pendula*. The relative process of wood formation in 1945. The thin curves show wood formation in the 8 trees described in Table V. The thick curves show the mean for trees Nos. 1—6:
..... In the stem in the middle of the crown. —— In the stem at 3 m height.

TABLE V.

Betula pendula ROTH. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
1944: The two trees whose wood formation was followed from July 4th Both were medium-sized trees in closed *Betula* stands										
1	25	12.3	12	4	0.35	3.0	3.3	30 cms slightly clayey sand. Coarse grained, deep and loose mould	Clayey sand. 1 m to ground water	*Urtica*, *Rubus fruticosus*
2	25	12.5	14	8	0.40	3.9	3.5			
1945: An open-grown tree over young *Picea abies*										
1	10	6.0	6	6	0.80	2.0	1.5	25 cms clayey sand. Coarse grained, fairly thin layer of mould	Sand to slightly clayey sand. Presumably 2 m to ground water	No herbaceous vegetation
II. Trees in closed *Betula* stand with a mixture of even-aged *Fagus silvatica*										
A. Dominant trees										
2	26	11.8	17	5	0.66	4.4	4.1	22 cms sand. Coarse grained deep, loose mould	Sand to 50 cms depth. Then slightly clayey sand. Ground water at 75 cms depth	Undergrowth of *Alnus glutinosa* (*Urtica*), (*Rubus idaeus* and *R. fruticosus*), (*Anemone*)
3	26	12.3	16	6	0.40	3.1	3.3			
4	26	13.0	16	5	0.54	4.0	3.7			
5	26	13.7	20	11	0.50	4.0	4.8			
6	26	14.0	19	10	0.58	4.2	5.0			
B. Intermediate trees with very small crowns (whips)										
7	26	10.2	7	3	0.14	1.5	1.2			
8	26	11.0	7	3	0.28	1.2	0.9			

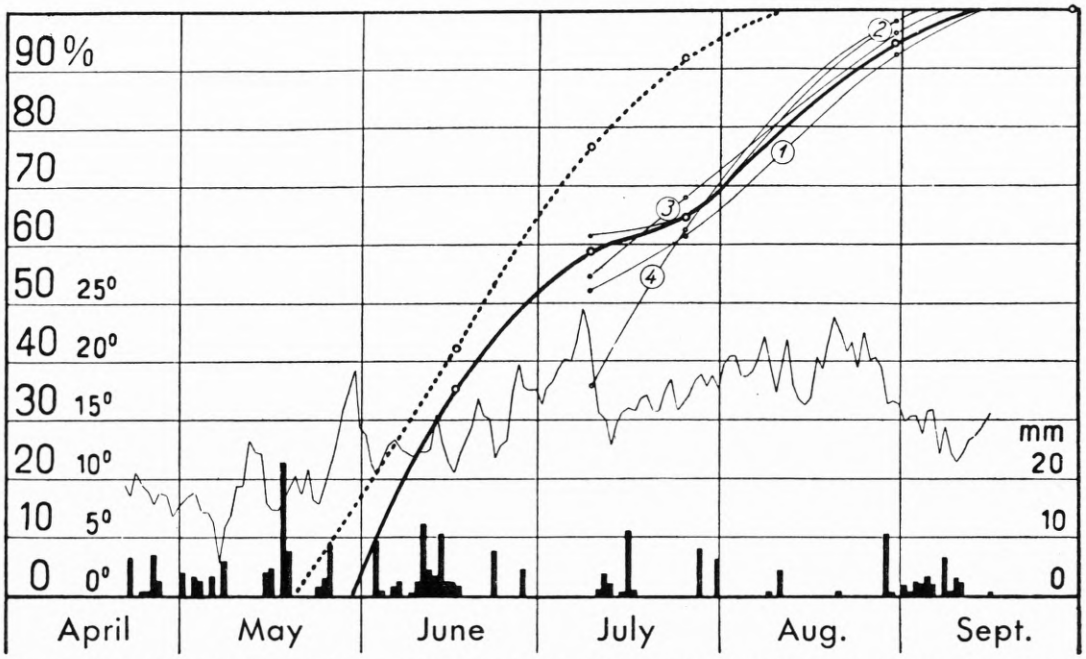

Fig. 17. *Alnus glutinosa*. The relative process of wood formation in 1944. The thin curves show wood formation in the 4 trees, that are described in Table VI. The thick curves show it in the mean for trees with medium sized to large crowns and in close-grown plantations in very watery swamp soil:
..... In 1.5 to 2 cms thick leafy branches in the upper half of the crown. —— At 1.3 m height in the stem.

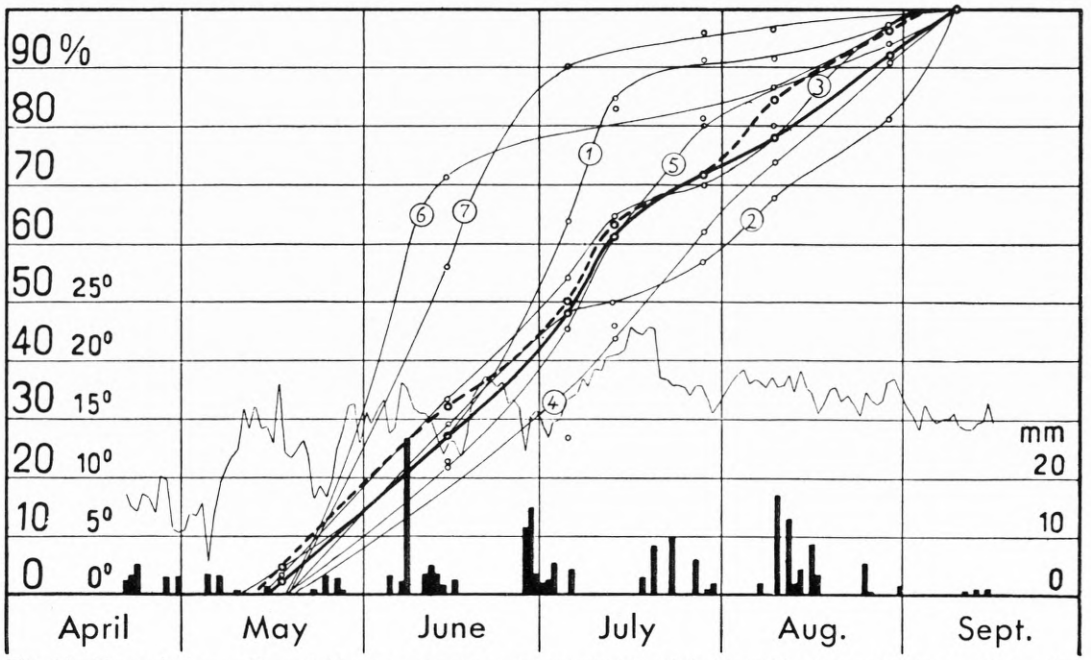

Fig. 18. *Alnus glutinosa*. The relative process of wood formation in 1945. The thin curves show wood formation in the 7 trees, that are described in Table VI. The thick curves show it in the mean for tree Nos. 1—5:
..... In the stem in the middle of the crown. —— In the stem at 1.3 m height.

TABLE VI.

Alnus glutinosa (L.) GAERT. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
1944: The four trees whose wood formation was followed from July 9th All trees in an uneven-aged *Alnus glutinosa* plantation										
1	10	6.1	5	8	0.50	2.5	2.2	Very moist marsh soil	Marsh still at 1 m depth. Ground water at 20—30 cms depth	Undergrowth of a few bushes, *Urtica*
2	14	8.0	8	8	0.45	2.9	2.5			
3	19	12.5	10	10	0.33	3.1	2.6			
4	25	12.7	18	10	0.33	3.2	4.0			
1945: Trees in pure *Alnus glutinosa* stands or mixed in even-aged ash stands A. Dominant trees										
1	14	7.6	8	6	0.40	3.1	2.0	18 cms clayey sand. Coarse grained, very humusrich and moist mould	Sand to stiff clay. Ground water at c. 50 cms depth	*Urtica*
2	18	9.0	13	13	0.60	5.1	3.3	60 cms rich and very wet swamp soil	Stiff clay. Ground water at 20—30 cms depth	Undergrowth of a few *Sambucus nigra*, *Urtica*, *Geranium*, *Galium*
3	—	9.1	10	9	0.45	2.8	2.2			
4	40	14.0	26	9	0.33	5.3	4.0			
5	55	18.1	33	8	0.53	4.3	6.1	24 cms clayey sand. Coarse grained, rich moist mould	Sand to stiff clay. Ground water at c. 50 cms depth	*Urtica*, *Rubus fruticosus*, (*Anemone*), (*Geranium*)
B. Intermediate and overshadowed trees with small crowns										
6	14	5.8	5	1	0.20	1.5	1.0	18 cms clayey sand. Coarse grained, very humus rich and moist mould	Sand to stiff clay. Ground water at c. 50 cms depth	*Urtica*
7	—	7.3	6	2	0.25	1.9	2.0			

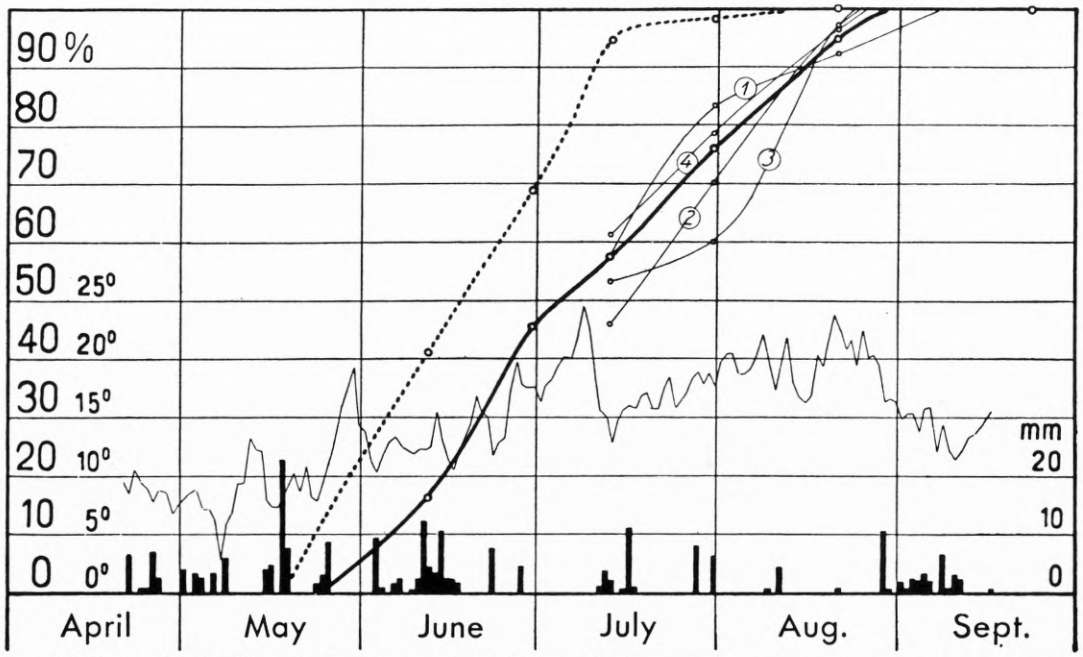

Fig. 19. *Fagus silvatica*. The relative process of wood formation in 1944. The thin curves show wood formation in the four trees, that are described in Table VII. The thick curves show the mean for trees with medium sized to large crowns and in close-grown plantations:
..... In 1.5 to 2 cms thick leafy branches in the upper half of the crown. —— At 1.3 m height in the stem.

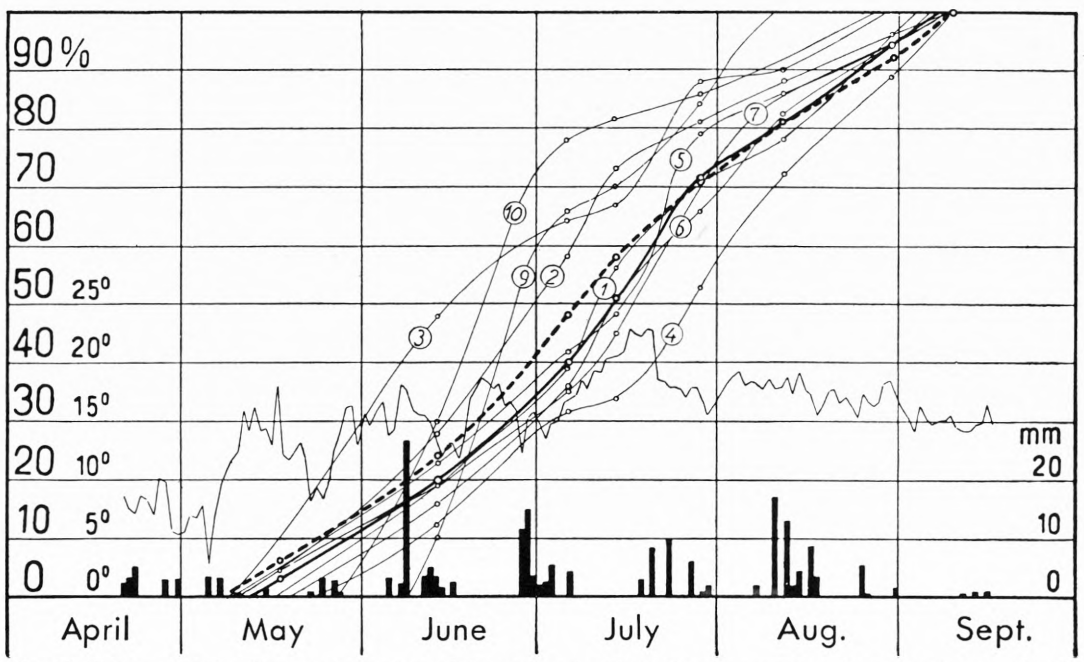

Fig. 20. *Fagus silvatica*. The process of wood formation in 1945. The thin curves show wood formation in 9 of the 10 trees, that are described in Table VII. The thick curves show it in the mean for trees Nos. 1—8:
..... In the stem in the middle of the crown. —— In the stem at 1.3 m height.

TABLE VII.

Fagus silvatica L. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
1944: The four trees whose wood formation was followed from July 12th										
All dominant trees in closed stands										
1	30	11.4	14	6	0.60	4.0	4.4	20—35 cms clayey sand. Coarse grained, rather deep mould	Sandy clay to clayey sand. 1.5 to 2 m to ground water	*Anemone, Asperula, Rubus idaeus*
2	45	15.9	23	12	0.50	4.8	5.2			
3	45	16.2	20	10	0.50	4.6	4.3			
4	60	21.0	24	6	0.60	5.5	5.0			
1945: I. Partly isolated trees										
1	40	14.0	31	11	1.00	6.7	9.2	45 cms sand. Coarse grained to fine-grained mould	Sand and gravel. Fairly high ground water level	*Urtica, Rubus idaeus*
2	70	18.6	43	8	0.90	9.8	9.2	40 cms clayey sand. Coarse-grained mould	Clayey sand to sandy clay c. 1.5 m to ground water	*Anemone, Asperula, Trientalis, Stachys*
II. Trees in closed stands										
A. Dominant trees										
3	14	5.1	5	6	0.50	2.1	1.9	20 cms clayey sand. Coarse-grained, rich mould	Lime-rich friable clay. Fairly high ground water level, swamp border	*Anemone*
4	28	12.8	17	10	0.64	5.0	4.1	20 cms slightly clayey sand. Coarse-grained, loose, deep mould	Sandy clay 1 to 2 m to ground water	*Anemone*
5	28	12.9	18	8	0.72	6.0	4.4			
6	28	14.1	20	12	0.58	4.8	5.0	24 cms clayey sand. Rich humusrich mould	Friable clay. Fairly high ground water level	*Anemone, Asperula, Urtica*
7	60	22.0	32	10	0.64	6.3	5.3			
B. Strongly suppressed trees										
8	26	10.1	4	0	0.10	0.9	1.1	15 cms clayey sand. Coarse- to fine-grained mould	Sandy clay. 1—2 m to ground water	*Anemone*
9	28	9.0	6	0.6	0.18	0.9	1.6	20 cms slightly clayey sand. Coarse-grained, loose, deep mould	Sandy clay. 1.5 to 2 m to ground water	*Anemone*
10	28	4.5	5	1	0.10	0.9	0.9			

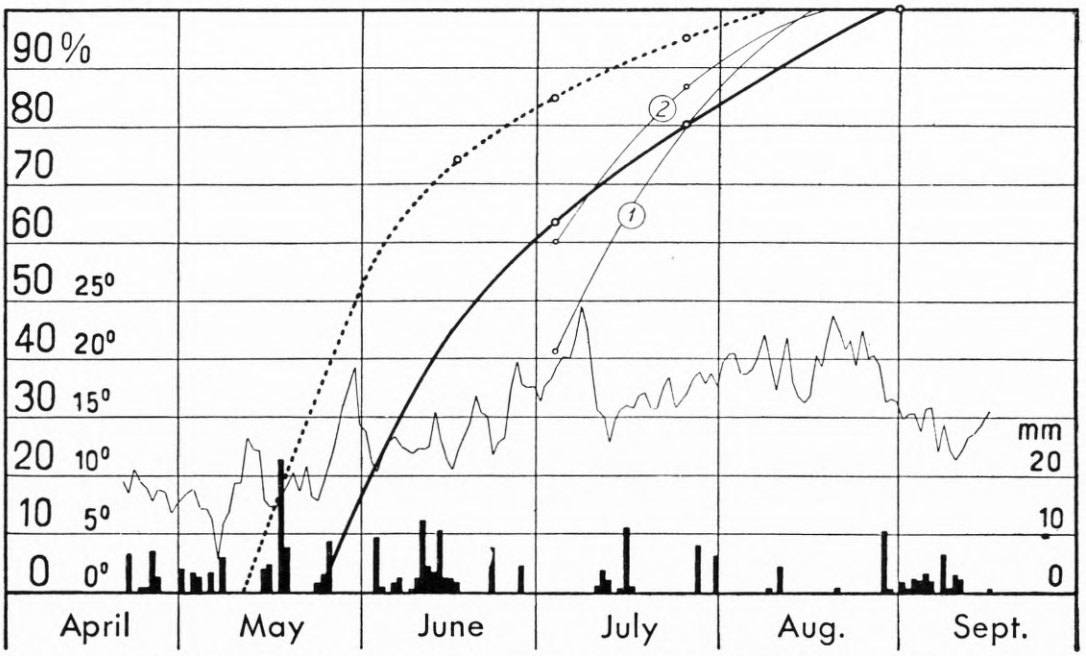

Fig. 21. *Acer pseudoplatanus*. The relative process of wood formation in 1944. The thin curves show wood formation in the two trees, that are described in Table VIII. The thick curves show the mean for trees with medium sized to large crowns and in closed stands in clayey soil:
..... In 1.5 to 2 cms thick, leafy branches in the upper half of the crown. —— At 1.3 m height in the stem.

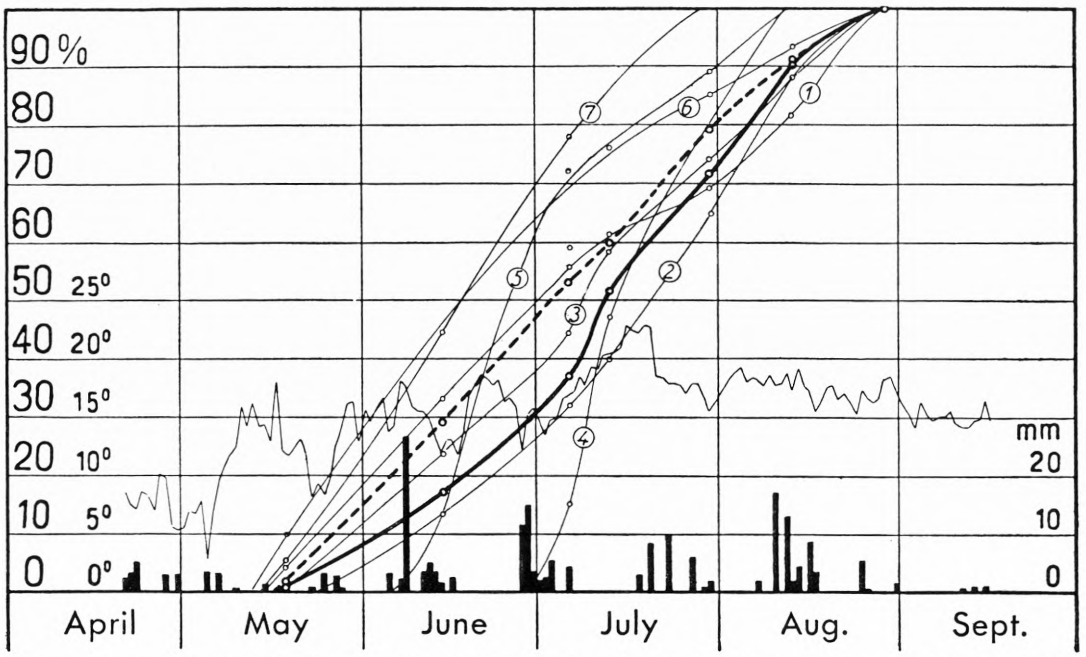

Fig. 22. *Acer pseudoplatanus*. The relative process of wood formation in 1945. The thin curves show wood formation in the 7 trees, that are described in Table VIII. The thick curves show the mean for trees Nos. 1—4:
..... In the stem in the midst of the crown. —— In the stem at 1.3 m height.

TABLE VIII.

Acer pseudoplatanus L. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
1944: The two trees whose wood formation was followed from July 3rd Trees in a stand of *Acer pseudoplatanus* and *Fagus silvatica*										
1	25	10.7	9	5	0.66	3.2	3.2	20—30 cms sandy clay to clayey sand. Coarse-grained, loose mould	Sandy clay to clayey sand. Presumably c. 2 m to ground water	Self-sown growth of *Acer pseudoplatanus*, *Anemone*, *Asperula*
2	25	15.5	14	5	0.38	5.2	4.1			
1945: Trees in stand of *Acer pseudoplatanus*, *Fraxinus excelsior* and *Fagus silvatica*.										
A. Dominant trees										
1	26	11.9	16	8	0.50	4.0	3.6	15 to 20 cms sandy clay to clayey sand. Coarse-grained, loose mould	Sandy clay. c. 1 m to ground water	*Anemone*, *Asperula*, *Melica*
2	—	14.6	19	7	0.65	4.1	3.0			
3	—	14.9	24	11	0.65	8.0	5.8			
4	35	15.8	32	5	0.50	6.6	5.8			
B. Undergrowth										
5	18	7.2	5	3	0.40	2.4	3.6	30 cms moist swamp soil	Stiff clay. Ground water at 50 cms depth	*Anemone*, *Hepatica*, *Geranium*, *Ficaria*, *Urtica*
6	20	8.1	4	2	0.35	2.6	2.0	60 cms clayey sand. Coarse-grained, humus-rich deep, loose mould	Stiff clay. Ground water at 65 cms depth	*Urtica*, *Milium Mercurialis*, (*Rubus fruticosus* and *R idaeus*)
7	—	9.0	3	3	0.40	2.4	1.8			

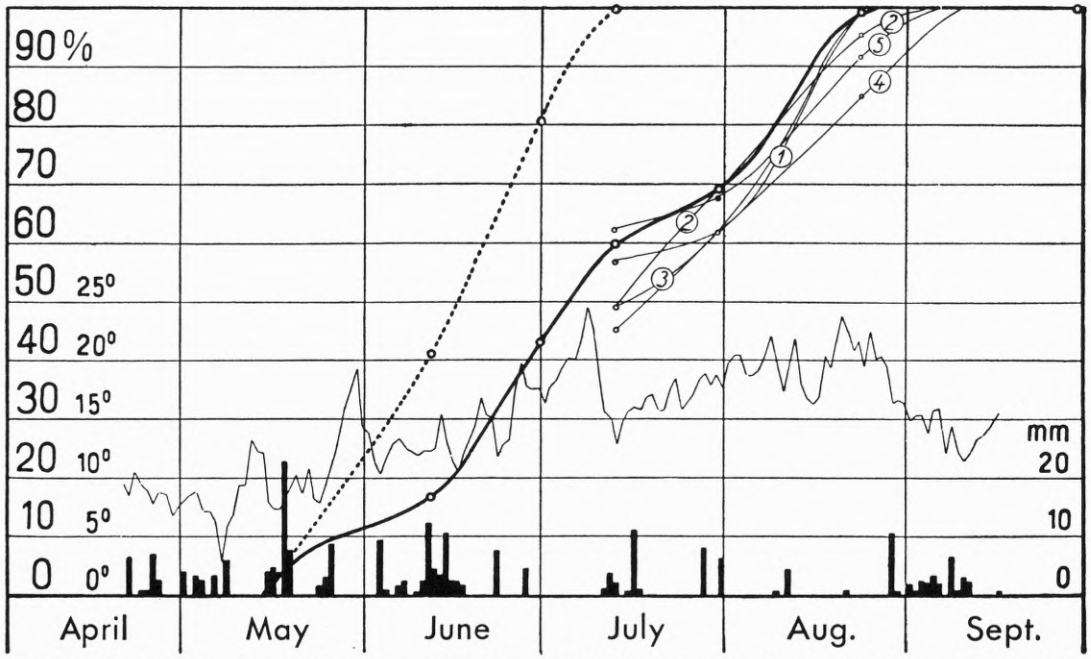

Fig. 23. *Quercus robur*. The relative process of wood formation in 1944. The thin curves show wood formation in the five trees, that are described in Table IX. The thick curves show the mean for trees with medium sized to large crowns in close-grown plantations in deep and clayey soil:
..... In 1.5 to 2 cms thick, leafy branches in the upper half of the crown. —— At 1.3 m height in the stem.

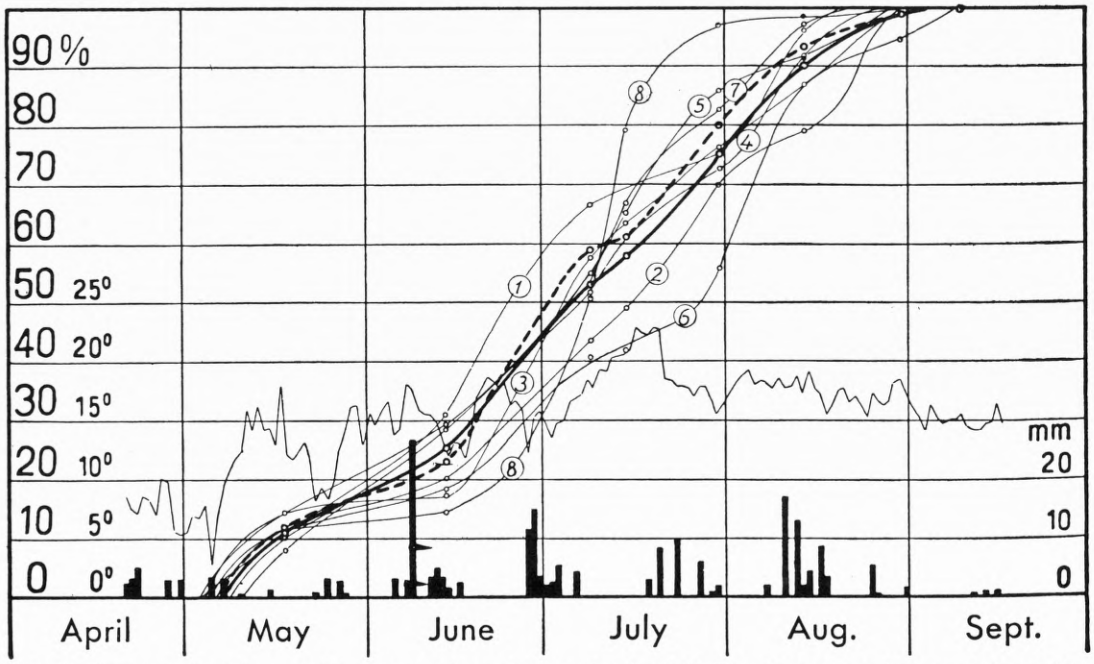

Fig. 24. *Quercus robur*. The relative process of wood formation in 1945. The thin curves show wood formation in the first eight of the ten trees, that are described in Table IX. The thick curves show the mean for trees Nos. 1—7:
..... In the stem in the middle of the crown. —— In the stem at 1.3 m height.

TABLE IX.

Quercus robur L. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
1944: The five trees whose wood formation was followed from July 12th										
All trees in a closed stand										
A. Dominant trees										
1	23	9.2	8	14	0.70	2.7	4.0	Clayey sand. Coarse-grained, rich mould. In patches remains of old morformation	Sandy clay. Presumably between 1 and 2 m to ground water	*Anemone* in patches *Pteridium aquilinum*
2	23	10.0	10	18	0.66	3.1	2.4			
B. Smaller trees (to be felled)										
3	23	8.1	6	8	0.50	1.9	2.1			
4	23	8.5	6	6	0.45	1.6	1.6			
5	23	8.7	8	8	0.50	1.7	2.0			
1945: I. Partly isolated trees										
1	14	6.5	7	10	0.79	3.3	2.9	30 cms sand. Coarse-grained, loose mould	Clayey sand. Between 1 and 1.5 m to ground water	*Urtica*
2	26	12.6	30	14	0.90	8.3	6.5	32 cms rich swamp-soil	Stiff clay. 75 cms to ground water	*Picea sitchensis* undergrowth
3	70	18.0	42	8	0.90	9.8	13.4	35 cms fine-grained strongly humus coloured mould	Gray sand and gravel. At beach. High ground water level	*Asperula, Pteridium aquilinum, Rubus fruticosus*
II. Trees in closed stand										
A. Dominant trees										
4	33	14.0	18	9	0.50	5.0	4.4	25 cms slightly clayey sand. Coarse-grained, loose, deep mould	Stiff clay, in patches sandy clay and marl. Between 1 and 2 m to ground water	*Anemone, Asperula, Rubus fruticosus* (*Deschampsia flexuosa*)
5	33	14.2	18	6	0.60	5.0	5.0			
6	33	14.6	22	6	0.45	3.3	4.3			
7	33	14.0	24	8	0.60	6.0	4.1			
B. Strongly suppressed trees										
8	33	7.6	5	1	0.14	0.9	0.7			
9	33	7.0	4	(0)	0.09	0.7	0.5			
10	33	8.1	4	(0)	0.11	0.7	0.8			

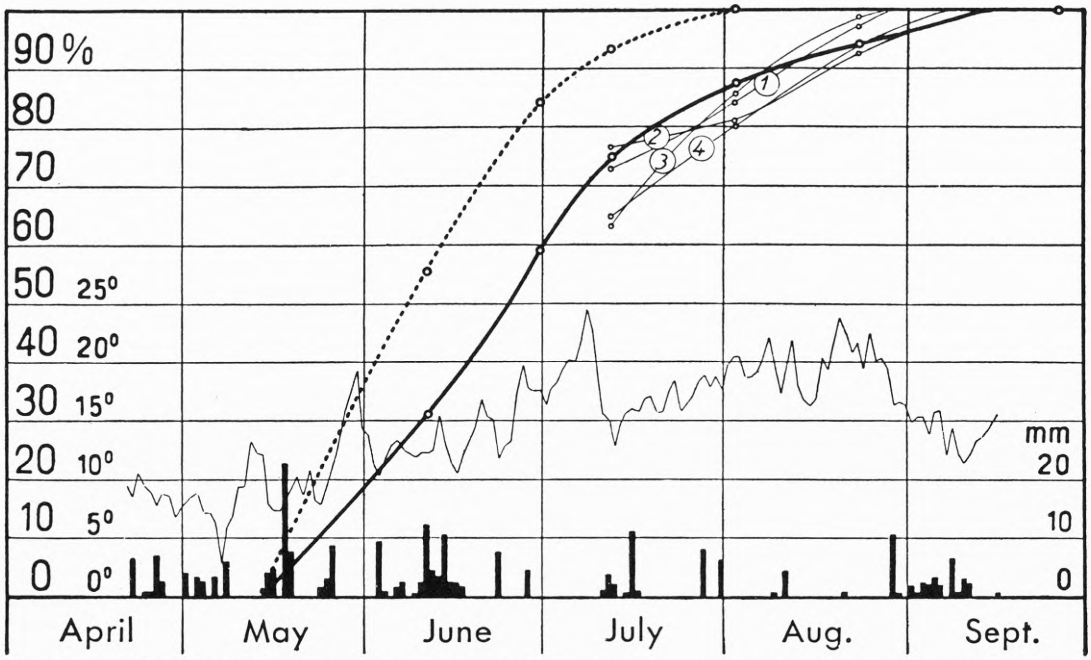

Fig. 25. *Fraxinus excelsior*. The relative process of wood formation in 1944. The thin curves show wood formation in the four trees, that are described in Table X. The thick curves the mean for trees with medium sized to large crowns and in closed stands on sandy and clayey soil as well as along the swamp borders and on well drained swamp soil:
..... In 1.5 to 2 cms thick leafy branches in the upper half of the crown. —— At 1.3 m height in the stem.

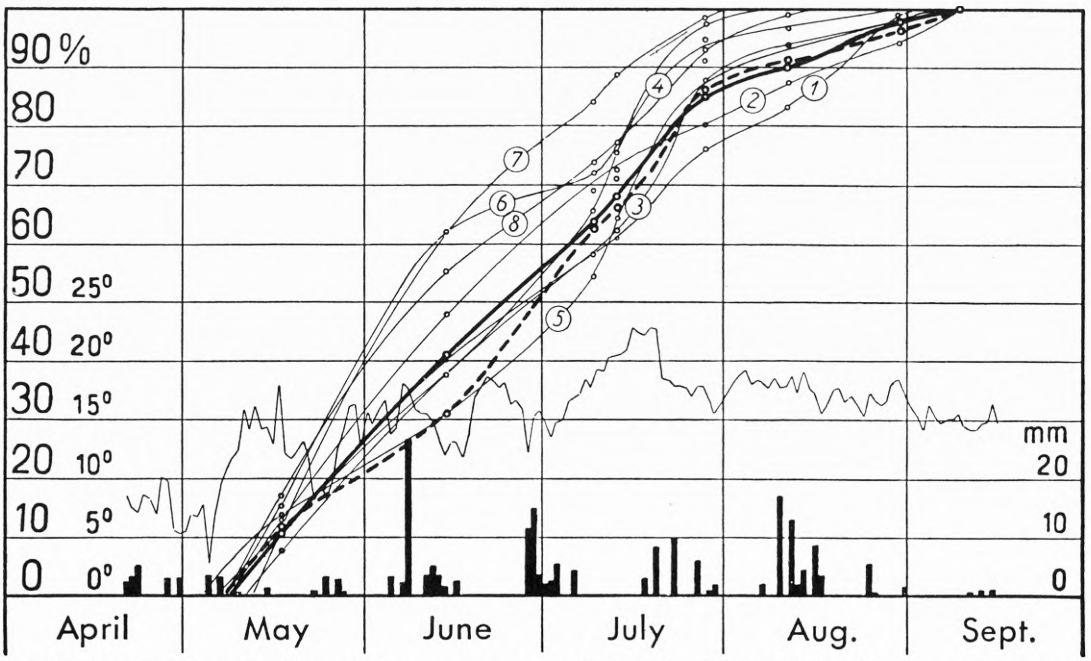

Fig. 26. *Fraxinus excelsior*. The relative process of wood formation in 1945. The thin curves show wood formation in the 8 trees, that are described in Table X. The thick curves show the mean for trees Nos. 1—4:
..... In the stem in the middle of the crown. —— In the stem at 1.3 m height.

TABLE X.

Fraxinus excelsior L. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
1944: The four trees whose wood formation was followed from July 12th										
All dominant trees in a closed stand										
1	17	7.4	8	15	0.50	3.1	2.2	30—40 cms swamp soil. Edge of a swamp	Stiff clay to sandy clay. High ground water level	*Urtica*, *Rubus idaeus*. Scattered *Alnus glutinosa bushes*
2	17	7.9	7	14	0.40	2.7	2.7			
3	17	8.1	7	8	0.50	3.3	3.6			
4	17	10.1	12	12	0.50	4.0	3.7			
1945: I. Trees in closed stands in relatively well drained soil										
A. Dominant trees										
1	28	12.1	18	11	0.50	5.0	5.0	Edge of a swamp. Coarse-grained, deep, rich and humus-rich soil	Marl and sandy clay. C. 50 cms to the ground water	Scattered *Alnus glutinosa* bushes. *Urtica. Geranium Impatiens*
2	28	13.2	19	10	0.40	4.0	3.8			
3	28	14.4	22	16	0.43	5.2	4.3	20 cms slightly clayey sand. Coarse-grained, loose and deep mould	Sandy clay. 1.5 to 2 m to ground water	*Anemone*
4	59	16.0	30	5	0.63	7.0	6.6	25 cms clayey sand. Coarse-grained, rich mould	Stiff clay, marl in patches. C. 50 cms to ground water	*Deschampsia caespitosa*
B. Suppressed tree										
5	28	8.0	5	4	0.12	1.1	1.6	20 cms slightly clayey sand. Coarse-grained, deep and loose mould	Sandy clay. 1.5 to 2 m to ground water	*Anemone*
II. Dominant trees in closed stands in very watery swamp soil										
6	20	9.0	10	8	0.85	2.6	2.7	Very watery swamp soil	Ground water at 25 cms depth. C. 30 cms deep ditches	*Urtica*, *Geranium Valeriana*
7	20	7.1	9	7	0.50	3.3	2.5			
8	20	10.5	18	6	0.50	6.0	4.1			

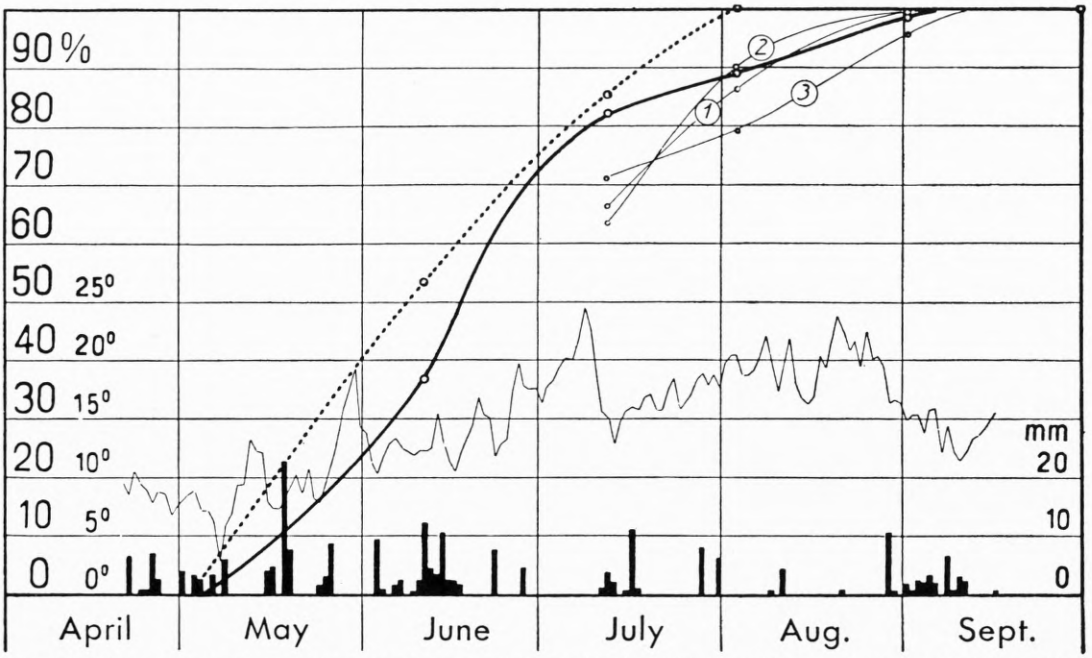

Fig. 27. *Ulmus glabra*. The relative process of wood formation in 1944. The thin curves show wood formation in the three trees, that are described in Table XI. The thick curves show the mean for wind-exposed trees with medium sized crowns in clayey soil:
..... In 1.5 to 2 cms thick leafy branches in the upper half of the crown. —— At 1.3 m height in the stem.

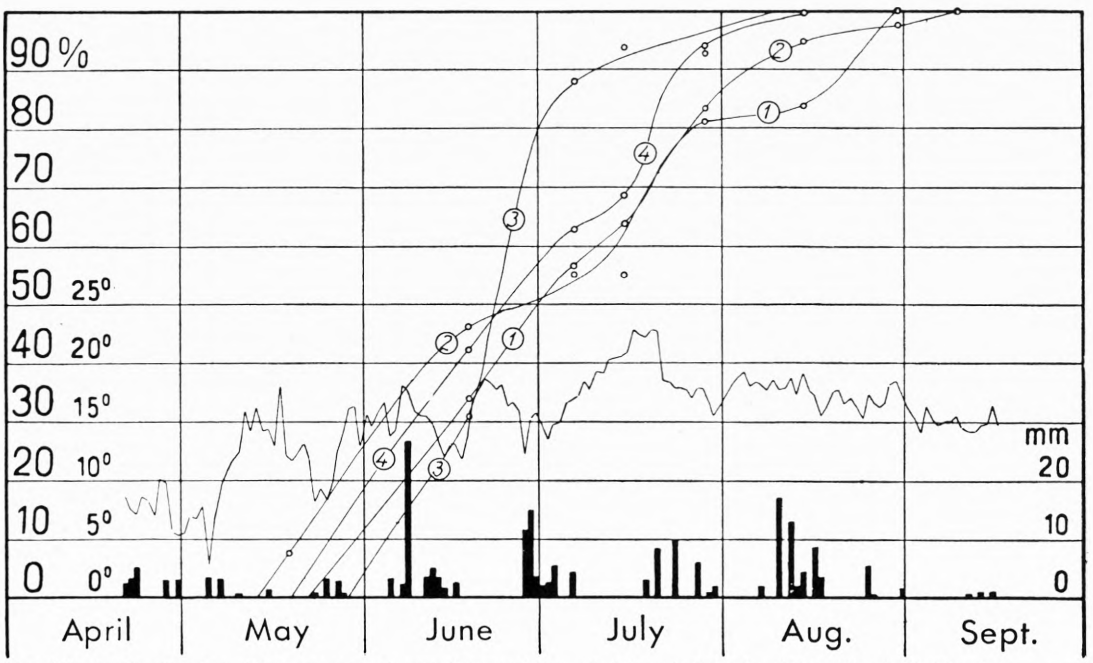

Fig. 28. *Larix decidua*. The process of wood formation at 1.3 m height in 1945. The individual trees are described in Table XII.

TABLE XI.

Ulmus glabra HUDS. 1944. Description of the Trees Whose Wood Formation was Followed from July 11th.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
All three trees intermixed in *Fagus silvatica* stands										
1	16	9.4	10	7	0.25	3.1	3.0	25 cms clayey sand. Coarse-grained mould	Sandy clay. Ground water at 0.5 m depth	*Anemone*, *Asperula*, (*Mercurialis*)
2	16	10.6	10	8	0.25	2.9	3.0			
3	45	16.9	29	14	0.40	5.5	4.1	20 cms clayey sand. Coarse-grained, loose mould	Sandy clay. Ground water at 65 cms depth	Undergrowth of *Alnus glutinosa* bushes. *Mercurialis*, *Urtica*

TABLE XII.

Larix decidua MILL. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
All four trees intermixed in even-aged *Fagus silvatica* stands										
A. *Larix leptolepis*										
1	13	8.0	7	10	0.75	2.2	1.8	30 cms clayey sand. Coarse-grained, deep and loose mould	Clayey sand. C. 1 m to ground water	(*Anemone*)
2	13	8.4	9	14	0.75	1.9	2.1	20 cms slightly clayey sand. Coarse-grained mould	Sandy clay. C. 1 m to ground water	*Anemone*
B. *Larix decidua*										
3	45	16.9	30	4	0.30	4.5	4.3	24 cms clayey sand	Friable clay. Fairly high ground water level	*Anemone*, *Asperula*, (*Rubus fruticosus*)
4	45	20.0	44	7	0.33	7.0	6.4			

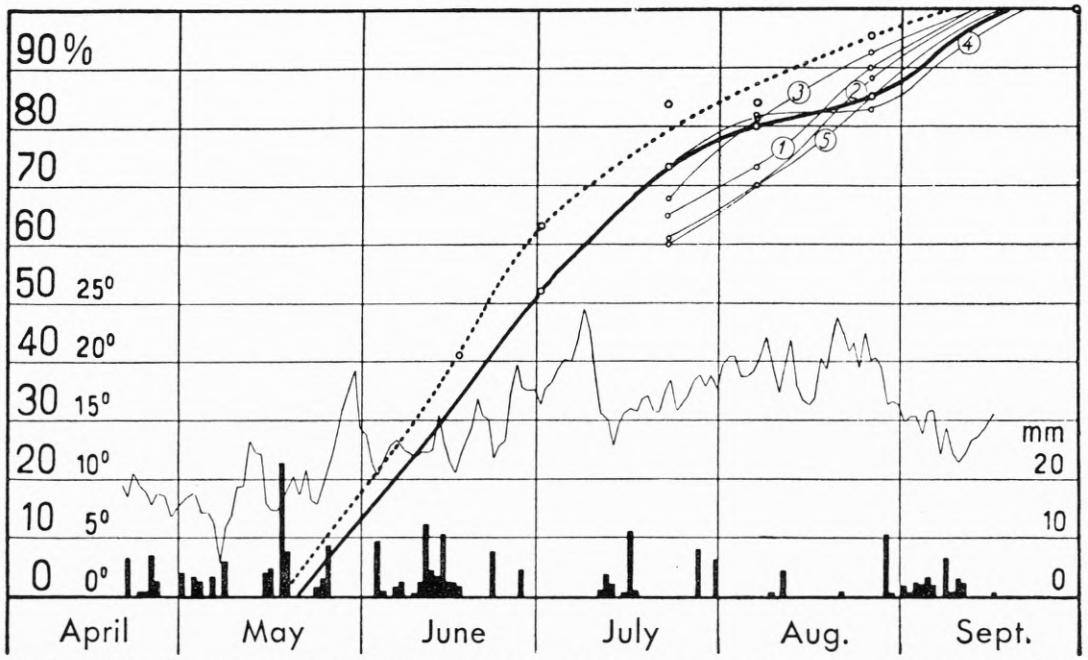

Fig. 29. *Picea abies*. The relative process of wood formation in 1944. The thin curves show wood formation in the five trees, that are described in Table XIII. The thick curves show the mean for trees with medium sized to large crowns in closed stands, in sandy and clayey soil:
..... In 1.5 to 2 cms thick, leafy branches in the upper half of the crown. —— At 1.3 m height in the stem.

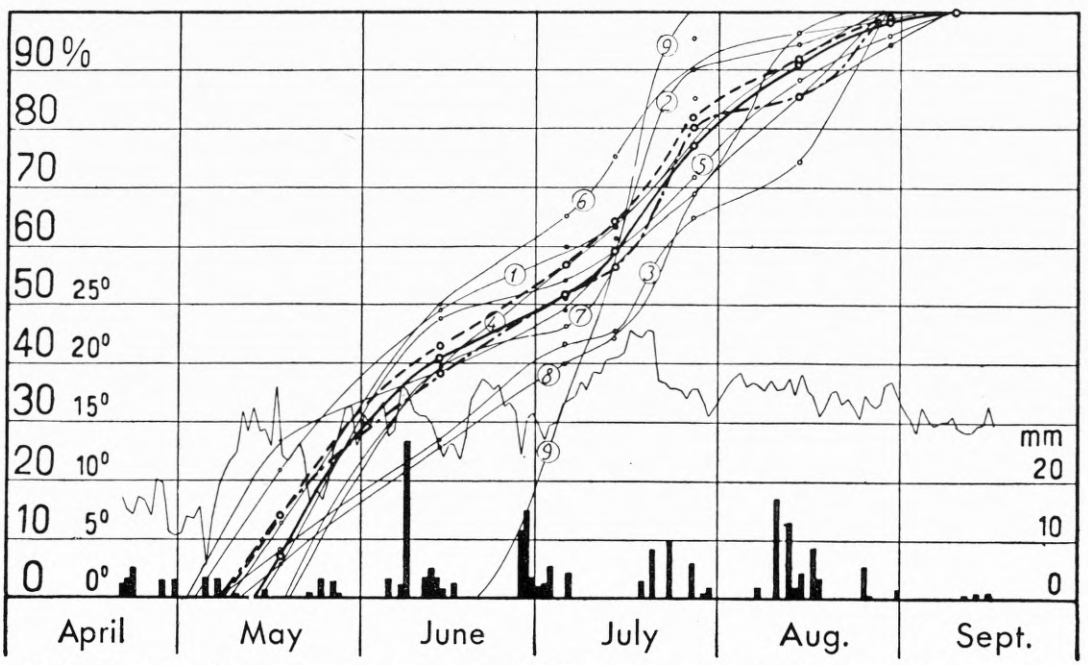

Fig. 30. *Picea abies*. The relative process of wood formation in 1945. The thin curves show wood formation in the first 9 of the trees described in Table XIII. The thick curves show the mean for
—.—.— 1.3 m height in the stem of trees Nos. 1—4. —— 1.3 m height in the stem of trees Nos. 5—8.
..... The stem in mid-crown of trees Nos. 5—8.

TABLE XIII.

Picea abies L. KARST. Description of the Individual Trees.

Tree No.	Age	Height m	Diameter cm	Diameter increment mm	Crown ratio	Crown diameter N-S m	Crown diameter E-W m	Soil: Surface soil	Soil: Subsoil	Ground flora
1944: The five trees whose wood formation was followed from July 22nd										
Border trees										
1	15	5.6	8	7	1.00	2.2	2.6	20—30 cms clayey sand. Coarse-grained to fine-grained mould	Clayey sand. C. 1.5 m to ground water	None
2	15	6.5	10	6	0.90	3.0	2.4			
3	15	6.9	10	7	0.90	2.1	2.1			
4	15	7.0	12	7	0.90	3.2	3.4			
5	15	7.2	9	4	0.90	3.4	3.5			
1945: I. Partly isolated trees										
1	10	4.0	5	8	1.00	2.2	2.4	20—30 cms slightly clayey sand. Coarse-grained to fine-grained mould	Sandy clay. Between 0.5 to 2 m to ground water	(*Oxalis*)
2	12	4.9	5	8	1.00	2.2	2.0			
3	16	6.8	8	6	0.80	3.0	3.2			
4	27	10.4	12	4	0.82	2.8	2.2			
II. Trees in closed stands										
A. Dominant trees										
5	27	13.6	16	6	0.64	3.6	3.8	30 cms slightly clayey sand. 1 cm raw humus	Clayey sand. C. 1.5 m to ground water	(*Oxalis*)
6	27	14.1	19	4	0.70	4.6	3.2			
7	35	19.8	22	5	0.40	4.8	2.9	20 cms slightly clayey sand. Coarse-grained to fine-grained mould	Sandy clay. C. 2 m to ground water	(*Anemone*)
8	35	22.0	38	8	0.50	6.8	5.1			
B. Strongly suppressed trees										
9	27	7.0	6	0.6	0.12	1.2	0.9	30 cms slightly clayey sand. Raw humus	Clayey sand. C. 1.5 m to ground water	(*Oxalis*)
10	27	7.1	6	0	0.20	1.5	2.0			
11	27	8.5	5	0	0.09	1.3	1.0			

Wood Formation in the Branches.

In the young branches the main part of the new annual ring is formed during the period in which the most active shoot extension takes place.

α) The Short Shoots.

The short shoots have a minimal growth in length and thickness. The extension growth is practically terminated when the foliage is completely expanded.

Wood formation often ceases at the end of May or during the first half of June.

As a rule only few new vessels are formed. Often there is no summer wood formation, so that it may be very difficult to distinguish the individual annual rings from each other (comp. HERRMANN (1916)).

β) The Long Shoots.

In *Quercus robur, Fraxinus excelsior, Ulmus glabra* and *Fagus silvatica* that have short shoot extension periods (see Table XVII) wood formation in the young branches is most active in May and at the beginning of June. In one-year-old branches $^3/_4$ of the new annual ring are often formed at the close of May.

In most branches wood formation is completed at the end of June or the beginning of July. The cambium, however, does not enter into the resting period (see Fig. 1) till September.

If repeated shoots are formed wood formation continues until these shoots are fully grown. Wood formation in the young branches has in such cases two annual maximum periods, one in May and the beginning of June, and one at the end of June and the beginning of July.

In *Acer pseudoplatanus, Betula pendula, Picea abies,* and *Larix decidua,* that have long shoot extension periods, wood formation proceeds more slowly in the young branches.

Maximum occurs in May and June. An almost equally great quantity of wood is formed during both months. At the end of June approximately $^3/_4$ of the new annual ring are formed in the one-year-old branches.

Wood formation generally terminates at the end of July or the beginning of August.

Literature offers little information only about wood formation in the branches.

R. HARTIG (1882b, pp. 118 and 119) found that in *Acer pseudoplatanus* and *Fagus silvatica*-branches wood formation terminates at the beginning of August, in *Larix decidua* in mid-August, and in *Pinus silvestris*-branches at the beginning of September. The age of the branches is not given.

JOST (1892) found that by July 1st 75 % of the new annual ring were formed in 2—4-year-old *Fagus silvatica*-branches and 90 % in 1—2-year-old *Quercus robur*-branches. In the *Fagus silvatica*-branches wood formation ceased in August, in the *Quercus robur*-branches in July.

ANTEVS (1917, p. 341) found that wood formation proceeds quickly in the branches and reaches maximum about the middle of June. It then continues "recht gleichmässig".

Wood formation is relatively more advanced in the terminal than in the basal parts of the branches. The difference may be very considerable, particularly in the younger parts of the branches (see Fig. 31) and it does not increase evenly downwards.

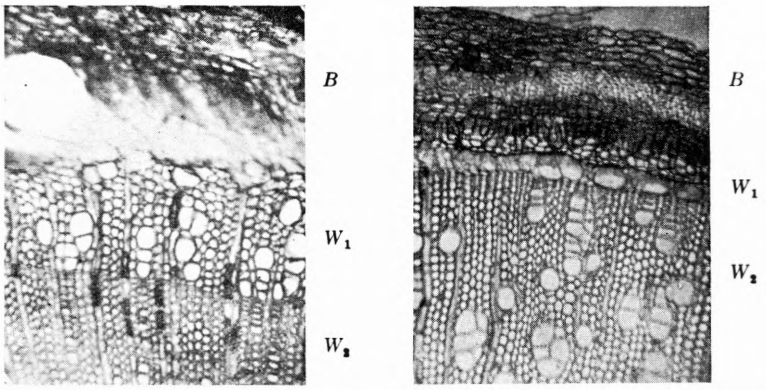

Fig. 31. Cross section through a one-year-old vigorous branch of a young *Acer pseudoplatanus* the section shows wood formation on April 27, 1945.

a = 5 cms and b = 30 cms from bud base (80 ×).
B = bark, W_1 = new formed wood, and W_2 = last year's summer wood.

There is a relatively greater difference among the one- and two-year-old branch parts etc. than in the two- and three-year-old branch parts, comp. SWARBRICK (1927a, p. 152). It is greatest in trees with short shoot extension period.

Wood Formation in the Stem.

The length of the wood formation period increases from the young branches and down into the stem, and a relatively greater part of the new annual ring is formed late in summer.

1. A Comparison between the Tree Species.

In Table XIV a general survey is given of the relative wood formation at breast height during the various months in 1944 and 1945.

It appears from the latter that there is some difference between the development of wood formation in the various species of trees. They may be divided into the following groups:

Fraxinus excelsior: It is among the trees examined the one in which the formation of the annual ring takes place at the relatively earliest time in summer. Wood formation is lively from the very start. About three fifths of the new annual ring are formed in May and June. After July there is little wood formation only (see Figs. 25 and 26).

Picea abies and *Larix decidua*: Wood formation is lively from the start as in *Fraxinus excelsior*. About half of the annual ring is formed in May and June. After July wood formation is not very active (see Figs. 28, 29 and 30).

Betula pendula, Fagus silvatica, Alnus glutinosa, Acer pseudoplatanus and *Quercus robur*: In most cases some time passes before wood formation becomes really active. Only between one third and one half of the annual ring is formed in May and June. In contrast to *Fraxinus excelsior, Picea abies* and *Larix decidua* wood formation is on the other hand very active still in August. Between one third and one fourth of the annual ring is formed in this month and during the first days of September (see Figs. 15, 16, 17, 18, 19, 20, 21, 22, 23 and 24).

TABLE XIV. The Relative Wood Formation (Formation of the Annual Ring) at Breast Height during the Various Months of 1944 and 1945. The Percentages are Read on the Thick Curves in Figs. 15—30[1] and Give the Average for Opengrown Trees and Dominant and Co-dominant Trees in Close Stands. The Mean Temperature and Precipitation is Measured at Bogø Meteorological Station (see Table I).

Species of Tree	Average Diameter-increment mm.	May	June	May–June	July	August	Sept.	Σ
1944:								
Betula pendula	—	6	33	**39**	26	33	2	100
Quercus robur	—	11	32	**43**	26	31	—	100
Fagus silvatica	—	5	41	**46**	30	24	—	100
Alnus glutinosa	—	4	48	**52**	17	26	5	100
Fraxinus excelsior	—	19	41	**60**	26	10	4	100
Average	—	9	39	**48**	25	25	2	100
Picea abies	—	14	37	**51**	27	10	12	100
Mean temperature	..	9.9	13.6	..	17.4	19.1	13.3	..
Precipitation	..	73	67	..	34	19	59	193[2]
1945:								
Fagus silvatica	9.3	12	22	**34**	40	22	4	100
Acer pseudoplatanus	8.7	12	26	**38**	38	24	—	100
Betula pendula	9.0	16	25	**41**	29	25	5	100
Alnus glutinosa	9.0	14	28	**42**	31	20	7	100
Quercus robur	8.4	18	26	**44**	32	23	1	100
Fraxinus excelsior	10.5	26	30	**56**	31	11	2	100
Average	..	16	26	**42**	34	21	3	100
Larix leptolepis	12.0	19	31	**50**	33	16	1	100
Picea abies	6.1	29	20	**49**	32	18	1	100
Mean temperature	..	11.6	15.3	..	18.0	17.3	13.9	..
Precipitation	..	18	80	..	45	58	16	201[2]

[1] *Acer pseudoplatanus* and *Ulmus glabra* are not included in 1944. It is because these tree-species grow under other conditions than the other species (see p. 38 and 53). In 1945 *Acer pseudoplatanus* No. 4 is left out (see Table VIII and Fig. 22). In the same year the average for *Betula pendula* is calculated for trees Nos. 3, 5 and 6 only (see Table V and Fig. 16). The other *Betulas* are left out as they showed small diameter increment only.

[2] Summary for May, June, July and August.

This difference among the tree species is on the whole confirmed by earlier investigations (see Table XV).

TABLE XV. The Relative Wood Formation (Growth in Thickness) during the Individual Months after Various Investigations Carried out Abroad. The Mean Temperature and Precipitation are Added in such Cases where Information has been Received on these Points.

Species of Tree	April	May	June	April May June	July	Aug.	Sept.	Oct.	Σ
Fagus silvatica									
R. HARTIG (1891)	—	(17)	(28)	**45**	39	16	—	—	100
(Germany)									
CHRISTISON (1889)	..	..	..	**38**	..	..	..	..	..
(Edinburgh, Engl.)									
JOST (1892)	1	14	32	**47**	27	20	5	1	100
(Strassburg, Germany)									
Mean temperature	9.0	14.5	17.1	..	18.1	18.6	15.6	10.0	..
Precipitation mm.....	28	73	74	..	76	45	46	84	..
FRIEDRICH (1897).....	2	23	33	**58**	28	10	3	1	100
(Mariabrunn, Austria)									
Mean temperature	10.6	13.2	16.3	..	19.1	16.8	13.0	7.8	..
Precipitation mm.....	75	78	121	..	79	69	31	..	..
GÄUMANN (1935).....	—	3	27	**30**	18	34	18	—	100
(Germany)									
Acer pseudoplatanus									
CHRISTISON (1889)	..	..	..	**38**	..	..	..	..	..
(Edinburgh, Engl.)									
JOST (1892)	1	15	33	**49**	31	15	4	1	100
(Strassburg, Germany)									
Mean temperature	9.0	14.5	17.1	..	18.1	18.6	15.6	10.0	..
Precipitation mm.....	28	73	74	..	76	45	46	84	.
Quercus									
CHRISTISON (1889)	..	..	..	**38**	..	..	..	..	..
(Edinburgh, Engl.)									
JOST (1892)	2	23	27	**52**	31	14	2	1	100
(*Quercus cerris*)									
(Strassburg, Germany)									
Mean temperature	9.0	14.5	17.1	..	18.1	18.6	15.6	10.0	..
Precipitation mm.....	28	73	74	..	76	45	46	84	..
Fraxinus									
LODEWICK (1925).....	10	15	40	**65**	30	5	—	—	100
(North America)									
Mean temperature	—	11.1	18.3	..	20.0	18.1	..	..	..
Precipitation mm.....	..	70	82	..	56	36	..	..	..
CHALK (1930)	6	11	32	**49**	39	12	—	—	100
(Oxford, Engl.)									
Mean temperature	8.3	10.8	14.6	..	16.5	17.1	..	..	..

TABLE XV (continued).

Species of Tree	April	May	June	April May June	July	Aug.	Sept.	Okt.	Σ
Picea abies									
MISCHKE (1890)	4	26	27	**57**	26	17	—	—	100
(Germany)									
Mean temperature	6.5	13.5	17.4	..	16.7	17.0	..	..	..
Precipitation mm.....	25	17	27	..	94	43	..	..	..
FRIEDRICH (1897).....	4	15	23	**42**	29	20	7	2	100
(Mariabrunn, Austria)									
Mean temperature	—	12.7	15.8	..	18.7	17.0	13.2	8.3	..
Precipitation mm.....	73	83	125	..	61	50	54	..	..
WIELER (1898)	..	..	..	(**47**)	..	..	..	..	..

Wood formation proceeds practically speaking in the same way in the upper and lower parts of the stem (see Figs. 16, 18, 20, 22, 24, 26 and 30).

In well-grown trees wood formation is terminated in the stem at the close of August or during the first half of September. The time varies somewhat according to the tree species[1] and the climate of the individual year (comp. Figs. 15—30).

2. The Individual Variation.

The individual variation is fairly considerable and to some extent relative to the diameter increment (comp. Figs. 16, 18, 20, 22, 24, 26 and 30 with Tables V, VI, VII, VIII, IX, X and XIII).

In trees with small radial growth wood formation is most lively up to the beginning or the middle of July. It varies somewhat according to the species of the tree. Thereafter it decreases quickly. It often terminates at the close of July or the beginning of August.

In trees with large diameter increment wood formation proceeds quite evenly all through summer. As a rule it only terminates at the close of August or the beginning of September.

The difference is most distinct in the diffuse porous and the conifers (*Picea abies*). In these trees one third of the annual ring is generally speaking formed after June, while $^2/_3$ are formed in trees with large diameter increment (see Fig 32).

The reason of this correlation between diameter increment and the formation of wood is no doubt that the more unfavourable the growth conditions are (decreasing growth in thickness) the more will the growth possibilities relatively decrease during the last half of the summer.

This may be due to the α) external conditions and β) the internal, nutrition physiological conditions.

[1] Wood formation does not continue later in autumn in *Fraxinus excelsior*, *Alnus glutinosa* and *Quercus robur* whose foliage keeps fresh and green till defoliation in October (comp. BURGER 1942) than in the broad leaved trees whose foliage begins to discolour relatively early in autumn.

α) External conditions.

The food material in the soil is greatest in May and during the first half of June. It thereafter decreases, cf. LUNDEGÅRDH (1925) and HONCAMP (1931). Particularly the nitrogen[1] content decreases. The reason is decreasing biological activity.

HONCAMP (1931, II, p. 84) writes: "Im Frühjahr erwacht mit steigender Wärme ein immer regeres Bakterienleben, das aber schon in der wärmsten Jahreszeit, Juli bis August, merklich nachlässt und erst zum Herbste hin wieder ansteigt, um dann gegen den Winter hin wieder einzuschlafen".

The growth retarding effect of this must according to the minimum law presumably be relatively stronger the poorer the soil is in food stuffs and particularly in nitrogen (sluggish assimilation, humus accumulation etc.).

β) Internal conditions of the physiology of nutrition.

During the first part of the growth period the volume increment is determined by the equation:

A) Consumption of reserve food + assimilation surplus[2] = volume increment + seed (if any).

The reserve nutrients are consumed during the leafing period and the first part of the shoot extension period, when great quantities are consumed during a comparatively short time for formation of leaves, shoots, and spring wood, cf. RAMANN and BAUER (1911)[3].

There exist no exact investigations showing how late in summer the reserve nutrients are consumed. After the many investigations made concerning the starch content of the trees etc. there is, however, every reason to assume that it is used up to 2 to 4 weeks after foliation, cf. R. HARTIG (1888c), FISCHER (1891), WOTCZAL (1890), LUTZ (1895), FABRICIUS (1905), RAMANN and BAUER (1911), KÜBLER (1912), PRICE (1915), BUTLER, SMITH, and CURRY (1917), CAMERON (1923), SWARBRICK (1927a), COCKERHAM (1930), WIGHT (1933), and GÄUMANN (1927 and 1935)[4].

In Denmark the growth of the trees presumably proceeds by means of reserve foods until the close of May to the middle of June. Probably it varies somewhat according to how long time the leaves take to expand, how long the shoot extension lasts, and whether the trees are seed-bearing or not.

[1] It is worth noticing that the trees at the same time require increased nitrogen supply, cf. RAMANN and BAUER (1911, p. 74).

[2] The assimilation surplus = the net assimilation of the leaves — loss of leaves — loss of branches — (root loss) respiration in the stem, branches, and roots, cf. BOYSEN JENSEN (1910).

[3] In older trees with well developed crowns only the young branches are completely depleted of reserve nutrients in spring, cf. SWARBRICK (1927), COCKERHAM (1930), and GÄUMANN (1927 and 1935). A complete depletion of reserve nutrients in the older branches and in the stem only takes place in seed years, cf. BOYSEN JENSEN (1943, p. 228).

A relatively greater quantity of the reserve food is consumed in quite young than in older trees, comp. RAMANN and BAUER (1911), KÜBLER (1912), and GÄUMANN (1935).

[4] According to MÜNCH (1938, p. 641) the branches only supply assimilates to the stem after the young shoots are fully developed.

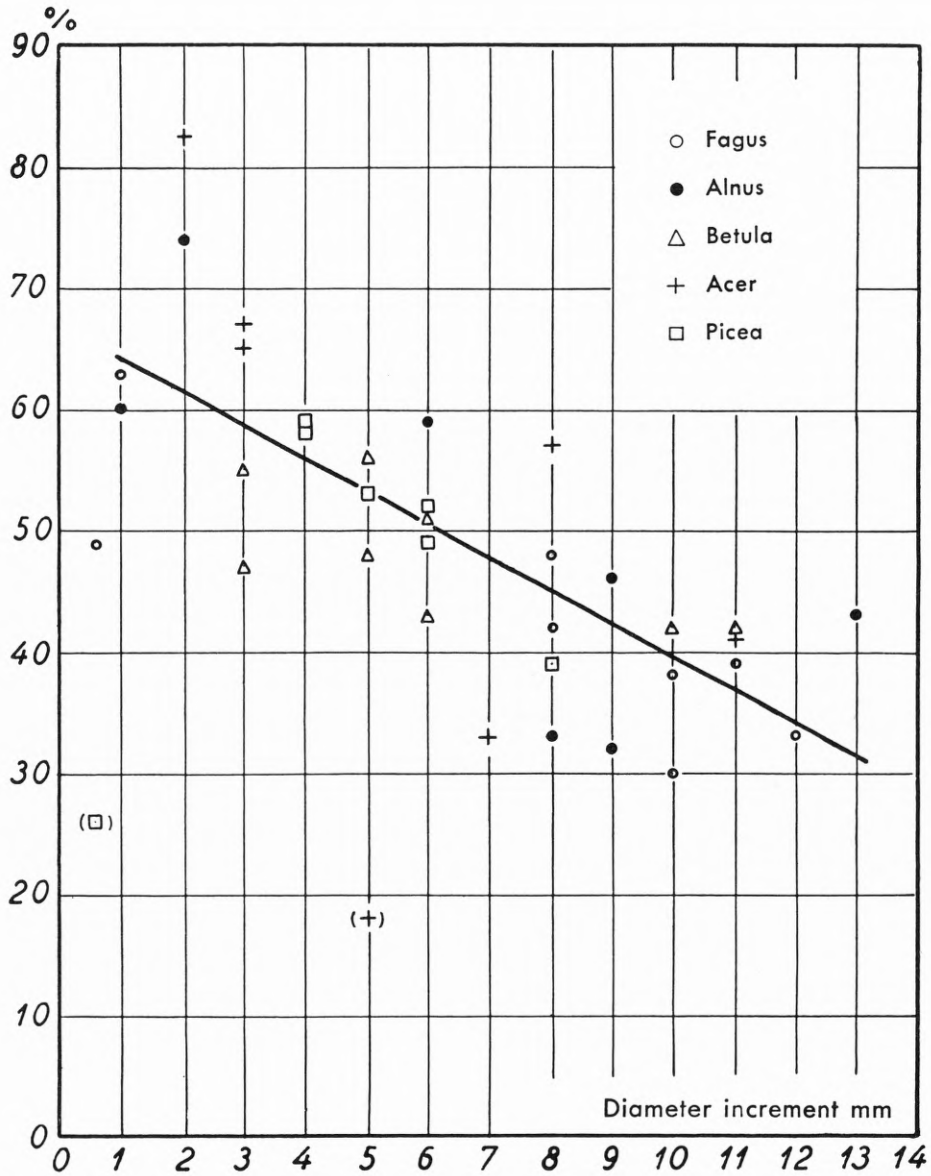

Fig. 32. The relation between the diameter increment of the trees and the relative annual ring formation per July 1, 1945.
The per cents give the mean for the stem in the middle of the crown and at brest height.
The curve is drawn assuming a rectilinear regression[1].
The correlation coefficient is 0.75[2].

[1] The regression equation is: $y = 67.10 - 2.74\,x$

[2] Judged by the t-criterion: $\frac{r}{m_r} = 6.5$; t = c. 2.

The volume increment during the last part of the growth period appears from the equation:

B) Assimilation surplus — reserve nutrients = volume increment + seed (if any).

In conformity with the minimum law it is to be assumed that the closer the assimilation surplus is to minimum wood formation will decrease relatively more by the transition from equation A) to B).

This may also explain why there is relatively less wood formation after June in the strongly suppressed trees with small crowns of scanty foliage (small diameter increment) than in trees with large crowns (large diameter increment).

The Course of Wood Formation in the Roots.

Judging by the sections taken from the roots wood formation in the latter proceeds very irregularly.

It terminates somewhat later than in the stem, often not until the beginning of October, comp. TH. HARTIG (1857, 1863a), GULBE (1888a und b), LODEWICK (1928) and REES (1929).

The Effect of Temperature and Precipitation on the Course of Wood Formation.

The correlation between the course of wood formation and temperature and precipitation is made the object of investigations in the following way:

a) By a comparison of the growth curves in 1944 and 1945 with mean temperature and precipitation.
b) By a comparison of the results of these investigations with the result of investigations carried on abroad in countries with a different climate. This comparison is made on the basis of the figures in Tables XIV and XV.

1. Temperature.

If we compare the thick growth curves in Figs. 15—30 with the temperature curve it will appear that wood formation was most active during the warmest periods.

TABLE XVI. The Correlation Coefficients for the Wood Formation and a) the Mean Temperature and b) the Precipitation in the Period from April—July. The Coefficients are Calculated after the Figures in Tables XIV and XV.

Species of Tree	Mean Temperature					Precipitation	
	r	%	F.V.	$\frac{r}{m_r}$	t	r	%
Acer pseudoplatanus	0.96	92	5	7.2	2.6	0.56	31
Fagus silvatica	0.80	64	12	4.6	2.2	0.25	6
Quercus	0.76	58	8	3.3	2.3	0.39	15
Fraxinus	0.73	53	11	3.5	2.2	0.16	2
Picea abies	0.72	52	12	3.6	2.2	÷ 0.06	(0)

A correlation calculation on the basis of the figures in Tables XIV and XV shows that in April, May, June and July there is a distinct positive correlation between wood formation and temperature (see Table XIV).

After July the course of wood formation seems chiefly to be autonomously determined.

2. Precipitation.

We get information of the effect of precipitation by examining how wood formation reacts in periods of drought.

July and August 1944 were by the Danish standard both warm and dry. In July the mean temperature was 1.0°, and in Aug. 3.2° over normal (see Table I). August was the warmest month of the year. Normally July is the warmest time.

Precipitation in July was only 34 mm against normally 71 mm, and in August 19 mm only against normally 67 mm (see Table I).

The water content in the ground under close-grown *Fagus silvatica, Acer pseudoplatanus, Quercus robur-* and *Picea abies*-stands in higherlying areas decreased in the uppermost 20 cms to only 11—14 % of the dry weight. A lower water content is scarcely reached in good forest soils in this country, except in quite exceptional periods of drought.

The *Fagus silvatica* and the *Quercus robur* did not react to this strong drying out of the soil (see Figs. 19 and 23). In the *Quercus robur* wood formation on the contrary reached maximum during the first half of August.

In a number of the *Picea abies* wood formation on the other hand decreased strongly in August (see Fig. 29). The wood that was formed during this month was typical summer wood with thick-walled tracheids of small widths.

When the drought ceased at the end of the month wood formation increased. During a short period wood was formed with proportionally thin-walled tracheids of fairly great widths.

In many of the trees a "false annual ring" appeared as a consequence of this.

The reason why the drought retarded wood formation in *Picea abies*, but not in *Fagus silvatica* and *Quercus robur*, may possibly be sought in the difference in the building of the root system. *Picea abies* has a shallow root and is therefore more sensitive to the drying up of the uppermost layer of the soil than *Fagus silvatica* that has a main root, and *Quercus robur* that has a tap-root. During periods of drought it is easier for these trees to get their supplies of water from the deeper lying layers of the soil than for *Picea abies*.

Fraxinus excelsior grew chiefly along swamp-borders where the soil was more watery. It is difficult on the basis of the curves to determine whether wood formation in this species of tree was retarded owing to lack of water under the drought (comp. Figs. 25 and 26).

In 1945 wood formation was at first relatively livelier in *Fraxinus excelsior* Nos. 6, 7, and 8, that were growing in watery marsh soil than in the other *Fraxinus excelsior*s on the

higher lands (see Fig. 26 and Table X). The reason of this may possibly be sought in a presumably livelier nitrification in the marsh soil during May and June when a vigorous and dense nettle-vegetation grew up here.

The *Betula pendula* and the *Alnus glutinosa* in most cases grew in moist marsh soil and have scarcely suffered from lack of water during the drought. On the contrary it must be supposed that the drought has improved the physical condition of the marsh soil. In both species of trees wood formation was accordingly also particularly lively during most of the drought-period (see Figs. 15 and 17).

According to the figures in Tables XIV and XV there is little positive correlation between wood formation and precipitation during the various summer months (see Table XVI).

Literature gives spare information only about the connection between the course of wood formation and external factors. Most investigators have paid little attention to this question.

MISCHKE (1890) followed wood formation in *Pinus silvestris* and *Picea abies* in a year of pronounced drought (see Table XIV) and found that drought retarded wood formation more in *Pinus silvestris* than in *Picea abies*.

FRIEDRICH (1897, p. 145) found: "... dass die Perioden der grössten oder grösseren Baumzuwachses mit den Perioden der höheren Lufttemperatur, und zwar sowohl hinsichtlich der mittleren als auch der maximalen zusammenfallen".

The investigations were carried out in a rainy area (see Table XIV) and therefore did not give any certain information about the effect of precipitation.

JOST (1892), CHRISTISON (1889), BROWN (1915), LODEWICK (1928) and CHALK (1930) found that wood formation has two annual maximum periods which stand in no relation to external factors.

KORSTIAN (1921) found no correlation between temperature and the course af wood formation in *Acer Negundo* L. and in *Picea pungens* ENGEL.

According to MACDOUGAL (1924) cold storms or short periods of drought may cause wood formation to decrease or terminate.

LODEWICK (1925) found that a decline in temperature may cause decreasing wood formation in *Fraxinus americana* L.

The influence of climatic factors on the width of the annual ring has on the other hand been the subject of many investigations. It would take us too far here to deal in detail with all of them. A survey of the older literature is to be found in ANTEVS (1914—17) and of later literature in KNUCHEL (1933) and ORDING (1940).

The investigations in Central- and Northern Europe chiefly comprise *Pinus silvestris* and *Picea abies*.

The main results may be summed up as follows:

In the colder climate of Sweden and Norway the width of the annual ring is chiefly determined by the summer temperature. The precipitation is on the other hand of inferior importance, cf. HESSELMAN (1904), WALLÉN (1917), KOLMODIN (1923 and 1935), EIDE (1926), AANDSTAD (1934), ERLANDSON (1936) and ORDING (1940—41).

In the warmer climates in Central Europe the width of the annual ring is on the other hand determined chiefly by the quantity of precipitation, cf. HENRY (1894), MER (1895), SCHWARZ (1899), CIESLAR (1907), WIEDEMANN (1925), KNUCHEL and BRÜCKMANN (1930) and KNUCHEL (1933).

Here in Denmark LÜTKEN (1891) found that in Bornholm the basal area increment of *Abies alba* is chiefly determined by the annual amount of precipitation: the mean temperature in April—October.

HOLMSGAARD (1945) has investigated the connection between precipitation and temperature and the variation in the width of the annual ring in *Picea abies* in Gludsted Plantation, where the soil on the whole is meagre. The measurements were carried out on 510 increment cores from 19 stands in the ages from 38—69 years.

He found that precipitation in April—July has a decisive influence upon the width of the annual ring. Of particular importance is the precipitation in May and June.

On the other hand he could not show any certain relation between the temperature and the width of the annual ring.

IX. The Thickening of the Cell Walls.

The thickening of the cell walls, which presumably takes place by apposition, continues later in autumn than wood formation (growth in thickness) by cell division and growth in size.

In well-grown broad leaved trees it ceases about the middle of September, in well-grown coniferous trees at the end of September or the beginning of October (see Fig. 33).

SIGMOND (1935) has made the same observation. He writes i. a. (p. 562): "Die Verstärkung der Spätholzeinheiten dauert bei der Fichte und sehr warscheinlich auch bei den übrigen Nadelbäumen unserer Breiten bis in den Herbst hinein an. Auf Grund gewisser Beobachtungen kann man sogar vermuten, dass die Vollendung des Spätholzanteiles erst während

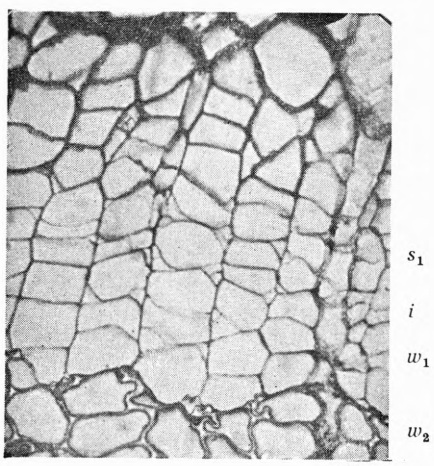

Fig. 33. The cambium of the *Larix decidua* in the middle of September, 1945. Transverse section taken at breast height from *Larix decidua* No. 2 (see Table XII). Cell division had ceased, it was at any rate impossible to prove further wood increment. On the other hand the cell walls of the summer wood cells had not yet ceased growing in thickness.

s_1 Young, undifferentiated sieve tube cells which presumably next spring will differentiate into spring tissue.
i The approximate position of the initial cell.
w_1 Young, undifferentiated wood cells, which presumably next spring will differentiate into spring wood.
w_2 Summer wood cells whose cell walls have not yet terminated their growth in thickness. Under the preparation the cell walls have shrunk to a certain extent.

des Winters, ja sogar noch im Laufe der darauffolgenden Wuchszeit erfolgt. Demnach bleibt das Kambium noch lange nach Abschluss der Teilungsvorgänge tätig, indem es die zur abschliessenden Verstärkung der letzten Spätholzeinheiten notwendigen Bildungsstoffe abgibt. Vereinzelte Fälle deuten sogar darauf hin, dass man Kambium während der Wuchszeit die verfügbaren Baustoffe nicht ausschliesslich für die Bildung des neuen Jahreszuwachses und gelegentliche Speicherung verbraucht, sondern auch zur Vollendung des vorletzten Jahres ringes verwendet".

X. The Change in the Width of the Vessels and Tracheids during the Growth Period.

An attempt has been made at elucidating the above mentioned change numerically and graphically by measurements on a number of sections taken from the stem during the summers of 1944 and 1945 from 1.3 m height.

Methods.

The measurements were carried out in the following way:

All vessels or tracheids within a limited area of the last lignified part of the new annual ring were by means of a Zeiss Zeichnenapparat traced on squared paper magnified 80, 120 or 240 times.

The conductive cross section area of the vessels or the tracheids was then calculated by counting how many squares were comprised.

The diameter of the vessels was calculated on the basis of the individual vessels' cross section areas by referring to MAX FRIEDRICH KUNZE: Hilftafeln für Holzmassen-Aufnahmen, 1928.

The period within which the measured sections of the annual ring was formed was approximately determined. The determination was based on curves of the previous course of wood formation. Errors in the determination have scarcely in any case exceeded one week to either side.

Tables and Figures.

The results are collected in Tables XVII and XVIII and appear graphically in Figs. 34, 35, 36, and 37.

The numbers in column 3 in the Tables refer to the trees, from which the sections examined are taken.

The mean annual ring width varied between c. 4 and 5 mm.

The total cross section area of the vessels in columns 8, 9 and 10 has been recorded in per cent of the whole cross section area of the examined core of the annual ring.

TABLE XVII. The Diameter of the Vessels and the Total Conductive Cr. Sect

1	2	3	4	5	6
Tree species	Year	Tree No.	Date	Vesse	
				Max. mm.	Min. mm.
Ring porous:					
Fraxinus excelsior	1945	1, 2, 3, 4, 5, 6, 7 and 8 (cf. Table X)	May 11—May 20	0.259	0.064
			May 20—June 1	224	24
			June 1—June 8	200	21
			June 16—June 25	106	12
			June 25—July 5	69	12
Quercus robur	—	1, 2, 3, 4, 5, 6 and 7 (cf. Table IX)	May 17—May 25	0.216	0.033
			May 25—June 8	262	33
			June 8—June 20	185	15
			June 20—July 1	62	12
			July 25—Aug. 8	46	12
Ulmus glabra	1944	..	May 2—May 25	0.161	0.032
			May 25—June 7	179	29
			June 25—July 6	121	15
			Aug. 1—Sept. 1	69	9
Diffuse porous:					
Carpinus betulus	1944	..	till June 15	0.081	0.016
			after July 15	48	6
Tilia cordata	—	..	till June 15	0.078	0.009
				46	7
Prunus avium	—	..	till June 15	0.073	0.017
			after July 15	47	6
Fagus silvatica	1945	1, 3, 4, 6 and 7 (cf. Table VII)	May 21—June 1	0.084	0.015
			June 1—June 9	100	15
			June 9—June 24	67	8
			July 13—July 21	50	8
			July 25—Aug. 10	58	8
Sorbus aucuparia	1944	..	till June 15	0.058	0.009
			after July 15	36	8
Corylus avellana	—	..	till June 15	0.097	0.007
			after July 15	73	7
Alnus glutinosa	1945	1, 2, 3, 4 and 5 (see Table VI)	May 21—June 1	0.069	0.009
			June 1—June 8	69	9
			July 10—July 25	82	9
			July 25—Aug. 5	51	7
Acer pseudoplatanus	—	1, 2, 3 and 4 (cf. Table VIII)	May 18—June 14	0.122	0.017
			June 14—July 1	96	17
			July 1—July 8	78	17
			July 20—July 30	78	17
			July 30—Aug. 8	74	9
Aesculus hippocastanum	1944	..	May 21—June 15	0.042	0.017
			June 15—July 5	50	14
			July 15—Aug. 5	32	8
Betula pendula	1945	2, 3, 4, 5, 6, 7 and 8 (cf. Table V)	May 17—June 14	0.105	0.024
			June 25—July 5	97	24
			July 25—Aug. 6	88	16
			Aug. 11—Aug. 29	82	13

Area in Wood Formed within Different Times of the Growth Period.

7	8	9	10	11
Diameter	The Total Cr. Sect. Area of the Vessels			Percentage relation between the Total Cr. Sect. Area of the Vessels in Summer and Spring Wood
Mean mm.	Max. %	Min. %	Mean %	%
0.165 ± 14.2	38	20	30 ± 1.8	
127 ± 18.4	35	10	17 ± 2.7	
72 ± 18.1	23	1	10 ± 2.6	
43 ± 8.6	3	0.5	2 ± 0.4	
38 ± 2.7	2	0.1	0.7 ± 0.2	6
0.161 ± 9.2	38	22	32 ± 2.2	
127 ± 20.0	42	10	23 ± 4.5	
46 ± 8.5	8.5	1.3	3.5 ± 0.9	
26 ± 1.5	3.5	0.3	2 ± 0.4	
26 ± 2.2	3.3	0.7	2 ± 0.4	7
0.127 ± 16.1	24	22	23 ± 0.4	
97 ± 14.6	16	11	15 ± 1.2	
53 ± 12.4	11	6	7 ± 1.9	
23 ± 5.7	8	2	5 ± 1.7	26
0.045 ± 6.0	5.7	2.3	3.8 ± 1.5	
23 ± 2.8	2.0	0.9	1.3 + 0.5	34
0.036 ± 6.1	22	7	13 ± 1.6	
24 ± 3.3	9	2	5 ± 1.4	38
0.057 ± 7.5	37	24	28 ± 2.4	
26 ± 3.6	17	8	12 ± 3.6	13
0.039 ± 7.9	31	21	26 ± 1.6	
52 + 7.4	28	15	19 ± 2.7	
46 ± 4.7	21	10	15 ± 1.8	
28 ± 3.8	18	4	11 ± 2.4	
29 ± 2.4	11	8	9 ± 1.1	44
0.034 ± 4.7	25	15	20 ± 1.8	
20 + 3.2	13	5	9 ± 1.2	45
0.026 ± 3.5	24	9	16 ± 1.9	
21 ± 3.2	12	6	8 ± 0.7	50
0.041 ± 7.1	29	13	20 ± 3.0	
33 ± 6.5	30	14	21 ± 2.5	
37 ± 7.5	18	12	15 ± 1.2	
29 ± 5.1	9	4	7 ± 0.8	54
0.062 ± 9.2	10	5	8 ± 1.1	
54 ± 8.4	7	4	6 ± 0.7	
45 ± 7.1	8	4	6 ± 0.8	
48 ± 7.1	6	3	5 ± 0.2	
43 ± 10.3	5	2	4 ± 0.8	64
0.026 ± 8.3	10	6	8 ± 0.5	
31 ± 3.5	7	5	6 ± 0.6	
18 ± 2.5	8	3	6 ± 0.8	75
0.060 ± 1.6	16	3	8 ± 1.6	
48 ± 1.1	11	6	8 ± 0.7	
47 ± 2.4	11	5	7 ± 1.2	
47 ± 1.8	9	4	6 ± 0.9	81

TABLE XVIII. The Cr. Sect. Area of the Tracheids in Wood

1 Tree species	2 Year	3 Tree No.	4 Date	5 The Cr. Sect. Area Individua Max. m²	6 Min. m²
Larix decidua	1945	1, 2, 3, and 4	May 18—June 5	0.00212	0.00044
			June 25—July 1	—	—
			July 10—July 20	—	—
			Aug. 1—Aug. 10	—	—
Picea abies	—	1, 2, 3, and 4 and 10	May 17—June 13	0.00176	0.00036
			June 25—July 3	—	—
			July 15—July 23	—	—
			Aug. 1—Aug. 10	—	—
			Aug. 15—Aug. 25	—	—

The Difference between Spring and Summer Wood and the Time of the Inception of Summer Wood.

1. Definition.

According to an arrangement of The International Association of Wood Anatomists (1933) spring wood = Früholz or Weitholz—is in the future to be called early wood, and summer wood = Spätholz or Engholz is to be called late wood.

The following definition was at the same time given:

Early wood is the loosely built wood with large cells in the first part of the growth ring.

Late wood is the densely built wood with small cells in the later formed part of the growth ring.

WIKSTEN (1944) uses the terms spring and summer wood. He gives the following definition for *Picea abies* and *Pinus silvestris* (see also MORK 1928)[1]:

As summer wood must thus be considered that part of the growth ring where twice the common cell wall constantly is equal to or larger than the lumen, while the remainder is considered as spring wood.

In such cases where the relation between the common cell wall and the lumen does not decline to 2.0 the relation between the tangential and the radial cell cross section $\left(\frac{t}{r}\right)$ must be used which for

Picea (gran) = 1.12
Pinus (tall) = 1.11
species = 1.10.

} or rounded off for both

The part of the annual ring is thus to be considered as summer wood where the relation between the cells' tangential and radial cross section $\left(\frac{t}{r}\right)$ constantly is equal to or larger than 1.10.

CHALK (1937) considers the small-porous part of the annual ring in the ring porous species as the equivalent of the whole annual ring in the diffuse porous. He writes (p. 326):

"It is suggested that the late or summer wood of ring-porous species is the equivalent of the whole ring in diffuse-porous species, and that the pore-zone represents an additional, highly specialised tissue.

The term early wood should imply early development in relation to the foliage and be limited to softwoods and ring-porous hardwoods".

[1] The Swedish text is translated into English.

Formed within Various Times during the Growth Period.

7	8	9	10	11
of the Tracheids	The Total Cr. Sect. Area of the Tracheids			Percentage Relation between the Total Cr. Sect. Area of Area of the Tracheids in Spring and Summer Wood
Mean m^2	Max. %	Min. %	Mean %	
0.00114	71	48	61 ± 5.8	
37	50	26	37 ± 4.9	
29	40	23	34 ± 3.7	
11	26	14	22 ± 2.7	46
0.00088	62	49	57 ± 2.5	
22	55	22	38 ± 5.2	
16	35	22	30 ± 2.5	
15	38	12	21 ± 4.6	
8	23	10	18 ± 2.3	34

For purely practical reasons the old-established term for spring and summer wood in Denmark is retained in this paper even if we agree with O. G. PETERSEN (1920, p. 70) that the term is somewhat misleading.

In cases where it is difficult to distinguish between spring and summer wood such wood as is formed before June 15th is considered as spring wood, while wood formed after July 15th is to be termed summer wood.

The first formed large-porous wood in the ring porous species is considered as spring wood.

2. The Successive Order of the Formation of Summer Wood.

The formation of summer wood begins first in the young branches and later in the stem. It may often be far advanced in the branches at a time, when spring wood is still being formed in the stem, see PRIESTLEY and SCOTT (1936).

3. A Comparison between the Tree Species.

a) HARDWOODS.

According to the difference between the size and total conductive cross section area of the vessels in spring and summer wood in the stem the hardwoods may be ranged in the following succession from typical ring porous to typically diffuse porous trees:

α) Ring porous.

Characteristics of the structure of the annual ring: Great difference between spring and summer wood. The vessels in the spring wood are very wide. In cross sections they are conspicuous to the naked eye as small cavities. The vessels in the summer wood are very small and scantily distributed in a tissue of wood fibres and wood parenchyma. The transition between spring and summer wood is abrupt.

Quercus robur and *Fraxinus excelsior* are typically ring porous trees.

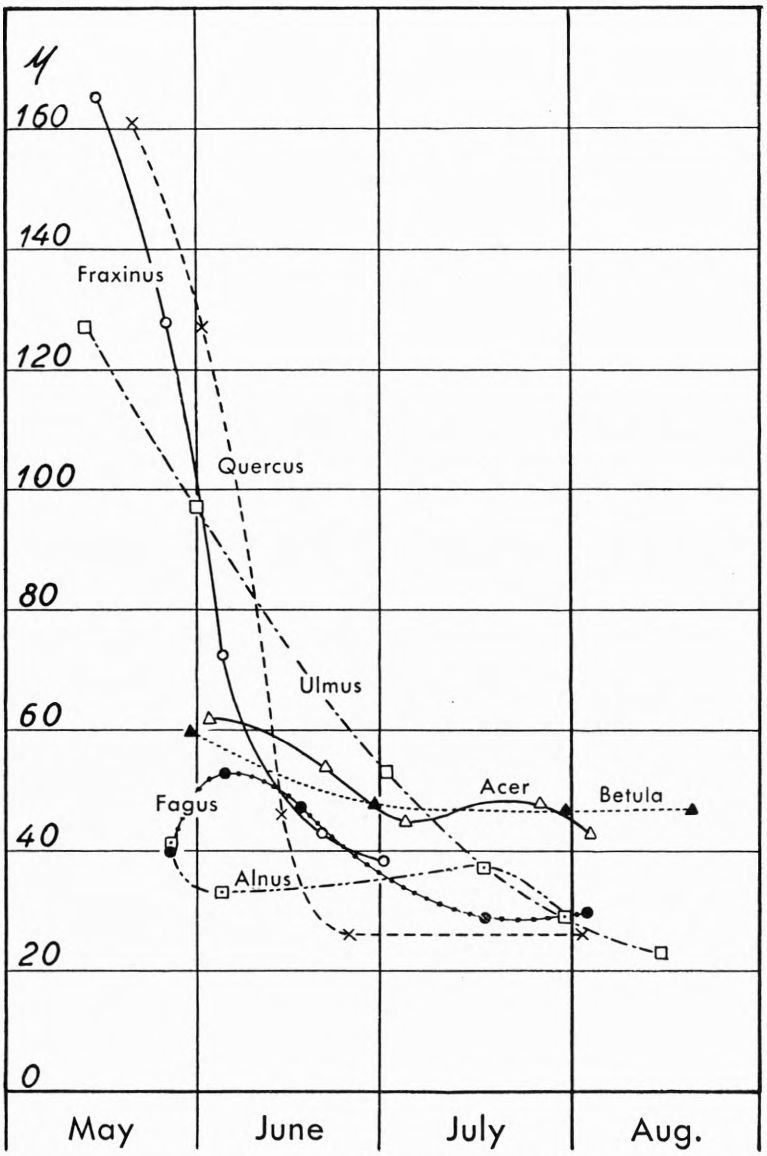

Fig. 34. The mean-diameter of the vessels formed in wood at different times in summer.

The first formed vessels in spring wood are very wide (mean diameter 0.16 mm) and cover scarcely one third of the total cross section area of the spring wood (see Table XVII and Figs. 34 and 35).

The diameter of the vessels and their total conductive cross section area is strongly decreasing till mid-June. About this time the formation of summer wood begins.

The summer wood contains only few and small vessels with a total conductive cross section area of only 2 % of the total cross section area of the summer wood.

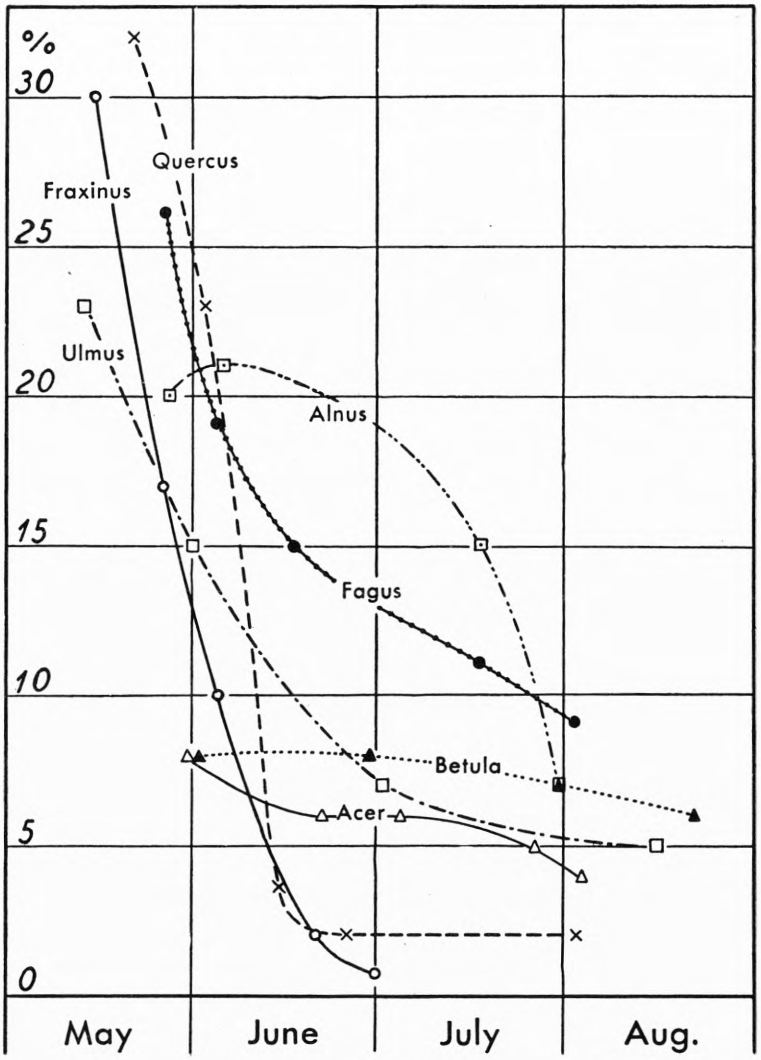

Fig. 35. The total conductive cross section area of the vessels in percentage of the cross section area of the wood formed.

Ulmus glabra is somewhat closer to the diffuse porous types.

It differs from *Quercus robur* and *Fraxinus excelsior* by having smaller spring vessels, by a more even transition from spring to summer wood, and by having more vessels in its summer wood (see Table XVII and Figs. 34 and 35).

β) Diffuse porous.

Characteristics of the structure of the annual ring: Small vessels both in spring and summer wood. Under good growth conditions the transition from spring to summer wood is even.

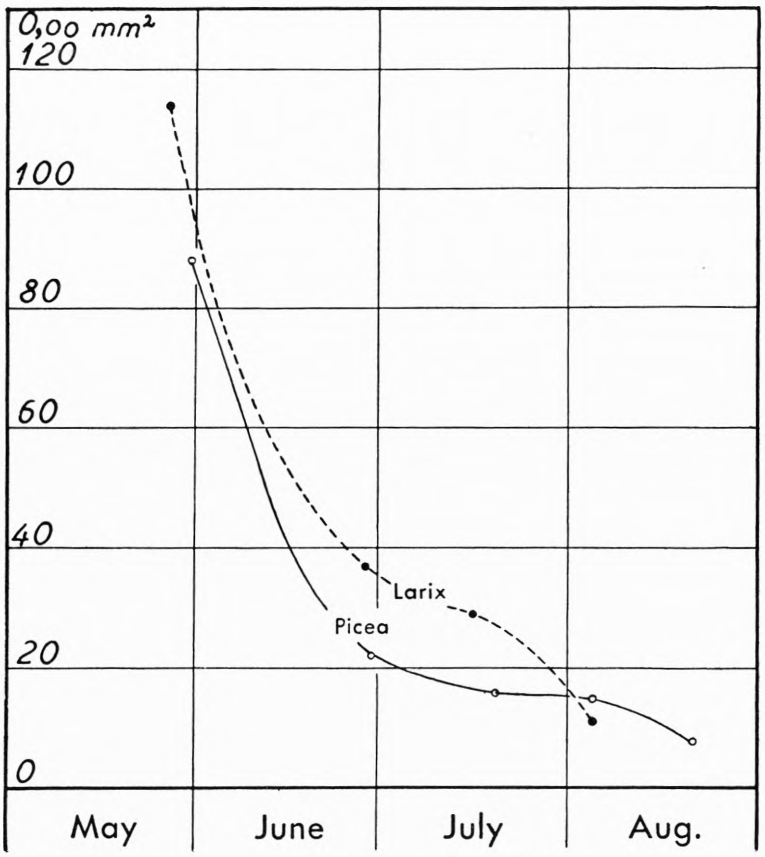

Fig. 36. The mean and cross section area of the individual tracheids in wood formed at different times in the course of summer.

Fagus silvatica, Alnus glutinosa, Prunus avium, Sorbus aucuparia, Tilia cordata, Corylus avellana and (*Carpinus betulus*) are those of the diffuse porous types that are closest to the ring porous.

In summer wood there are considerably fewer and smaller vessels than in spring wood. The difference is so conspicuous that in most cases it may easily be seen on cross sections under a good magnifying glass.

In *Prunus avium* and *Fagus silvatica* the total cross section area of the vessels in spring wood is almost as large as in *Quercus robur* and *Fraxinus excelsior* (see Table XVII and Figs. 34 and 35).

Carpinus betulus has very few vessels in its spring as well as in its summer wood.

In *Fagus silvatica* the commencement of summer wood formation may averagely be considered to take place from the end of June, in *Alnus glutinosa* from mid-July.

Betula pendula, Alnus glutinosa and *Aesculus hippocastanum* are typically diffuse porous trees.

The number and size of the vessels are on the whole alike both in spring and

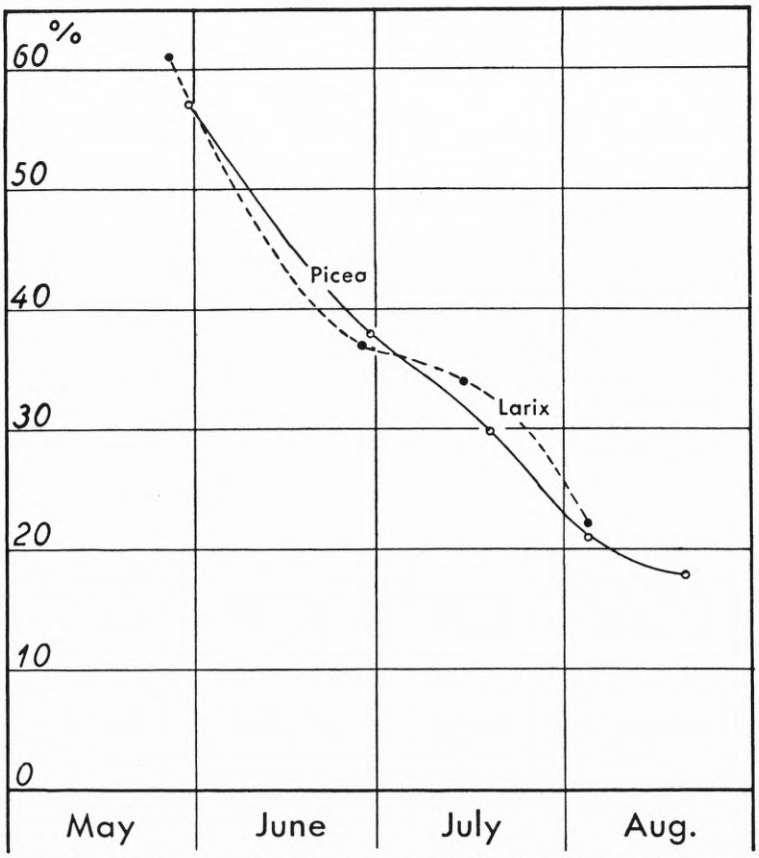

Fig. 37. The total conductive cross section area of the tracheids in percentage of the cross section area of the wood formed.

summer wood (see Table XVII and Figs. 34 and 35). Even under the microscope it may often be difficult to notice any distinct difference between spring and summer wood.

The border of the annual ring is therefore often not sharply outlined.

The number of vessels is relatively small both in spring and summer wood. In spring wood their total conductive cross section area thus makes only 8 % of the total cross section area of the spring wood.

b) CONIFERS.

Characteristics of the structure of the annual ring: Considerable difference between spring and summer wood. The spring-tracheids are thin-walled and have a fairly large volume. The summer-tracheids are thick-walled, somewhat compressed radially, and have a small volume only.

The transition between spring and summer wood is most often even.

Picea abies and *Larix decidua* have almost the same annual ring structure (see Table XVIII and Figs. 36 and 37).

The total conductive cross section area in the spring wood is double as large as that of the ring porous types (comp. Tables XVII and XVIII).

The commencement of summer wood formation may averagely be considered to take place from the beginning of July (see Fig. 36).

Literature gives the following information about the time of the inception of summer wood formation in the different tree species:

Quercus robur: The middle of June (Mer 1892c and Antevs 1914—17).
The middle of July (Priestley and Scott 1936).

Fraxinus excelsior: The middle of June (Lodewick 1925, Chalk 1930 and Priestley 1936).

Picea abies: The middle of August (Mer 1892c).
The end of July (Wieler 1898).

Picea rubra L.: The middle of July (Rees 1929).

4. The Width of the Annual Ring.

In hardwoods the percentage of summer wood increases with the width of the annual ring, and in the conifers it decreases at the same rate (cf. R. Hartig (1891) and Antevs (1917).

According to Wiksten (1944, p. 457) the width of the transition zone between spring and summer wood in conifers (*Picea abies* and *Pinus silvestris*) increases with the width of the annual ring.

The Cause of the Difference between Spring and Summer Wood.

1. Literature.

Ever since the first half of last century botanists have tried to find the cause of the difference between spring and summer wood.

Literature offers many more or less hypothetic explanations. Some of the most important are the following:

a) difference in nutrition.

Schacht (1856) and R. Hartig (1891) think that the reason is that the cambium is better supplied with food substances at the height of the summer season and late in summer than early in summer, when the temperature still is relatively low and the assimilation has not yet reached full height.

Wieler (1887) and Klebs (1914) also seek the reason in the difference of the food supply of the cambium. But in contrast to the above mentioned investigators they think that summer wood formation is due to declining food supplies.

André (1920) has shown by experiments that spring wood is only formed when there is an excess of nutrients and the water supply is abundant.

b) BARK TENSION.

KRAUS (1867), SACHS (1868), DE VRIES (1872, 1874, 1875, and 1876) and BURNS (1910) maintain that summer wood formation is due to increasing bark pressure on the wood cylinder, when this in the course of summer increases in circumference owing to wood increment.

KRABBE (1882 and 1884) and WIELER (1885 and 1887) have by experiments shown that this assumption is incorrect.

c) TURGOR.

RUSSOW (1881) seeks the reason of summer wood formation in declining turgor.

d) WATER CONTENT.

LUTZ (1895) thinks that summer wood formation is due to decreasing water content in the bark and the young wood regions.

e) MECHANICAL POINTS OF VIEW.

METZGER (1908) explains the difference between spring and summer wood from purely mechanical points of view.

f) TELEOLOGY

HABERLANDT (1884), STRASBURGER (1891), R. HARTIG (1894) and HOLTERMANN (1907) explain the difference from teleological points of view. The spring wood is wide porous, because the trees at this time of the year, when leaf expansion takes place, require great water supplies. Later in summer when the foliage has hardened and the request for water supply decreases so much and extensive water conductive tissue is no longer necessary. Therefore at this time more thick-walled wood elements are formed to strengthen ". . . die Festigkeit des Stammes" (HABERLANDT 1884, p. 638).

g) HORMONE EFFECT.

COSTER (1927) has in tropical countries made the observation that wood of the spring wood type is only formed as long as foliage is developing. When the leaves are fully expanded summer wood formation begins.

He advances the theory that wood formation is under influence of growth hormones issuing from the foliage. The difference between spring and summer wood he explains in this way, that other hormones are formed in the foliage while it is developing than in the fully developed leaves.

h) VASCULAR CONNECTION.

PRIESTLEY and SCOTT (1936) have undertaken some investigations of summer wood formation in the ring porous types. They found that only the large vessels in

the spring wood stand in direct connection with the leaf traces. The small vessels in summer wood on the other hand issue from the bud scales and the embryonal shoot- and leaf-organs in the new formed buds.

2. A Comparison between the Length of the Shoot Extension Period and the Difference between the Size and Number of the Vessels in Spring and Summer Wood.

When considering the material from the investigations carried on in the first year I come to the result, that the difference between the size and number of the vessels in spring and summer wood may possibly be explained by a corresponding differense between the length of the shoot extension in the individual tree species. To try out the theory I measured the length of the shoot extension period in 1945 in the species of trees mentioned in Table XIX. The measurements were all carried out on trees of good growth, and at 7—14 days interval I measured the elongation growth in respectively,

a) the three uppermost vigorous top branches,
b) and the three lowest vigorous lateral branches.

Then the length of the shoot extension period in each species was calculated by taking the mean figure for the duration of the shoot extension in both categories of branches. The results are recorded in Table XIX.

TABLE XIX. The Length of the Shoot Extension Period in 1945.

1	2	3	4	5	6
Tree Species	No. of Trees	Age	Average for Top branches (a) days	Lower branches (b) days	All branches $\frac{(a+b)}{2}$ days
Hardwoods:					
a) Ring porous					
Quercus robur	7	10—15	35	20	27.5
Fraxinus excelsior	8	7—12	43	20	31.5
Ulmus glabra	6	10—20	45	40	42.5
b) Diffuse porous					
Fagus silvatica	7	10—15	47	39	43
Sorbus aucuparia	2	c. 15	61	43	52
Prunus avium	1	c. 10	68	—	(60)
Corylus avellana	3	c. 10	68	56	62
Acer pseudoplatanus	9	10—20	77	53	65
Alnus glutinosa	5	10—15	92	48	70
Betula pendula	9	5—12	105	68	86.5
Conifers:					
Picea abies	5	10	70	45	57.5
Larix decidua	5	7	(110)	(70)	(90)

In Table XVII in column 11 is recorded how great the difference is between the total conductive cross section area of the Vessels in spring and summer wood respectively in the said hardwoods. The difference is recorded in per cent.

In Fig. 38 these percentages are given as ordinates, while the length of the shoot extension period (Table XIX, column 6) is given as abscissa.

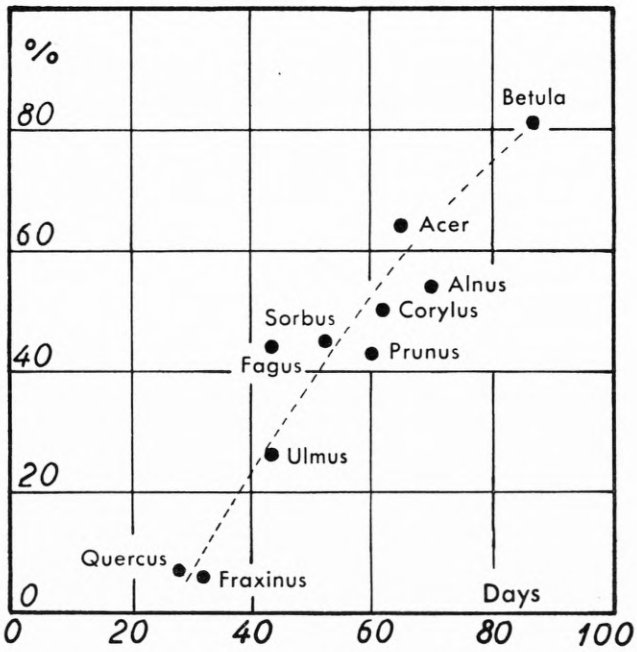

Fig. 38. A comparison between the mean length of the shoot extension period and the percentage relationship between the total conductive cross section area of the vessels in summer and spring wood.

It appears from the figure that there almost exists an inverse proportion between the length of the shoot extension period and the difference between the total conductive cross section area of vessels in spring wood and summer wood.

After this result there is reason to suppose that the size and the distribution of the vessels within the annual ring in the individual broad leaved trees, and thus one of the most essential differences between wood formation in spring and summer wood, is due to a difference in the length of the shoot extension period, comp. COSTER (1927). This explanation is confirmed by the fact that there, so to speak, is no difference between spring and summer wood in tropic tree species with leaves and shoots developing all the year round.

The reason of this connection may presumably be sought in:

a) The close connection which according to PRIESTLEY and SCOTT (1936) exists between formation of vessels in the leaves and large vessels in the wood.

b) Relatively larger hormone production during the last part of the summer in

trees with a long shoot- and leaf-developing period than in trees with a short one, cf. pp. 34—36.

c) Presumably it is also of importance how long time passes between the differentiation of the vessels in the young branches and lower down in the stem. A long interval in time (the diffuse porous) must be supposed to cause a more even distribution of vessels than a short interval (the ring porous), comp. the figures in Table XVII, column 11, with the time that passes between the beginning of wood formation at bud base and at breast height (Figs. 7 and 8).

XI. Water Transportation.

On the basis of the figures in Tables XVII and XVIII and HUBER and SCHMIDT's (1936) figures for the velocity of the water flow some estimates have been made concerning the amount of transportation in *Quercus robur, Fraxinus excelsior, Fagus silvatica, Alnus glutinosa, Betula pendula, Acer pseudoplatanus, Picea abies* and *Larix decidua.*

TABLE XX. Calculation of Water Transportation in the Middle of the Day in the Outermost Annual Ring in a 20 cms Thick Stem, when the Annual Ring is 5 mm Wide (diameter increment = 1 cm).

1	2	3	4	5	6	7	8
Tree Species	Tree	Mean annual ring width	Total conductive cross section area	Water Transportation in the Middle of the Day at Breast Hight			
				velocity	per cm² annual ring	in the whole outermost annual ring	relative for Quercus robur
	No.	mm.	%	m/hour	cm³/hour	Liter/hour	100
Ring porous:							
Quercus robur	1, 2, 3, 5 and 7	4.9	8.2	43.6	358	10.74	100
Fraxinus excelsior . . .	1, 2, 3, 6, 7 and 8	5.1	8.8	25.7	226	6.78	64
Diffuse porous:							
Alnus glutinosa	2, 3, 4 and 5	5.0	11.4	2.00	23	0.69	6
Fagus silvatica	1, 3, 4, 6 and 7	5.0	12.6	1.07	14	0.42[1]	4
Acer pseudoplatanus .	1 and 3	4.8	5.4	2.40	13	0.39	4
Betula pendula	3, 5 and 6	4.7	7.2	1.60	12	0.36	3
Conifers:							
Picea abies	3 and 6	5.0	39.4	(0.50)	(20)	(0.64)	(6)
Larix decidua	3 and 4	5.5	47.3	2.1	99	2.97	28

[1] Water transportation in the outermost annual ring in a 120-year-old *Fagus silvatica* quality class 2 is after corresponding calculations 0.66 liters/hour. DETLEV MÜLLER (1943, p. 161) has by other methods approximately estimated it at 0.7 liters/hour.

Water Transportation in the Outermost Annual Ring.

In Table XX is shown a calculation of the water transportation in the middle of the day through the outermost annual ring in a 20 cms thick stem when the annual ring is 5 mm wide.

The figures in column 2 refer to the trees described in Tables V—XIII. They are here selected in such a way, that the mean annual ring width is as close to 5 mm as possible (column 3).

The total conductive cross section area (column 4) is given in per cent of the cross section area of the whole annual ring. It is calculated after curves for the relative course of wood formation (Figs. 16, 18, 20, 22, 24, 26, 28 and 30) and curves for the total conductive cross section area in wood formed within various times of the growth period.

The velocity of flow (column 5) is taken after HUBER and SCHMIDT (1936).

In the ring porous species (*Quercus robur* and *Fraxinus excelsior*) the water transportation in the outermost annual ring is 10 to 30 time larger than in the diffuse porous (*Alnus glutinosa, Fagus silvatica, Acer pseudoplatanus* and *Betula pendula*).

As the conductive cross section area is approximately the same for both groups taken in sections the difference is chiefly due to the much greater velocity of flow in the ring porous species (column 5).

In *Picea abies* the velocity of flow must be supposed to be very small (see HUBER and SCHMIDT 1936, p. 411). Thanks to the large conductive cross section area the total water transportation in the outermost annual ring is nevertheless just as great as in the best yielding among the diffuse porous.

In *Larix decidua* the velocity of flow is approximately as in the diffuse porous types (*Acer pseudoplatanus* and *Alnus glutinosa*). But on account of the much larger conductive cross section area the water transportation in the outermost annual ring is 5 to 10 times larger.

Total Water Transportation.

In order to be able to calculate the total water transportation we must know how many annual rings are engaged in it.

According to RUMBOLD (1920), PRIESTLEY, SCOTT and MALINS (1933) and HUBER and SCHMIDT (1936) the water transportation in the ring porous species almost exclusively takes place in the outermost annual ring.

In the diffuse porous on the other hand it takes place through several annual rings. As to how many we have only uncertain information. WIELER (1888) states that in branches of *Fagus silvatica* 3.6, and in the stems of *Betula pendula* over 15 annual rings are water conductive. DETLEV MÜLLER (1943) has approximately estimated that in 120-year-old *Fagus silvatica* between 10 and 20 of the outermost annual rings are engaged in water transportation.

In June 1944 I have carried out the following investigations of how many annual rings participate in the water transportation in *Quercus robur, Fraxinus excelsior, Fagus silvatica, Acer pseudoplatanus* and *Betula pendula.*

At a week's interval a tree was felled within each species. The trees were 15 to 20 years old. They were all well-grown, stood in close stands and had medium sized crowns.

The trees were felled at about nine o'clock. They were felled in such a way, that they did not fall to the ground, but remained standing, leaning against neighbouring trees.

Immediately after the felling the trees were placed in containers with water stained with red ink.[1]

The weather was each time warm with sunshine and a cloudless sky.

About 6 p.m. the stems were cut and examined.

The following annual rings participated in the water transportation:

Quercus robur and *Fraxinus excelsior* (ring porous):

1. Annual ring (under formation): All vessels.
2. — — : Most of the small and c. $^1/_5$ of the large vessels.
3. — — : C. one half of the small and a few of the large vessels.
4. — — : A few small vessels.

According to estimates roundly speaking 75 % of the total water transportation take place in the outermost annual ring.

Fagus silvatica, Acer pseudoplatanus and *Betula pendula* (diffuse porous):

Almost all vessels in all annual rings (up to 20). But the velocity of the water transportation decreases much inwards. It is 5 to 15 times greater in the outermost than in the innermost annual rings, comp. R. Hartig (1888a, p. 223) and Antevs (1914—17, p. 353).

After measurements and curves water transportation in the outermost annual ring is calculated at:

Fagus silvatica	10.4 %	of the total water transportation
Acer pseudoplatanus	9.1 %	- - - - -
Betula pendula	8.9 %	- - - - -

After these results and the figures in column 7 in Table XX the total water transportation in the middle of the day in a 20 cms thick stem with 5 mm wide annual rings may be estimated at:

Ring porous:		
Quercus robur	14.1	liter/hour
Fraxinus excelsior	9.1	—
Diffuse porous:		
Fagus silvatica	4.0	—
Acer pseudoplatanus	4.3	—
Betula pendula	4.0	—

[1] First experiments were made with a solution of methyl blue which Huber and Schmidt used (1936) in some of their experiments. The result was not, however, completely satisfactory as the colouring matter was strongly absorbed by the cell walls of the vessels and therefore took comparatively long time to enter the vessels. Diluted red ink rose considerably quicker.

We have too little information about the velocity of the flow at other hours of the day and night to undertake a calculation of the total transpiration during 24 hours.

HUBER and SCHMIDT (1936, Table 5) give some figures for the velocity of the flow in the evening in branches and stem. According to these figures the transpiration flow between 6 and 8 p.m. in a c. 20 cms thick stem with 5 mm wide annual rings may approximately be calculated at:

Ring porous:	
Quercus robur	1.1 liter/hour
Fraxinus excelsior	2.2 —
Diffuse porous:	
Fagus silvatica	2.7 —
Acer pseudoplatanus	1.4 —

From the calculations appears that in the middle of the day the transpiration flow is two to three times greater in the ring porous than in the diffuse porous species. In the evening it is on the other hand almost alike within both groups.

This seems to indicate, that the water transportation in the ring porous types shows a greater adaptability towards the much increased transpiration in the middle of the day than in the diffuse porous types. The reason must be sought in the much larger vessels, the strong concentration of the transportation tissue (chiefly the outermost annual ring), and a wide margin in the velocity of flow.

From the point of view of production it presumably means that the ring porous types[1] utilize the warm, sunny hours of the day relatively better than the diffuse porous (the stomata keep open longer?). Possibly it is the reverse in the hours of morning and evening.

XII. Comparisons.

1. Hardwoods.

In Table XXI the above main results are collected in a graphic summary of the anatomic-physiological differences among the hardwoods.

Compared with Figs. 5—8 it appears that the ring porous species differ from the diffuse porous by:

a) Much wider spring vessels and smaller and fewer summer vessels.
b) Much higher top yield in water transportation.
c) 75 % of the total water transportation take place in the outermost annual ring against only 9—10 % in the diffuse porous.

[1] The ring porous are all light trees (see DETLEV MÜLLER 1943, p. 166). After investigations by STÅLFELT (1924) and BOYSEN JENSEN (1932) the light leaves of the light trees may get a considerably higher production capacity by strong light (full daylight) than the leaves of the shade trees.

TABLE XXI. Graphic Summary of the Anatomica

1 Tree Species	2 Mean diameter of the vessels in spring wood mm.	3 Tissue length m.	4 Percentage relation between the total conductive cr. sect. area in summer and spring wood %	5 Water Transportation. Highest velocity the middle of the day at breast heigth m/hour	6 The water transportation in the outermost annual ring in % of the total water transportation %
Ring porous:					
Fraxinus excelsior	0.165	> 1	6	25.7	75
Quercus robur	0.161		7	43.6	
Ulmus glabra	0.127		26	6.0	
Diffuse porous:					
Carpinus betulus	0.045	< 0.5	34	1.25	—
Tilia cordata	0.036		38	—	—
Prunus avium	0.057		43	—	—
Fagus silvatica	0.039		44	1.09	10.4
Sorbus aucuparia	0.034		45	—	—
Corylus avellana	0.026		50	—	—
Alnus glutinosa	0.041		54	2.0	—
Acer pseudoplatanus	0.062		64	2.4	9.1
Aesculus hippocastanum	0.026		75	0.80	—
Betula pendula	0.060		81	1.6	8.9

The figures in column 3 are quoted after DETLEV MÜLLER (1943, Table 3).
The dates for leaf expansion in column 7 are quoted after BRUUN (1919).

d) Averagely later leafing (except in elm).
e) Shorter interval between bud break and complete leafing.
f) Shorter shoot extension period (if no repeated shoots are formed).
g) Much shorter interval between the commencement of wood formation at bud- and stem-base.
h) More active wood formation in May and June.

TABLE XXII. Graphic Summary of the Anatomical-Physiologica

1 Tree Species	2 Conduction Tissue. The mean cr. sect. area of the tracheids in spring wood mm^2	3 Percentage relation between the total conductive cr. sect. area in summer and spring wood %	4 Water Transportation. The highest velocity in the middle of the day at breast height m/hour
Picea abies	0.00088	34	(0.50)
Larix decidua	0.00114	46	2.1

* Short Shoot.

Physiological Differences among the Hardwoods.

7	8	9	10	11	12	13	14
Leafing and Shoot Extension			Periodicity of Wood Formation				
Mean date of leafing	No. of Days between bud break and complete leafing	Length of shoot extension period	No. of Days between beginning of wood formation at bud base and at breast height	At breast height wood formation begins the following no. of days		Relative annual ring formation per July 1.	Force-readiness in winter
				before bud break	after bud break		
	Days	Days	Days	Days	Days	%	
$^{5}/_{6}$	18	32	2	8	..	58	Difficult to force
$^{29}/_{5}$	15	28	2	6	..	44	
—	—	43	2	0—3	..	—	
$^{17}/_{5}$	28	—	9	..	7	—	
—	—	—	11	..	6	—	
—	—	(60)	19	..	15	—	
$^{11}/_{5}$	14	43	16	..	14	40	Difficult to force
—	—	52	16	..	11	—	
—	..	62	27	..	26	—	
$^{16}/_{5}$	25	70	35	..	35	47	Comparatively easy to force
$^{12}/_{5}$	24	65	29	..	23	38	
$^{9}/_{5}$	—	—	27	..	22	—	
$^{13}/_{5}$	24	87	32	..	31	40	

The growth periodicity of the ring porous types seems to be more autonomously determined and the growth to have a more marked optimum than in the diffuse porous types.

In the typically ring porous types (*Quercus robur* and *Fraxinus excelsior*) the buds, irrespective of temperature, do not begin to move till May. But then things also happen in quick succession. Leafing proceeds quickly, shoot extension terminates in the course of relatively short time, and in branches as well as in stem comparatively much wood is formed in May and June.

Differences between *Picea abies* and *Larix decidua*.

5	6	7	8	9
	Periodicity of Wood Formation			
Length of the shoot extension period	No. Days between inception of wood formation at bud base and at breast height	At breast height wood formation begins the following no. of days		Relative annual ring formation per July 1
		before bud break	after bud break	
Days	Days	Days	Days	%
58	8	5	..	50
(90)	6	..	36*	50

Outside the growing period the ring porous (*Quercus robur* and *Fraxinus excelsior*) are very difficult to force, cf. LAKON (1912) and KÜHN (1916).

The diffuse porous types are more sensitive towards the increase in temperature in spring. If the latter is mild the buds begin to swell already in March. But it takes a long time before the growth really increases. Leafing, shoot extension, and wood formation begin at a slow rate. Wood formation takes a long time before it spreads in basipetal direction. In the stem between one third and one half of the annual ring only is formed in May and June

Outside the growth period the typical diffuse porous (*Acer pseudoplatanus, Aesculus hippocastanum* and *Betula pendula*) are comparatively easy to force.

Among the diffuse porous *Carpinus betulus, Tilia cordata, Prunus avium* and *Fagus silvatica* are nearest the ring porous. Particularly *Fagus silvatica* has a few qualities in common with them. Its growth periodicity thus seems to be autonomously determined. It develops fairly late in spring. Its shoot extension period is relatively short. Outside the growth period it is very difficult to force, cf. JOHANNSEN (1906), HOWARD (1906), MOLISH (1908 and 1909), WEBER (1911), LAKON (1912), and KÜHN (1916).

There is some reason with DETLEV MÜLLER (1943, p. 165) to believe that the diffuse porous types phylogenetically are older than the ring porous ones. "Ring porous condition is a higher development and more specialised."

In the anatomy and physiology of the ring and diffuse porous types a certain adaptation may be traced to the climatic conditions under which the trees have their greatest distribution.

The ring porous species chiefly grow within the area of summer green forests of hardwoods[1] (see DENGLER (1930, Table I)). In the warmest part of this area (*Castanetum*) they are conspicuous: *Castanea, Quercus, Carya, Morus, Robinia* and *Ailanthus*. With HUBER and SCHMIDT (1936, p. 404) they may be considered as outposts in the warm and relatively dry border areas towards the steppes where on account of their greater top yield in water transportation it is easier for them to grow than the diffuse porous.

To the North and in direction from the marked continental towards the Atlantic climate the ring porous decrease in species and in dominance. At the same time the diffuse porous species spread and particularly those which are nearest the ring porous types. In the intermediate and northern parts of the area of the summer green forests of hardwoods (*Fagetum*) the beech (*Fagus*) and the oak (*Quercus*) are dominant with an intermixture of *Fraxinus, Ulmus, Tilia, Carpinus, Acer,* and *Alnus.*

In the northernmost and coldest part of the area the ring porous are less conspicuous.

Within the area of conifers in the cold climates only diffuse porous trees are on the whole to be found. At the polar forest border there are of hardwoods only *Populus trémula, Salix* and *Betula pendula* (typically diffuse porous species).

[1] In the tropical countries there are almost no ring porous trees, cf. FORSAITH (1926, pp. 83—84). On the whole the number of ring porous species is only small. CHALK (1937, p. 325) mentions that out of 1700 genera collected in Imperial Forestry Institute less than 3 % have species with ring porous wood.

2. Conifers.

In Table XXII a graphic summary is made of the most important anatomical-physiological differences between *Picea abies* and *Larix decidua*.

Physiologically they are nearest the diffuse porous species. They both show adaptation to a relatively cold and moist climate, which fact is confirmed through their distribution.

XIII. Summary.

1. During the resting stage in winter the cell walls of the cambium generally appear sharply and distinctly outlined under the microscope. In transverse sections the cell form is most often markedly rectangular.

2. When temperature rises in March or April the appearance of the cambium changes. The walls of the cells become semi-transparent and the protoplasm proceeds from a gel- to a sol-like condition. At the same time the radial cell walls begin to extend (size increment) and the cambial ring increases in width.

3. The change (the preliminary change of the cambium) begins at bud base end from here spreads in basipetal direction. In *Picea sitchenses* and *Pseudotsuga taxifolia* it starts at a mean temperature of 4° to 5° C. In *Pinus silvestris, Larix decidua, Picea abies, Betula pendula, Alnus glutinosa, Corylus avellana, Carpinus betulus, Ulmus glabra, Tilia cordata, Aesculus hippocastanum, Acer pseudoplatanus, Prunus avium* and *Sorbus aucuparia* it starts after a few warm spring days at the end of March or the beginning of April with a maximum temperature over 12° C. In *Fagus silvatica, Quercus robur* and *Fraxinus excelsior* the change in the cambium does not set in till the last half of April. In the latter species the time seems to be more autonomously determined than in the former.

4. When the cambium is in the preliminary change it is sensitive to frost.

5. One to four weeks after the change has started in the cambium cell division begins. It starts at bud base and from here spreads in basipetal direction.

6. In the ring porous species cell division begins at bud base one to nine days before bud break. In the diffuse porous species with considerable shoot extension before bud break (*Sorbus aucuparia, Acer pseudoplatanus, Aesculus hippocastanum* and *Prunus avium*) it starts up to a week before bud break; in the other diffuse porous at the earliest two days before bud break.

In conifers it begins five to fifteen days before bud break.

7. Cell division spreads quicker in basipetal direction in the ring porous species than in the diffuse porous and the conifers.

In the ring porous and the evergreen conifers cell division begins in the lower part of the trunk some days before or at the latest simultaneously with bud break. In the diffuse porous and *Larix decidua*, on the other hand, it does not begin till after the leaves (the short shoots in *Larix decidua*) are completely or partly expanded.

8. In the roots cell division only takes place when the temperature of the soil has reached up between 10° to 13° C.

9. The elongation growth of the roots precedes their growth in thickness.

10. The reason that cambial activity begins at bud base and from there spreads in basipetal direction is that growth hormones are formed in the buds of the trees when they begin to swell in spring. From the buds (and inflorescence) the growth hormones proceed down through the branch-, stem- and root-cambium and stimulate it to a resumption of growth.

11. There is reason to assume that the change in the cambium before its preliminary change is due to a beginning downward progress of growth hormones from the swelling buds.

12. In the young branches the main part of the annual ring is formed within the period when the liveliest shoot extension takes place.

13. The length of the wood formation period increases gradually from the young branches and down into the stem, and a relatively greater part of the annual ring is formed later in summer.

14. There is a difference in the course of the wood formation in the stems of the various species of trees. They may be divided into three groups:

Fraxinus excelsior: Wood formation is lively from the very start. About one half of the annual ring are formed in May and June. After July there is only slight wood formation.

Picea abies and *Larix decidua*: Wood formation is lively from the start as in *Fraxinus excelsior*. About half of the annual ring is formed in May and June. After July wood formation is not particularly active.

Betula pendula, Fagus silvatica, Alnus glutinosa, Acer pseudoplatanus and *(Quercus robur):* Some time often elapses before wood formation actually becomes active. Only between one third and one half of the annual ring is formed in May and June. On the other hand wood formation is very lively in August. Between one third and one fourth of the annual ring is formed in this month and during the first days of September.

15. The less the trees grow in thickness the earlier in summer wood formation declines. The reason may be sought in external as well as in internal nutrition-physiological conditions.

16. In well-grown trees wood formation in the stem terminates in the last half of August or the beginning of September.

17. In the roots wood formation often continues into October.

18. In April, May, June, and July there is a distinct positive correlation between wood formation and temperature.

19. Only in *Picea abies* can it be proved with certainty that protracted drought retards wood formation.

20. The growth in thickness (apposition) of the cell walls terminates two to four weeks later than the cell division.

21. In the ring porous species (*Quercus robur, Fraxinus excelsior,* and *Ulmus*

glabra) summer wood formation begins about mid-June, in beech at the end of June, in *Alnus glutinosa* about mid-July, and in *Picea abies* and *Larix decidua* about the beginning of July.

22. The diameter of the spring vessels is approximately three times larger in the ring porous than in the diffuse porous species.

23. The total conductive cross section area for spring and summer wood in sections is averagely about equally large in the ring porous and the diffuse porous species. In conifers it is four to nine times greater than in hardwoods.

24. There exists an almost inverse proportionality between the length of the shoot extension period and the difference between the total conductive cross section area of the vessels in spring and summer wood.

The difference between the distribution of the vessels within the annual ring, and thus the difference between spring and summer wood in hardwoods, may therefore partly be referred to a difference in the length of the period of the shoot- and leaf-expansion.

25. In the ring porous species (*Quercus robur* and *Fraxinus excelsior*) the water transportation in the outermost annual ring is in the middle of the day ten to thirty times greater than in the diffuse porous species (*Alnus glutinosa, Fagus silvatica, Acer pseudoplatanus* and *Betula pendula*).

26. The difference is due to the much greater velocity of flow in the ring porous species.

27. In *Picea abies* the water transportation in the outermost annual ring is in the middle of the day almost of the same size as in the diffuse porous species. In *Larix decidua* it is five to ten times greater.

28. In the ring porous species (*Quercus robur* and *Fraxinus excelsior*) the whole water transportation takes place in the four outermost annual rings. 75 % of the total water transportation, however, take place in the outermost annual ring.

29. In the diffuse porous species (*Fagus silvatica, Acer pseudoplatanus,* and *Betula pendula*) the water transportation takes place through many annual rings (over twenty). But the velocity of the flow is five to fifteen times greater in the outermost than in the innermost annual rings. Approximately 10 % of the total water transportation take place in the outermost annual ring.

30. In the middle of the day the total transpiration flow is two to three times greater in the ring porous than in the diffuse porous trees. In evening and morning it is on the other hand alike within the two groups.

From the view of production this presumably means that the ring porous utilize the warm and sunny hours about noon relatively better than the diffuse porous. In the hours of the morning and evening the case is probably reversed.

31. In the anatomy and physiology of the ring and diffuse porous species a certain adaptation may be traced to the climatic conditions under which the trees have their greatest distribution.

The ring porous have their chief distribution within the area of the summergreen hardwood forests. In the warm and dry regions of the latter they dominate

as they thrive better here than the diffuse porous owing to the higher top yield in the water transportation.

Towards the North and in direction from the Continental towards the Atlantic climate the ring porous decrease in species and dominance, and simultaneously the diffuse porous gain ground, in the first line those that are nearest to the ring porous types. Within the area of conifers in cold climates there are so to speak diffuse porous trees only.

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BY

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København
i kommission hos Ejnar Munksgaard
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1. Introduction.

The isle of Læsø lies in the northern part of the Kattegat between Jutland and Sweden. Apart from some higher dune areas in the northern and eastern part the level surface rarely exceeds 30 feet above the sea. The island is entirely built up of alluvial deposits, and most soils consist of sand or sand covered by a mor layer. More than half is not cultivated, being chiefly occupied by various dwarf shrub heaths, *Molinieta*, a number of different dune vegetations and salt marshes. The eastern part in the vicinity of the village Østerby is a narrow peninsula about five miles in the direction west-east and two miles from north to south (fig. 1). In this part less than a quarter is now cultivated and the influence of man in the uncultivated areas is very limited. Along the shore the vegetation may be almost entirely natural and thus very well suited for ecological research.

The Østerby region was visited by me in 1939 and 1948. In both years most importance was attached to observations of the vegetation rich in lichens which is developed on drift sand or sandy gravel behind the beach. Some of the results from 1939 were published in a previous paper (1941 b), which further contains some analyses of lichen heaths from the northernmost part of Jutland (the Skaw). The lichen-dune vegetation of the latter area was first studied by RAUNKIÆR (1913; see RAUNKIÆR 1934 pp. 332—338). Other analyses of lichen heaths on dune soils in different parts of Denmark are found in BÖCHER 1941 a, 1945, and 1947.

From the previous paper on the dune vegetation of Læsø (1941 b) we may summarize the following facts:

(1) Profile transects on various points on the north side of the peninsula from the beach to the closed dwarf shrub vegetation (the dune heath) reveal rather few zones owing to the low content of carbonates and the low pH values of the sand on the foreshore and the youngest dunes. The green fixed dune communities which in other parts of Denmark are frequently inserted between the white and the typical grey dunes with acid soils are absent or fragmentarily developed owing to insufficient supply of basic particles blown in from the sea shore. On the other hand the grey dune vegetation with abundant lichens and *Corynephorus canescens* covers large areas and varies very much. It is found on the old inner coastal dunes as well as on the inland dunes and in the blow-outs formed on the dune heaths.

(2) The lichen heath vegetation of the grey dunes comprises the following sociations:

(a) *Corynephorus-Cornicularia aculeata*-soc. frequently rich in *Polytrichum piliferum*. On acidic sand and gravel; frequent in blow-outs of the inland dunes, here succeeding a pioneer stage dominated by *Polytrichum*.

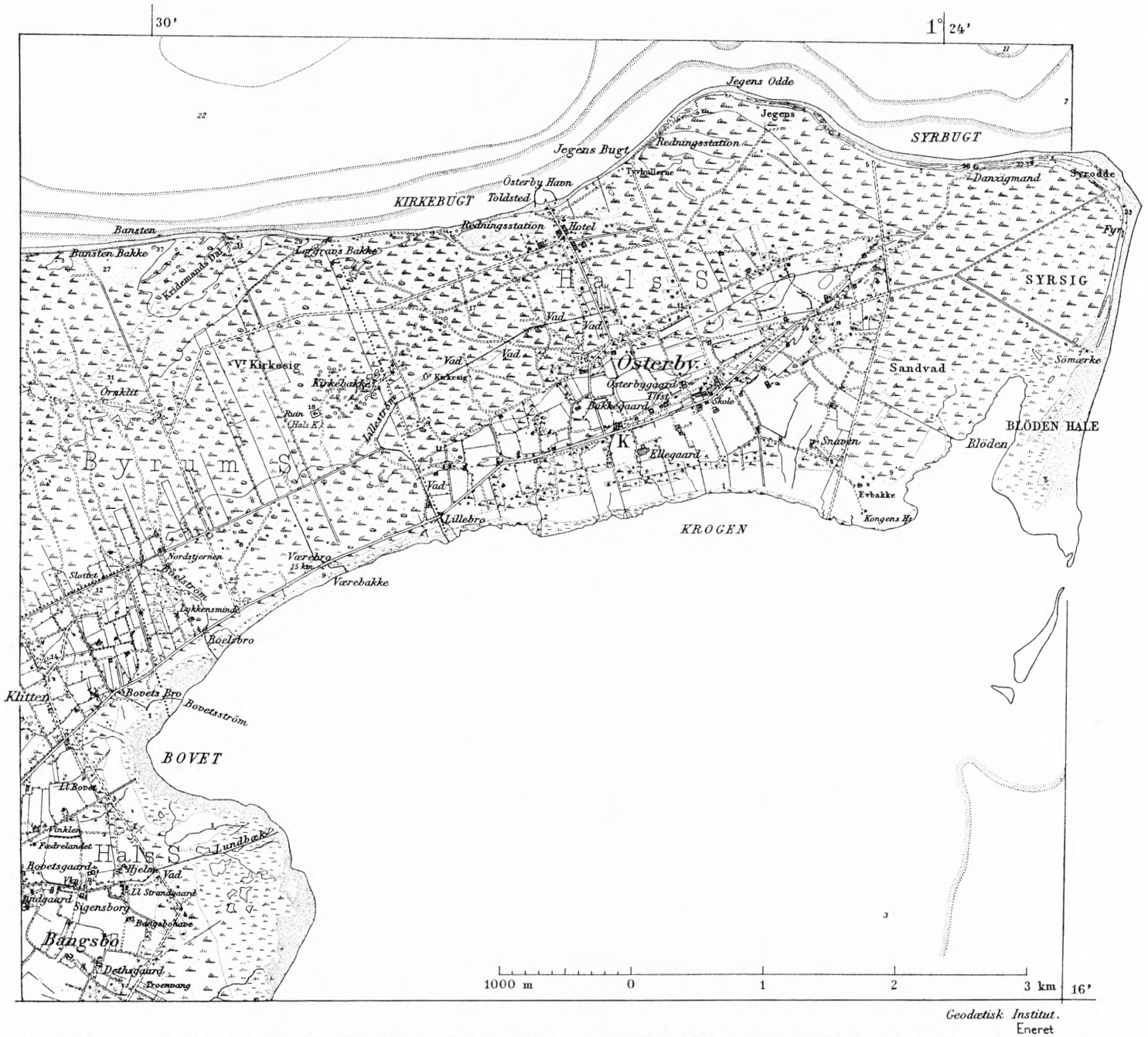

Fig. 1. Map showing the eastern part of the isle of Læsø (the Østerby peninsula). Most of the analyses of vegetation contained in the present paper were undertaken on the north side of the peninsula between Bansten Bakke and Syrodde.

(b) *Corynephorus-Cladonia destricta*-soc. On acid sand, as a rule exposed to wind, sometimes even in places where a slight removal of sand takes place. Occurs together with the preceding sociation or mixed with it. Many observations make a succession from a *Corynephorus-Cornicularia*-soc. to a *Corynephorus-Cl. destricta*-soc. very probable.

(c) *Corynephorus-Cladonia rangiformis-* and *furcata*-sociations. These sociations are mainly found on the coastal dunes, in places with moderately acid soil. In similar places a *Corynephorus-Cladonia alcicornis*-soc. occurs. The latter is furthermore found as very small patches in inland dunes.

(d) *Corynephorus-Cladonia mitis*-soc., the most important type of lichen heath dominated by *Cladinae*, in particular *C. mitis*, but also containing *C. sylvatica*, *tenuis*, *impexa*, and *rangiferina*. *Carex arenaria* and *Ammophila* sometimes abundant. The type occurs as the typical grey dune vegetation on old coastal dunes and inland dunes. The lichen carpet is very dense. The soil is acid with a somewhat higher content of organic matter than in the preceding sociations. Where the organic content increases further, as in the oldest parts of the peninsula, *Corynephorus* is subordinate, while *Festuca ovina* is most dominant, forming a dense *Festuca ovina-Cladina*-soc.

(e) *Corynephorus-Cetraria nivalis*-soc. occurs together with the *Cladina*-type, but prefers less protected places where the competition with the species of *Cladina* is less intense. Lichen heaths with *Cetraria islandica* as a dominant, on the other hand, are mainly found on somewhat sheltered spots.

The floristic composition of these types of lichen heath appears from Tables 2, 8, and 9 in BÖCHER (1941 b).

(3) Blow-outs are formed in the white and grey dunes as well as on the dune heath (*Calluna-Empetrum*-heath) farther inland. Where the blow-outs are surrounded by lichen heath or *Calluna-Empetrum*-heath a number of successions from open sand to lichen heath and further to dwarf shrub heath may take place. In many blow-outs the bottom is soon colonized by *Empetrum*, *Salix arenaria*, and *Calluna*. From these central heath patches where the soil may be less dry, the heath vegetation expands and invades open sand as well as lichen heath on the slopes of the hollows, but it is hardly able to settle on the driest spots and those parts of the slopes where the wind erosion is particularly strong.

(4) On the border between the *Calluna-Empetrum*-heath and the lichen heath of the grey dunes a similar succession may take place resulting in a formation of a dwarf-shrub subclimax vegetation. In many cases, however, a degeneration of the dwarf shrubs occurs. In particular *Calluna* is inclined to die, thus forming spaces (destruction hollows or areas) which are colonized by lichens or *Empetrum*. In certain cases blow-outs may be formed where the dwarf shrubs have disappeared.

During the author's stay on Læsø in 1939 some permanent quadrates were selected for a close study of the successions. In some cases the degree of cover per square metre was estimated for all species by means of the HULT-SERNANDER scale and the distribution of the dwarf shrubs and the lichen heath mapped. The selected areas were marked out by means of four concrete poles in the corners (fig. 4). In 1948 the permanent quadrates were reinvestigated. The results of these reinvestigations as well as a number of supplementary studies of the lichen heaths and of the succession of the vegetation leading from embryonal dune to lichen heath are contained in the present paper.

2. The succession from embryonal dune vegetation to lichen heath ("grey dune" vegetation).

The Østerby peninsula ends in a spit of land called Bløden Hale (fig. 1). In the southern part of this spit as well as on the small islet of Knotten south of the point of Bløden Hale the dunes are very young and low.

Fig. 2. Large newly formed area on the southernmost part of Bløden Hale. Low dunes covered by *Agropyrum repens* and *Salsola kali*. *Ammophila* is invading some of the dunes. T.W.B. phot. 1948.

They are formed on a very broad sandy beach which constantly increases owing to the supply of fresh sand being washed ashore by the south-going current. The first stages are characterized by the occurrence of plants which are halophilous and demand an admixture of manure, in particular from dead seaweeds.

(1) *Suaeda maritima* stage on saline and more or less manured and moist sand.

(2) *Salsola kali-Cakile maritima* stage on somewhat saline and manured sand, which is drier. Subordinate species are *Atriplex hastata, A. sabulosa, Suaeda maritima, Agropyrum repens, A. junceum, Agrostis stolonifera, Plantago maritima,* and *Glaux maritima.*

(3) *Agropyrum-Elymus* stage on very low, embryonal dunes, repeatedly subject to changes during springtides. Soil almost as at the preceding stage, but less manured, whenever *Agropyrum junceum* dominates. *A. junceum*- and *Elymus*-sociations are only developed on the islet of Knotten, not on the southernmost part of the spit, which may be due to the cattle grazing there. On the other hand, the southern point of the spit has large areas covered with *Agropyrum repens*-soc. (fig. 2) containing *Cakile* and *Salsola*, the latter sometimes in great abundance.

(4) *Ammophila* stage. *Ammophila* invades low, young dunes which may be comparatively stabilized and consist of neutral sand with a very low content of salt or manure. pH in the soil was measured at 6.6—6.8 and the electrical conductivity varied between 56 and 58.[1] Frequent: *Honckenya peploides*. Scattered: *Elymus, Agropyrum junceum, A. repens, Festuca rubra, Eryngium maritimum, Circium vulgare, C. arvense, Taraxacum* sp., and *Carex arenaria*. (See also fig. 2).

Stages 1—4 are the only ones occurring on the islet of Knotten and the southernmost part of Bløden Hale. In order to follow the succession a number of squares forming a belt transect from the eastern to the western beach of the islet were analyzed. The line was marked in 1939 by a concrete pole and a large wooden pole. Unfortunately both poles had disappeared in 1948. The concrete pole had probably been covered by drift sand and the wooden pole set adrift by the sea. Although the exact position of the transect could not be localized again it was clear that the area occupied by *Ammophila* had been enlarged considerably, thus giving evidence of the succession *Agropyrum-Elymus* stage → *Ammophila* stage.

Evidence of successions from stages like (1)—(2) to *Agropyrum-Elymus* stages and further on to an *Ammophila* stage was obtained by observations in another part of Denmark (Korshage, cf. Böcher 1952).

From the southern point of Bløden Hale and northwards the land becomes older and older and at the same time the dunes grow higher. One mile from the point they reach a height of 7 feet and at the lighthouse near the northeast corner of Læsø (Syrodde) 23 feet. The highest dunes (38 feet) are found west of Syrodde and on Jegens Odde. With increasing age the soil changes from circumneutral to acid reaction and a leaching of the sand becomes more pronounced. In the vegetation these changes lead to a succession from white to grey dune vegetation. The belts found from south to north on the Bløden Hale evidently correspond to successional stages:

(5) *Carex arenaria—Festuca rubra—Ceratodon* stage. The invasion of *Carex arenaria* or *Festuca rubra* frequently results in the formation of a ± closed vegetation which, however, in the first stages frequently lacks cryptogams. Several sociations belong to this stage, thus (a) *Ammophila*-soc. with *Festuca rubra, Jasione montana, Hypochoeris radicata,* and *Viola tricolor*; (b) *Carex arenaria-Honckenya-Galium verum*-soc.; (c) *Carex arenaria*-soc. sometimes with abundant *Eryngium maritimum* and patches of *Galium verum*; (d) *Festuca rubra-Galium verum*-soc. with *Bromus mollis,*

[1] The figures given are the rest-conductivity, $K_{20°} - (K_H{}^+)_{20°} \cdot 10^6$, (specific conductivity at 20° C from which the conductivity of the hydrogen ions is subtracted, cf. H. Sjörs 1946).

Cerastium semidecandrum, Sedum acre, Poa pratensis, Agrostis tenuis, and *Potentilla anserina.* (e) almost as the preceding but with *Ceratodon, Tortula ruralis,* and *Brachythecium albicans*; (a) occurs mainly on dune slopes while (b)—(e) cover the more or less level areas between the dunes. The variation in the vegetation undoubtedly is a result of rather important soil differences. *Carex arenaria* seems to indicate a soil which is poor in easily soluble salts while *Festuca-Galium-Sedum acre,* etc., may be connected with richer soils. In a place with abundant *Carex arenaria* pH was 6.2 and the conductivity value 18. Another spot dominated by *Festuca-Galium* showed a pH-value of 6.1 and a conductivity value of 58, thus a value of the same magnitude as that found at Stage 4.

(6) *Hypnum cupressiforme-Cladonia* stage. This stage may follow stages with *Ceratodon* or *Tortula-Brachythecium albicans. Hypnum cupressiforme* is dominant together with *Festuca rubra,* but it is still possible to find weak specimens of *Brachythecium albicans.* Characteristic is the frequent occurrence of a number of lichens as well as *Dicranum scoparium, Rhacomitrium canescens, Corynephorus canescens, Hypochoeris radicata, Hieracium pilosella, Teesdalea nudicaulis, Trifolium arvense* and *Rumex acetosella.* Among the lichens the following are most important: *Cladonia alcicornis* (sometimes dominant), *C. furcata* (sometimes dominant), *C. rangiformis, C. fimbriata, C. chlorophaea, Cornicularia aculeata* and *Peltigera canina. Cladonia mitis* is very rare. There are also at this stage several sociations. The *Festuca-Galium verum-Hypnum cupressiforme*-soc. occurs on somewhat less dry ground than the *F. rubra-Cladonia alcicornis-furcata*-soc. pH in these sociations was measured to be 5.5 and 5.3 and the rest conductivity to be 38 and 32.

(7) *Cladina*-stage. The first patches dominated by species of the *Cladina* group occur a little more than a mile north of the southern point of Bløden Hale. The most important lichens are *Cladonia mitis* and *Cornicularia aculeata.* Of secondary importance are *Cladonia sylvatica, rangiferina, impexa, uncialis, gracilis, pityrea, chlorophaea, furcata, alcicornis, Cetraria islandica, nivalis* (very rare), *Peltigera canina, P. rufescens* and *malacea. Corynephorus* and locally *Empetrum nigrum* may dominate. Characteristic are further *Calluna, Juniperus, Viola canina, Hieracium umbellatum, Armeria vulgaris,* and *Aira praecox.* At this stage species like *Galium verum, Trifolium arvense, Agrostis tenuis* and *Brachythecium albicans* may still occur indicating a moderate poorness of the soil. pH and conductivity were measured in an *Ammophila-Corynephorus-Cladonia mitis-Cornicularia*-soc. and in an *Empetrum-Cladonia mitis-impexa*-soc. The pH values were 5.1 and 5.7 and the rest conductivity values 40 and 36, thus figures about the same level as at the preceding stage.

(8) *Calluna-Empetrum-Cladina* stage. At this final stage the heath invades the *Cladina*-vegetation. A stable subclimax heath may result, in particular on somewhat protected or less dry spots. In exposed or very dry places a degeneration of the dwarf shrubs may take place and frequently heath and lichen-vegetation are almost at equilibrium (see below). Particularly characteristic of this stage is a number of lichens occurring on old dead or dying twigs of the dwarf shrubs (*Parmelia physodes, Cetraria glauca, C. chlorophylla, Usnea hirta*) or on the ground where *Calluna* (or *Empetrum*)

have disappeared: *Cladonia glauca* and *C. floerkeana*. From this stage which is reached at Syrodde (the northeast corner, cf. fig. 1) there are three soil analyses giving the pH-values 4.3, 4.6, and 5.2 and the rest conductivity values 15, 30, and 14. These values are in good agreement with those found in still older vegetations on the Østerby peninsula and therefore this stage seems to constitute a termination of more or less complete stoppage also with regard to the soil development. There is further good agreement with the pH and conductivity values from *Corynephorion* and related communities in South Sweden (Andersson & Waldheim 1946).

The succession of mosses and lichens described above reminds highly of that mentioned by Richards (1929) from Blakeney Point in Norfolk. According to Richards the first invaders are *Brachythecium albicans*, *Ceratodon* and *Tortula*. Later settlers are *Cornicularia aculeata* and *Cladonia furcata* and finally *Cladonia sylvatica*.

3. The succession from lichen heath to dwarf-shrub heath.

This succession was studied in particular on Jegens Odde, the northernmost part of the Østerby peninsula (cf. fig. 1), on two permanent quadrates (I—II). On both quadrates the vegetation was mapped. In the large Quadrate II a system of connected squares each of 1 square metre were laid down and within these the degree of cover was estimated for all species. The analyses were made in 1939 and 1948.

Quadrate I (fig. 3). This quadrate was placed on a spot where *Calluna* had formed a heath patch surrounded by lichen heath (*Cladina* heath). The spot is seen on fig. 8 in Böcher 1941 b. In 1939 the southeast corner of the *Calluna* patch was bordered by an *Empetrum* patch, which seemed to enlarge its area fairly rapidly. The *Calluna* patch itself seemed also to be enlarging, but at the same time the *Calluna* had died away from three central areas and formed three enlarging rings. In the three destruction areas a colonization of lichens and *Empetrum* took place. The spot seemed particularly interesting as enlarging and dying-away of *Calluna* and competition between *Calluna* and *Empetrum* could be observed simultaneously there. In 1948 a considerable extension of the *Calluna* rings as well as of the *Empetrum* patches could be recorded (see fig. 3). The system of *Calluna* measured 4×2.3 m in 1939 and 5×2.8 m in 1948. The *Empetrum* patches inside the *Calluna*-area were considerably enlarged and had been able to gain a foothold in areas occupied by living *Calluna*. *Empetrum* shoots began bridging two of the destruction areas (B—C in fig. 3). Other *Empetrum* shoots from the large patch in the southeast corner of the quadrate tried to bridge the *Calluna* ring. The flora in the destruction areas was not considerably changed. This appears from analyses of Areas B and C:

1939: On the ground: *Cornicularia aculeata*, *Cladonia floerkeana*, *coccifera* (?), *glauca*, *furcata*, *destricta*, *alcicornis* (the latter only in Area C) and more scattered *C. mitis*, *impexa*, *Hypnum cupressiforme*, *Corynephorus canescens*, and (only Area C) *Galium verum*. On old or dying twigs of *Calluna*: *Parmelia physodes*, *Cetraria glauca*, and *C. chlorophylla*.

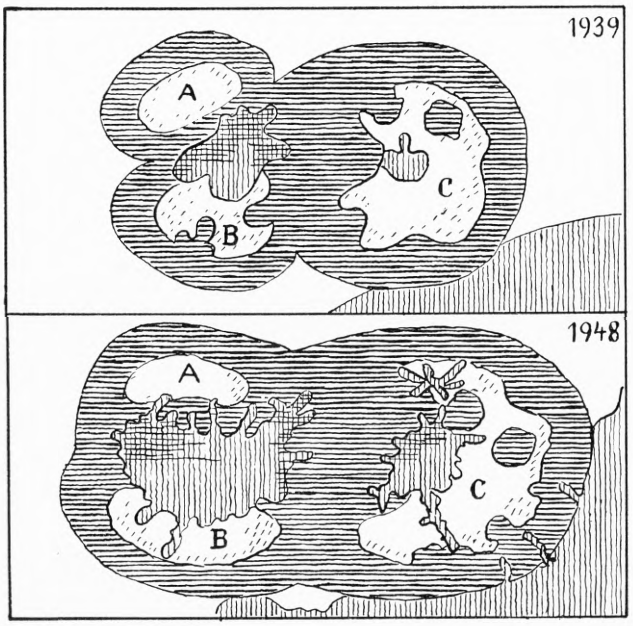

Fig. 3. Permanent Quadrate I (6 × 3 m) showing the development of a system of *Calluna* rings and *Empetrum* patches. Vertical hatching: *Empetrum*. Horizontal hatching: *Calluna*. Interrupted oblique hatching: *Parmelia physodes* on old twigs of *Calluna*. No hatching: *Cladina* mat. A.B.C. three destruction areas, cf. text.

1948: Additional plants in Area B not observed in 1939: *Cladonia uncialis, Usnea hirta, Dicranum scoparium, Hieracium umbellatum,* and *Lotus corniculatus.* Additional plants in Area C.: *Cladonia tenuis, uncialis,* and *Hieracium umbellatum.* Not refound: *Hypnum cupressiforme, Cl. coccifera* (?).

The centrifugal growth of *Calluna* reminds of the fairy-ring formation of different macromycetes. It seems probable that *Calluna* in the course of years makes the soil unfavourable for itself and, therefore, it can only thrive and flower in the periphery of the rings. In inland heath districts of Jutland *Calluna* generally dies away after a period of 30 years. This disappearance of *Calluna* may also be a result of changes in the soil produced by the plant itself. At all events it takes very long time before new *Calluna* plants appear on the spots or within such enlarging destruction areas as those in Quadrate I, where seedlings of *Calluna* were absent in both years of observation. On the other hand young *Calluna* plants occurred in several places outside the rings in the *Cladina* carpet. *Empetrum* may be less particular with regard to the soil and this seems to explain its ability to invade the destruction areas of *Calluna*. In addition to the two plants observed in 1939 a third plant occurred in 1948 in the northern corner of destruction area C. (Cf. fig. 3).

Quadrate II (figs. 4—6). This large quadrate was subjected to a more detailed analysis. From the mapping of the vegetation the following facts appear. In 1939 the eastern part of the quadrate (4—8, c—g) was occupied by a wide *Calluna*-ring with a large central *Empetrum* patch. The resemblance to Quadrate I was great,

but the stage seemed much more advanced. The ring was closed no longer; in the northeast corner (8 c—d) and at another point (7 f) *Empetrum* had broken through it or had filled out a gap in it. In 1948 the *Calluna*-ring was breaking up into small isolated parts. In some of these the *Calluna* shoots were almost hidden in the vigorous

Fig. 4. Permanent Quadrate II in the grey dune areas at the point Jegens Odde. A vertical line through the middle of the picture cuts two of the corner pegs (1 g to the southwest in the foreground, 8 a behind, cf. figs. 5—6). Quadrate III is to the right of the blow-out in the background in the higher coastal dunes. T.W.B. phot. 1948.

Cladina-mat (e. g. 6 c), in others the *Calluna* shoots seemed able to compete with the lichens. The situation in 1948 may probably show the final stage of the development of the *Calluna*-ring. Future investigations will probably demonstrate the complete disappearance of it.

In the squares 6—7, b—c, a strong *Calluna* plant occurred in 1939. This plant had been able to enlarge its area in spite of the vigorous lichen mat surrounding it. Another young, very small plant in 3 a perished. If such plants succeed in competing

with the lichens they will undoubtedly be starting points of larger *Calluna* patches which later enlarge and finally die away in the central parts.

A very intricate system of expanding *Calluna*-patches occurred 1939 in Squares 1—4, e—g. The individual patches merged to some extent and some of them

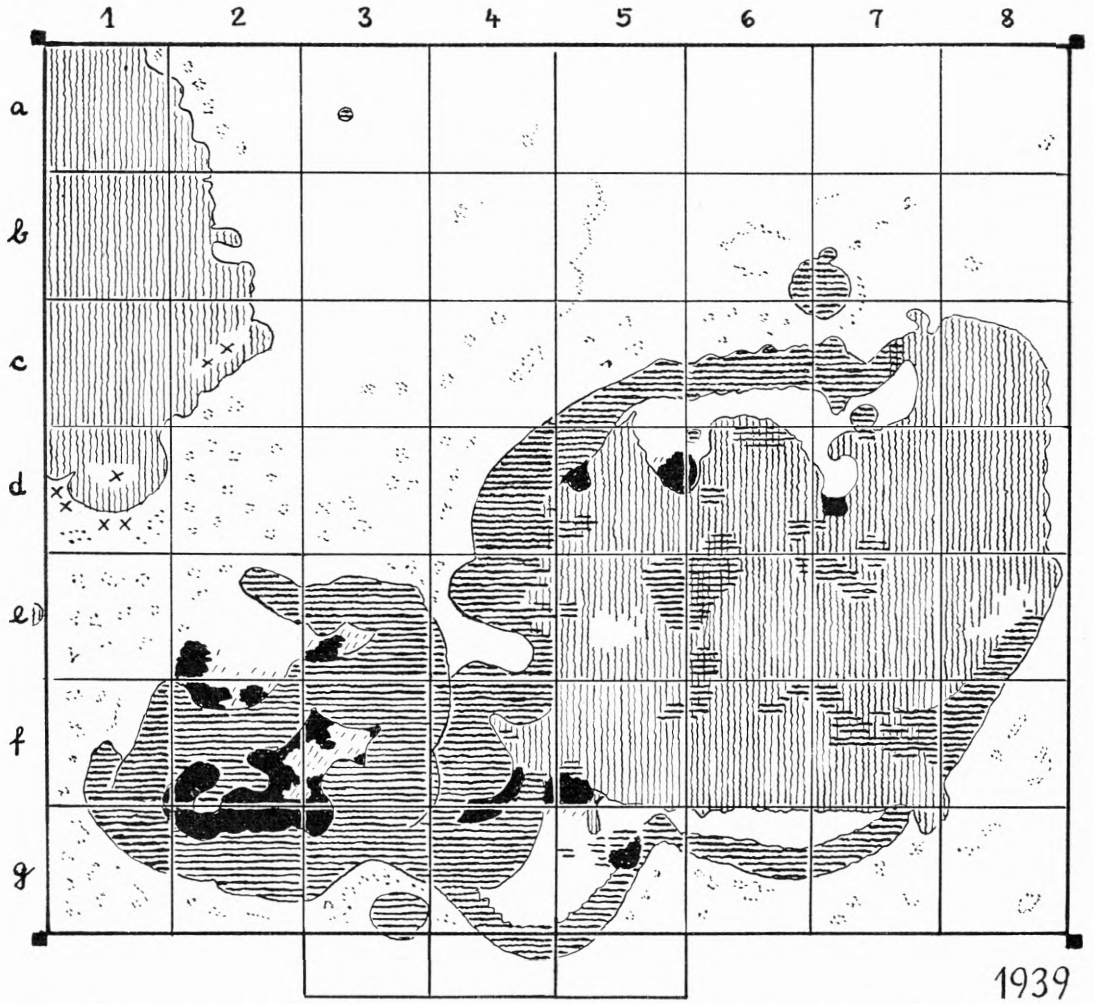

Fig. 5. Permanent Quadrate II in 1939, showing the grid and the distribution of the same species or communities as in fig. 3. Black: dead *Calluna*, × : dead *Empetrum*. Small dots: open sand spaces in the *Cladina* mat. Other signatures cf. fig. 3.

had central destruction areas which also merged. From the observations made in 1948 it became evident that one of these vigorous *Calluna* patches (in 2—3 f) had been able to invade an old destruction area of another *Calluna*-patch, thus showing that the rule mentioned above is not without exceptions or that it must be confined only to apply to seedlings of *Calluna*, which also were missing in all destruction areas in Quadrate II.

Two large *Empetrum* patches could be studied in the quadrate. One of them was surrounded on all sides with *Cladina* heath, but only the eastern part of it got inside (Squares 1—2, a—d). The other, as already mentioned, had developed in an old destruction area of a *Calluna* patch. The growth of the first *Empetrum* patch

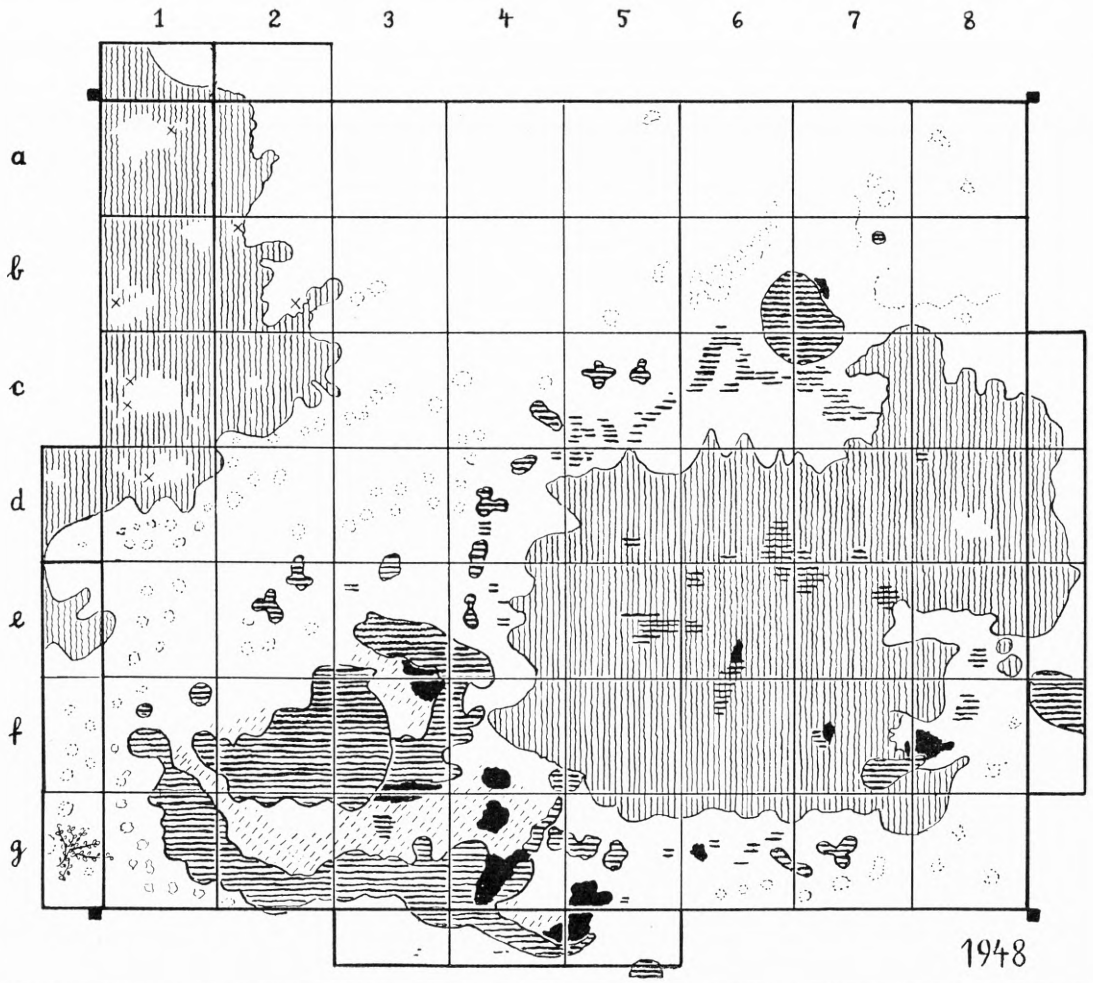

Fig. 6. Permanent Quadrate II in 1948. In 1 g a specimen of *Salix arenaria* has just got a shoot inside. More vigorous *Calluna* areas have contours whereas *Calluna* almost hidden in the *Cladina* mat is without a contour. Otherwise as in fig. 5.

during nine years was not very impressive, and it was evident that the shoots in 1948 were more scattered and that some small openings had appeared in the patch which to a great extent had been occupied by *Cladina*. The patch which first was surrounded by a *Calluna* ring showed an interesting divergent behaviour. Those parts which developed behind the extending *Calluna*-ring were clearly checked while those parts which in 1939 had broken through the ring generally showed more progress (see 8 c—d, 7—8 f—g) although a slight retrogression could be recorded in parts of 8 c.

Table 1 contains a summary of all occurrences and covering values in the two years of observation. The first three columns concern the whole permanent quadrate, the last two give the constancy percentage and average covering for ten selected *Cladina* heath squares (3 abc, 4 ab, 5 ab, 6 a, 7 a and 8 a) and ten dwarf-shrub heath squares (2 f, 3 f, 4 f, 5 ef, 6 def, 7 ef). Owing to the subjective moment in the determination of the degree of covering only large differences in covering values can be regarded as significant. On the other hand rather small differences between the two years with regard to occurrences or constancy must be considered significant. A considerable decline for *Ammophila, Corynephorus, Festuca rubra, Hypochoeris radicata, Jasione, Cladonia impexa, C. rangiferina,* and *Cornicularia aculeata* can be established and simultaneously an increase for *Hieracium umbellatum, Empetrum, Cladonia mitis, C. gracilis, Cetraria islandica, C. chlorophylla, Parmelia physodes* and the bryophytes. A moderate decrease in covering is found for *Calluna vulgaris* in the dwarf-shrub squares, a fact which corresponds very well to the more luxuriant growth of the epiphytes on old *Calluna* twigs, especially *Parmelia physodes.* The total number of occurrences in 1939 (662) is only slightly higher than that in 1948 (635) a fact which in particular may be connected with the decrease in occurrence of *Ammophila, Corynephorus,* and others. The decrease for *Ammophila* and *Galium verum* and the increase of the bryophytes may be results of a change in the soil complex (increase in acidity) while the decrease for *Corynephorus, Hypochoeris, Jasione,* and perhaps *Carex arenaria* may be connected with climatic conditions (cold winters) during the passed nine years (see below p. 16).

From the year 1939 we have a pH measurement from the soil underneath the *Cladina* mat in Quadrate II. The value (5.1) is higher than that from the same vegetation in 1948 (4.6). A soil sample from a place with degenerating *Calluna* collected in 1948 proved to be very different from that of the *Cladina* carpet the same year. Apart from its higher content of organic matter it was more acid (pH 3.9), but otherwise its conductivity value even after subtraction of the conductivity of the hydrogen ions was comparatively high (68 as against 30 in the soil under the lichen carpet).

The most important fact which appears from the investigation of Quadrate II is the very limited progress of the dwarf-shrub heath taken as a whole. The total covering for the two dwarf shrubs is 184 (1939) and 202 (1948) thus giving a difference of 18, which is hardly sufficient for a demonstration of an advance of the *Calluna-Empetrum* heath. As moreover a number of lichens have increased in frequency it seems in this case more adequate to speak about an equilibrium between lichen heath and *Calluna-Empetrum* heath. This is very interesting and gives an explanation of the apparent stable arrangement of the vegetational zones along the sea. The typical "grey dune"-vegetation (lichen heath) almost always occupies a zone between the white dunes or green fixed dune-communities and the dwarf-shrub heath. In certain cases the dwarf shrubs may invade lichen heath and fairly rapidly change it into a dwarf-shrub heath; with decreasing distance from the beach this advances more and more sluggishly and finally the succession may stop or go the other way when sometimes the lichen mat recovers lost ground. In this connection it may be mentioned

TABLE 1.

Permanent Quadrate II	1939					1948					
	Nos. of occurrences (max: 56)	Sum of covering values[1]	Highest covering value[2]	Constancy per cent and average covering; lichen heath	Constancy per cent and average covering; dwarf-shrub heath	Nos. of occurrences (max: 56)	Sum of covering values[1]	Highest covering value[2]	Constancy per cent and average covering; lichen heath	Constancy per cent and average covering; dwarf-shrub heath	
Ammophila arenaria	48	79	3	**100** 2.4	70 1	27	31	2	**80** 1	10 1	>
Corynephorus canescens .	37	49	3	**100** 1	0	14	14	1	30 1	0	>
Festuca rubra	10	10	1	70 1	0	6	6	+	10 1	10 1	>
Carex arenaria	56	87	3	**100** 1.3	**100** 1.4	55	59	2	**100** 1.1	**100** 1.1	>
Hieracium umbellatum ..	38	38	1	**100** 1	50 1	41	52	2	**100** 1.7	20 1	<
Hypochoeris radicata ...	29	29	1	**100** 1	0	7	7	1	0	0	>
Jasione montana	19	19	1	50 1	0	12	12	1	10 1	0	>
Galium verum	13	13	1	0	50 1	9	9	1	0	20 1	>
Plantago maritima	0	0	—	0	0	1	1	+	0	0	(<)
Calluna vulgaris	32	91	5	10 1	**100** 3.2	33	81	5	0	**90** 2.6	>
Empetrum nigrum	30	93	5	0	**80** 4.1	37	121	5	20 1	**80** 4.9	<
Viola canina	5	5	+	10 1	0	5	5	1	10 1	10 1	—
Salix arenaria	0	0	—	0	0	1	1	+	0	0	(<)
Sum...	317	513				248	399				
Cladonia mitis — sylvatica — tenuis [3]	56	207	5	**100** 4.2	**100** 2.6	56	218	5	**100** 4.7	**100** 2.5	(<)
— impexa	35	38	2	30 1	**80** 1.2	27	27	1	20 1	70 1	(>)
— rangiferina	52	103	5	**100** 3.7	70 1	44	80	5	**100** 3	20 1	>
— furcata	1	1	+	0	0	2	2	+	0	0	—
— gracilis	29	29	1	40 1	20 1	36	36	1	50 1	40 1	<
— uncialis	24	24	1	30 1	20 1	20	20	1	10 1	0	(>)
— destricta	4	4	1	0	0	4	4	1	10 1	0	—
— cornuta	0	0	—	0	0	2	2	+	0	0	(<)
— coccifera	2	2	+	0	0	8	8	+	0	0	<
— floerkeana	7	7	1	0	20 1	12	12	1	0	30 1	<
— fimbriata	3	3	+	0	10 1	5	5	+	10 1	10 1	(<)
— chlorophaea ...	18	18	1	10 1	40 1	16	16	+	20 1	20 1	—
— pityrea	0	0	—	0	0	1	1	+	0	0	(<)
— glauca	15	15	1	20 1	20 1	17	17	1	30 1	30 1	(<)
— verticillata	0	0	—	0	0	2	2	+	0	0	(<)
— alcicornis	12	12	1	10 1	0	11	11	1	0	0	—
Cetraria nivalis	9	12	2	0	0	8	10	2	0	0	—
— islandica	3	3	1	0	0	8	9	2	0	10 1	<
— glauca	11	11	1	0	30 1	11	11	1	0	40 1	—
— chlorophylla ...	1	1	+	0	0	7	7	+	0	30 1	<
Cornicularia aculeata ...	41	55	2	60 1.1	30 1	34	37	2	50 1	0	>
Parmelia physodes	18	18	1	0	50 1	29	35	3	0	**80** 1.4	<
— subaurifera	0	0	—	0	0	2	2	+	0	0	<
Parmeliopsis ambigua ...	0	0	—	0	0	1	1	+	0	0	(<)
Usnea hirta	2	2	+	0	10 1	2	2	+	0	10 1	—
Evernia prunastri	0	0	—	0	0	1	1	+	0	10 1	(<)
Sum...	343	565				366	575				
Dicranum scoparium ...	2	2	1	0	0	13	13	1	10 1	30 1	<
Hylocomium schreberi ..	0	0	—	0	0	1	1	+	0	10 1	(<)
Hypnum cupressiforme ..	0	0	—	0	0	7	7	+	0	40 1	<
Sum...	2	2				21	21				

[1] In the calculation the covering values + (the species only just present) and 1 (covering below $^1/_{16}$ of the square) have both been reckoned as 1.

[2] Covering scale according to Hult-Sernander: 5 (covers more than $^1/_2$ of the square, 4 (covering between $^1/_2$ and $^1/_4$ of the square), 3 (between $^1/_4$ and $^1/_8$), 2 (between $^1/_8$ and $^1/_{16}$), 1 (below $^1/_{16}$), + only just present in a single specimen and with an extremely low covering.

[3] Mainly typical *C. mitis, C. sylvatica* occurring much scattered and *C. tenuis* only intermixed with the other *Cladina* species in a few squares.

that *Cladina*-species can invade the destruction areas which are first colonized, in particular by *Cladonia floerkeana* and *glauca*. This happened in the northern corner of Area C in Quadrate I, where in 1948 a vigorous *Cladina*-mat was developing.

4. Lichen-heath vegetations in relation to sand supply and sand removal by the wind.

Heavy sand accretion as well as strong erosion will destroy any type of lichen heath, whereas more moderate covering or wind influence will lead to ecologically different types of lichen heath. In the dunes or gravelly flats along the north coast of the Østerby peninsula both extremes occur.

On the point Jegens Odde a special study was made of the influence of sand covering. In 1939 a permanent quadrate (No. III) was established immediately behind the higher "white" sea-coast dunes (see fig. 4 in the background). West of the quadrate there were a large and a small blow-out from which sand was carried away and deposited more easterly. The quadrate, which was 25 square metres included two vegetational units. The ten northernmost and the five westernmost square metres were occupied by an *Ammophiletum* with scattered lichens (in particular *Cladonia mitis, sylvatica,* and *Cornicularia aculeata*), whereas the southeast corner had more the character of a lichen heath (Table 2). Although the lichens obtained rather high covering values it was always possible to see the sand between the individuals. In 1948 the small blow-out west of the quadrate had expanded in an easterly direction and consequently the sand covering had gradually become severer. Table 2 gives a number of values showing a number of minor changes which undoubtedly mainly are the results of the increased sand supply. The lichens seem to have difficulties in keeping up with the covering; only vigorous podetia of *Cladonia mitis-sylvatica* or vigorous specimens of *Cornicularia* hold their own. On the other hand the increasing sand supply had been of advantage to *Festuca rubra, Carex arenaria, Hieracium umbellatum,* and perhaps *Viola canina*. The decrease for *Corynephorus* may be due to frost during the very cold winters 1940—42. In Rørvig in North Zealand this effect was followed more closely in the same couple of years and it was quite evident there that this species in 1948 had not recovered its old frequency from before the severe winters. This weakening influence of heavy frost agrees with the suboceanic distribution of *Corynephorus,* and the decrease for other suboceanic species (*Hypochoeris radicata, Jasione*) in Quadrates II—III may further accentuate this connection. It is not probable that the sand itself should weaken *Corynephorus*. This species will endure a much stronger sand covering by sending new shoots up through the sand (Warming 1909 fig. 66). It is surely a somewhat acidophilous plant, but the fresh sand from the blow-outs is moderately acid (pH 5.0—6.4, mostly about 6.0) and may thus be very suitable for it.

In 1939 pH in sand from the quadrate was found to be 5.9 and in 1948 the same figure was recorded in the northern part (with few lichens), while a pH of

TABLE 2.

Permanent Quadrate III	1939					1948					
	No. of occurrences (Max: 25)	Sum of covering values	Highest covering value	Constancy per cent and average covering. Northern area	Constancy per cent and average covering. Southern area	No. of occurrences (Max: 25)	Sum of covering values	Highest covering value	Constancy per cent and average covering. Northern area	Constancy per cent and average covering. Southern area	
Ammophila arenaria	25	66	4	**100** 3.1	**100** 2.3	25	66	5	**100** 3.8	**100** 1.7	—
Corynephorus canescens.	25	54	3	**100** 1.6	**100** 2.7	22	24	2	**80** 1	**90** 1.1	>
Festuca rubra.....	0	0	—	0	0	18	18	1	50 1	**90** 1	<
Carex arenaria.....	25	26	2	**100** 1	**100** 1.1	25	30	2	**100** 1.3	**100** 1.2	(<)
Hieracium umbellatum..	25	26	2	**100** 1	**100** 1.1	25	42	2	**100** 1.7	**100** 1.6	<
Hypochoeris radicata ...	4	4	1	0	40 1	1	1	+	10 1	0	>
Jasione montana.....	2	2	+	0	20 1	1	1	+	10 1	0	(>)
Viola canina.....	5	5	1	0	40 1	9	9	+	20 1	50 1	(<)
Sum...	111	183				121	191				(<)
Cladonia mitis } ...	25	58	5	**100** 1.2	**100** 4.0	21	33	3	70 1	**100** 2.2	>
— sylvatica }											
— tenuis	1	1	1	0	10 1	5	5	1	0	50 1	<
— impexa	1	1	1	0	10 1	1	1	1	0	10 1	—
— scabriuscula...	0	0	—	0	0	1	1	+	10 1	0	(<)
— rangiformis....	0	0	—	0	0	2	2	+	20 1	0	<
— furcata	12	12	1	30 1	70 1	9	9	1	20 1	50 1	(>)
— gracilis	2	2	1	0	20 1	0	0	—	0	0	>
— uncialis.....	1	1	+	0	10 1	1	1	+	0	10 1	—
— coccifera.....	0	0	—	0	0	1	1	+	10 1	0	(<)
Cetraria islandica.....	2	2	+	0	0	2	2	+	0	0	—
Cornicularia aculeata ...	23	23	3	**80** 1	**100** 2.0	19	23	2	40 1	**100** 1.4	>
Sum...	67	110				62	78				>

5.4 was found in the southeast corner where the sand supply was less. Here the rest conductivity value was very low, being 15 against 47 in the northern part of the quadrate. The further succession in Quadrate III will probably be in the direction of an *Ammophiletum* rich in *Festuca, Carex,* and *Hieracium,* but almost without lichens.

The succession on Bløden Hale and northwards from embryonal dunes on the beach to lichen-grown grey dunes has already been mentioned. This transition depends on increasing age and acidity but is rather independent of sand supply or removal of sand. Locally increasing supply or removal can stop, check, or modify the succession, but these factors will always be of local importance in newly formed dune areas until the chemical soil development approaches or has reached a final stage. The age and the soil development being the most important factors in the dune areas between Syrodde (the northeast corner) and Bløden Hale, the removal of sand and direct influence of wind upon the vegetation increases in importance from the point Syrodde and westwards. This appears from the fact that the higher coastal dunes disappear in that direction, and erosion by the sea becomes more and

more violent. In the vicinity of Østerby a low erosion slope is formed and from time to time areas covered with lichen heath or *Empetrum-Calluna*-heath fall down and are removed by the sea (cf. fig. 7 in Böcher 1941 b). The strongest wind erosion results in the formation of blow-outs and it is a very common feature that destruction areas or hollows in the dry *Calluna-Empetrum* heath form starting points for blow-outs. With regard to the blow-outs and especially the importance of different lichen vegetations for the recolonization of them reference may be made to the author's previous paper. In what follows the subject is the dependence of certain vegetations on such wind influences as do not result in or have not yet resulted in blow-out formation.

Weak influences of this kind produce only minor differences in the composition of the lichen heath, while influences which reach the level of erosion transform the vegetation entirely. Large lichen podetia and loose sand, especially the smallest sand particles, are removed by the wind and a more or less gravelly or stony flat forms with a very special lichen flora. A number of lichens seems to prefer this kind of vegetation, thus in particular *Alectoria vexillifera, chalybeiformis, Stereocaulon* sp., *Cladonia destricta,* and *C. cervicornis.*

There are also, however, lichens which profit by a weaker wind action presumably owing to a decrease in vitality of the typical *Cladonia mitis* as well as of *C. sylvatica* and *impexa.* In particular *Cetraria nivalis* and *Cladonia alpestris* may belong to this category.

Cetraria nivalis (L.) Ach. The first scattered specimens occur in the dune slopes at Syrodde (constancy percentage in 2 quadrates of 10 m^2 10—20, covering: +). At Jegens Odde (Quadrate II Table 1) it occurs also very scattered but obtained in a single square (8 g) the covering value of 2. Between this point and the harbour of Østerby it reaches dominance on west-facing, very gently sloping ground. Here it occurs in vegetation which is also dominated by *Cladonia destricta* and contains much *Corynephorus* and *Cladonia mitis* var. *prostrata.* Similar vegetations are described in the previous paper from dune areas farther inland. All these vegetations are rich in *Corynephorus* and frequently contain open spaces where sand and gravel are laid bare. A dense lichen mat mainly dominated by *Cetraria nivalis* occurs frequently in Scandinavian mountains as well as at the heads of the Southwest Greenland fjords, but is very rare in Denmark. In 1948, however, such a vegetation was found on the Østerby peninsula in the oldest parts of the area in some low inland dunes a little north of the main road and south of the lost village of Hals which was destroyed by sand-drift long ago. Five analyses (squares) of this *Cetraria nivalis* heath are surveyed in Table 3. The vegetation differs from the more open vegetations of the dunes or gravelly flats along the north coast by the occurrence of species like *Festuca ovina, Agrostis tenuis, Luzula multiflora,* and *Achillea millefolium.* It covers rather a large area so that the yellow colour of the dominant can easily be seen at quite a long distance. The vegetation alternates with patches dominated by *Calluna* or *Empetrum* together with *Cetraria* and on less exposed parts of the area with patches of *Cladina*-heath with the same dwarf shrubs and *Salix arenaria.* It very much resembles

lichen heaths with *Cetraria nivalis* described from Northwest Zealand and Central Jutland (BÖCHER 1947 and 1941 a).

Cladonia alpestris (L.) Rabh. This lichen is not so frequent as *Cetraria nivalis*. It is absent from Syrodde—Jegens Odde, but occurs between the latter point and the harbour of Østerby scattered in the *Cladina* heath. Only in one place it obtains a

Fig. 7. *Cladonia alpestris* forming patches in the grey dune areas between Jegens Odde and the harbour of Osterby. T.W.B. phot. 1948.

high covering value (Table 3 No. 6, fig. 7). This place was on a low flat hill and was more protected than the *Cetraria nivalis-Cladonia destricta*-vegetation and less so than the pure *Cladina* heath. In other parts of the Østerby peninsula the species occur on *Empetrum* heaths on exposed ridges and sometimes in destruction hollows in the heath (BÖCHER 1941 b Table 10 Nos. 11—16 and fig. 10).

Cladonia destricta Nyl. occurs much scattered at Jegens Odde but farther west soon gets a prominent place in the vegetation. It is clearly the most important *Cladonia* in the most exposed situations on acid and poor soils. Only *C. mitis* var. *prostrata* may sometimes on less exposed ground be of the same importance. In five

TABLE 3.

No.	1	2	3	4	5	Constancy per cent Nos. 1—5	6
pH	4.7	—	4.5	—	4.5		4.3
$K_{20°} - (K_{H+})_{20°} \cdot 10^6$	51	—	29	—	22		15
Corynephorus canescens	3	—	—	—	+	40	+
Festuca ovina	+	—	—	2	1	60	—
— rubra	+	—	—	—	—	20	1
Agrostis tenuis	1	1	2	2	—	80	—
Ammophila arenaria	+	—	1	1	1	80	1
Carex arenaria	+	+	+	+	—	80	+
Luzula multiflora	—	—	+	—	—	20	—
Hieracium umbellatum	1	+	1	1	1	100	—
— pilosella	—	—	—	—	—	0	+
Hypochoeris radicata	—	+	—	—	—	20	—
Achillea millefolium	—	—	—	+	—	20	—
Jasione montana	1	1	1	1	1	100	—
Galium verum	—	—	+	—	+	40	—
Calluna vulgaris	1	—	2	2	+	80	—
Empetrum nigrum	—	—	—	—	—	0	2
Viola canina	—	—	—	—	—	0	1
Rumex acetosella	—	—	+	—	+	40	—
Cladonia alpestris	—	—	—	—	—	0	**5**
— mitis	2	2	1	2	1	100	**4**
— sylvatica	—	—	+	+	+	60	—
— tenuis	—	—	+	+	+	60	—
— rangiferina	—	—	1	+	+	60	+
— impexa	—	—	1	1	1	60	—
— scabriuscula	—	—	+	—	+	20	—
— uncialis	—	—	+	+	—	40	—
— gracilis	+	—	+	+	—	60	+
— glauca	—	—	+	+	—	40	—
— fimbriata	—	—	—	+	+	40	—
— chlorophaea	+	+	—	+	+	80	—
— coccifera	—	+	—	—	—	20	+
Cetraria nivalis	**5**	**5**	**5**	**5**	**5**	100	1
— crispa	—	—	—	+	—	20	—
Cornicularia aculeata	+	1	1	1	1	100	1
Polytrichum piliferum	+	—	—	—	+	40	
Dicranum scoparium	+	+	—	+	+	80	
Hypnum cupressiforme	—	—	+	—	+	40	
Webera nutans	—	+	+	—	—	40	
Cephaloziella sp.	—	+	+	+	—	60	

of the square analyses in Table 4 (Nos. 6—10) which were made in the inner zone of the gravelly flat west of the Østerby harbour the species was constant and obtained high covering values. As distinct from the two above-mentioned species it will stand a moderate removal of sand. It has a very vigorous system of rhizines which adhere to the grains of sand and small stones and will therefore withstand very violent winds. It is certainly a very characteristic element in the vegetation of the exposed gravelly flats, but it is not exclusive to this habitat. It occurs in pure acid sand at exposed stations and also on bare wet raw humus in heather moors (see BÖCHER 1941 a, 1941 b).

Alectoria vexillifera (Nyl.) Stzbrgr (= *A. cincinnata* (Fr.) Lynge). This arctic lichen seems completely bound to the windy gravelly flats. As the vegetation in which it occurs is of special interest a number of square analyses were undertaken partly at the station where I detected it in 1939 west of the harbour of Østerby (Table 4

Fig. 8. Gravelly flat on the north coast of Læsø at "Bansten Bakke". (1) maritime belt with scattered herbs and squamulate *Cladoniae*. (2) transitional belt with thin lichen vegetation composed mainly by *Cornicularia—Cladonia destricta*. (3) *Cornicularia—C. destricta* soc. with *Alectoria vexillifera*. (4) Dense *Cornicularia—Cladonia destricta—C. mitis prostrata*-heath with *Empetrum*-patches. T.W.B. phot. 1948.

Nos. 1—10), partly at a new station "Bansten Bakke" farther west (Table 4 Nos. 11—15). A profile transect from the first locality is mentioned in Table 3 and p. 10 in Böcher 1941 b). The area at "Bansten Bakke" resembles that at the harbour very much. Just above a low erosion slope at the beach there is a gravelly plain with much scattered plants. *Plantago maritima* and *Armeria vulgaris* are here

TABLE 4.

No.	1	2	3	4	5	Constancy per cent. Nos. 1—5	6	7	8	9	10	Constancy per cent. Nos. 6—10	11	12	13	14	15	Constancy per cent. Nos. 11—15
pH	5.2		4.7		5.4		5.4			5.0				4.5			5.3	
$K_{20°} - (K_{H+})_{20°} \cdot 10^6$	18		23		18		23			21				9			32	
(1) Corynephorus canescens	1	1	1	+	2	100	+	1	1	+	+	100	1	1	—	+	1	80
Festuca rubra	+	+	+	—	—	60	1	+	1	1	+	100	+	—	—	—	—	20
Hieracium umbellatum	—	—	—	—	—	0	—	+	+	+	1	80	+	—	+	+	—	60
Jasione montana	—	+	+	1	+	80	1	1	+	—	1	80	+	+	—	—	—	40
Plantago maritima	—	—	—	—	—	0	—	—	—	—	—	0	1	—	+	+	—	60
Armeria vulgaris	1	—	+	—	—	40	—	—	—	—	—	0	—	—	—	—	—	0
Empetrum nigrum	—	+	—	—	—	20	—	—	—	—	1	20	+	1	—	+	+	80
Viola canina	—	—	—	—	—	0	—	+	1	+	+	80	+	—	—	—	+	40
Lotus corniculatus	—	—	—	—	—	0	—	—	—	—	—	0	+	—	—	—	—	20
(2) Alectoria vexillifera	1-2	2	2	1	1	100	1	+	+	+	1	100	1	+	1	1	1	100
— chalybeiform.	—	—	+	1	+	60	—	—	—	—	—	0	—	—	—	—	—	0
Cladonia destricta	+	+	1	—	+	80	**4**	**4**	**3**	**5**	**4**	100	—	1	+	—	+	60
— cervicornis	+	—	+	+	+	80	+	+	—	+	—	60	—	+	—	1	+	60
— cf. pyxidata	—	—	—	+	+	40	—	—	—	+	—	20	—	—	—	—	+	20
— strepsilis	—	—	—	—	+	20	—	—	—	—	—	0	—	—	—	—	—	0
Stereocaulon sp.	+	+	+	+	+	100	—	+	+	+	+	80	—	—	—	+	+	40
(3) Cladonia mitis var. prostrata	—	—	+	—	—	20	+	—	—	—	—	20	+	+	+	1	—	80
— furcata	—	—	—	—	—	0	—	—	—	—	—	0	—	+	+	—	—	40
— gracilis	—	—	—	—	—	0	—	—	—	+	—	20	—	—	—	—	—	0
— coccifera	—	—	—	—	+	20	+	+	+	—	—	60	+	—	+	+	+	80
— floerkeana	—	—	—	—	—	0	+	—	—	+	—	20	—	—	—	—	—	0
— chlorophaea	—	—	—	—	—	0	—	—	—	—	—	0	—	—	—	—	+	20
— glauca	+	—	—	+	+	60	+	—	—	—	—	20	—	—	—	+	—	20
— alcicornis	1	+	+	+	+	100	2	+	+	+	1	100	2	+	—	1	+	80
Cornicularia aculeata	+	2	2	1	1	100	**4**	**4**	**4**	2	**3**	100	**5**	**4**	**5**	**5**	**4**	100
Lecidea granulosa	—	—	+	—	—	20	—	—	—	—	—	0	—	—	—	—	—	0
(4) Parmelia saxatilis	—	—	—	—	—	0	+	+	—	—	—	40	—	1	—	—	—	20
— mougeottii	+	—	—	—	—	20	+	—	—	—	—	20	—	+	—	—	—	40
Rhizocarpon obscuratum	2	+	+	1	2	100	2	+	+	+	+	100	+	1	—	2	+	80
— reductum	+	—	—	+	—	40	—	—	—	—	—	0	—	—	—	—	—	0
Sarcogyne simplex	+	—	—	—	—	20	—	—	—	—	—	0	—	+	—	—	—	20
Acarospora smaragdula	+	—	—	—	+	40	—	—	—	—	—	0	—	—	—	—	—	0
Lecidea erratica	—	—	—	+	+	40	—	—	—	—	—	0	—	—	—	—	—	0
— sorediza	—	—	—	—	—	0	—	—	—	—	—	0	—	+	—	1	+	60
— pycnocarpa	—	—	—	—	—	0	—	—	—	—	—	0	—	—	—	+	—	20
Lecanora polytropa	+	—	—	—	—	20	—	—	—	—	—	0	—	—	—	+	—	20
— badia	—	—	—	—	—	0	—	—	—	—	—	0	—	—	—	+	—	20
(5) Polytrichum piliferum	—	+	+	—	—	40	1	1	+	1	+	100	+	1	2	+	2	100

(1) Flowering plants, (2) lichens which are characteristic of the community, (3) lichens occurring on sand, (4) lichens on the small stones (kindly determined by M. SKYTTE CHRISTIANSEN, M.Sc), (5) bryophytes.

rather important, less so are *Corynephorus*, *Jasione*, *Hieracium umbellatum*, *Cladonia alcicornis*, and *cervicornis*. This extreme belt may be influenced by salt spray; on fig. 8 it is called (1). The next belt (Fig. 8 (2)) contains the first specimen of *Alectoria*

vexillifera and there the lichens are more abundant, especially *Cornicularia* and *Cladonia destricta*. Of some importance is likewise *Polytrichum piliferum*. Among the higher plants *Festuca rubra, Viola canina, Lotus corniculatus,* and *Empetrum* have entered the vegetation. The analyses in Table 4 (Nos. 11—15) are all from the third belt (3). In the background on the left this belt is rather broad (in fig. 8 indicated by arrows). Here *Alectoria vexillifera* is constant and rather abundant. In this belt the lichen flora of the small stones further is best developed, it consists mainly of *Rhizocarpon obscuratum*. In the fourth belt (4) the lichens cover the ground. A *Cornicularia-Cladonia destricta-mitis* var. *prostrata*-heath occurs which, however, frequently is interrupted by *Empetrum* patches or small sandy or gravelly areas with the same vegetation as in belt (3). In the closed lichen mat small stones may protrude and not rarely they are overgrown by *Parmelia saxatilis*.

In Southwest Greenland *Alectoria vexillifera* grows in places which from an ecological point of view resembles the Læsö type of habitat very much. I saw it in 1946 on gravelly ridges or stony fell fields (barrens) in places highly marked by wind influence. At Ivigtut it occurred in the very characteristic *Salix uva ursi* barren land community. The analyses of this community will appear in a later paper on the Greenland vegetation.

Alectoria chalybeiformis (L.) Röhl. is another characteristic species of the gravelly plains. It was seen in some of the squares at Østerby. I have further noticed it at Rørvig on exposed lichen heaths at the sea (cf. Böcher 1945 p. 152). Dahl (1950) found it in Greenland on rocks and on the top of windy hills together with *Alectoria vexillifera* and *ochroleuca*.

In 1939 two rather small permanent quadrates were made in vegetations rich in *Cladonia destricta* on the gravelly plains. Both had a bad fate. One was placed in belt No. 5 in the profile transect at Lergravsbakke mentioned on p. 8 in Böcher 1941 b. But there the more extreme belts 2—3 in 1948 were removed by the sea and the next two belts covered with fresh sand. The only plants left in the quadrate were a specimen of *Empetrum*, which had been able to form a low dune, and further *Festuca rubra, Hieracium umbellatum,* and *Plantago maritima*. All lichens and several others had disappeared.

The other quadrate was made on the *Alectoria vexillifera* locality west of the harbour of Østerby. In 1948 the corner pegs were taken away by someone and it was therefore impossible to find the place exactly. The quadrate, however, was cut by a line indicated by two sea-marks and its approximate situation could be established through counting of steps along this line. It was therefore possible to ascertain that no larger changes had occurred in that area during the nine years. It thus appears that such gravel-plain communities as are the result of strong wind influences can be very stable unless new blow-outs are formed or removal of sand takes place and disturbs the balance.

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BY

MATHIAS THOMSEN

København
i kommission hos Ejnar Munksgaard
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Introduction.

The concept of neurosecretion is especially due to ERNST and BERTA SCHARRER and to HANSTRÖM. It is not necessary to cite here all the earlier papers on neurosecretion, as the literature has been repeatedly reviewed in recent years (see BARGMANN and E. SCHARRER 1951, B. SCHARRER 1948 and 1952c, and B. SCHARRER 1954); a few facts, especially with regard to neurosecretion in insects, however, ought to be mentioned.

WEYER (1935) was the first to observe neurosecretory cells in the brain of an insect, the honey-bee (*Apis mellifica*), and this observation was confirmed by B. SCHARRER (1937), who also found similar cells in *Bombus* sp. HANSTRÖM described secretory cells in the brain of the hemipteran *Rhodnius* (1938), and these cells were again pictured by WIGGLESWORTH (1940), who showed that they secrete a hormone connected with moulting.

Later, cells containing secretory material have been described in the nervous system of a number of insects belonging to different orders (HANSTRÖM 1940, 1943, DAY 1940a and b, PEREZ 1940, B. SCHARRER 1941 and later, VOGT 1942, WILLIAMS 1948, M. REHM 1950, E. THOMSEN 1948 and 1952, M. THOMSEN 1951 and 1954, DUPONT-RAABE 1951 and 1952, L'HÉLIAS 1950 and 1952).

Important progress in the staining technique was made by BARGMANN's detection (1949) that the chrome-hematoxylin-phloxin stain of GOMORI is of value to the study of the neurosecretory cells of the vertebrates; these cells, which are situated in the diencephalon, and their axons going to the neurohypophysis, assume a very distinct dark blue colour with the chrome-hematoxylin, while the surrounding tissue stains light red.

During the last few years several papers have appeared which are based on the use of the chrome-hematoxylin-phloxin stain in insects. B. SCHARRER (1951) used it for the blattid *Leucophaea*; STUTINSKY (1952) studied *Gryllus, Blatta, Periplaneta, Carausius,* and *Dytiscus*; ARVY and GABE investigated *Odonata* (1952) and *Ephemeroptera* (1953); ARVY, BOUNHIOL and GABE (1953) *Bombyx mori*; HANSTRÖM (1953) described the conditions in the apterygote insect *Petrobius*; and NAYAR (1953) showed the occurrence of neurosecretory cells in *Iphita* (*Hemiptera*).

In most cases the neurosecretory cells occur in the dorsal part of the protocerebrum, where they generally form two medial and two lateral groups, though the latter may be less distinct and sometimes have not been found at all. The medial cells are situated in the pars intercerebralis.

As found by HANSTRÖM (1940) and later confirmed by other investigators the fibre bundles comprising the axons of the two medial groups after crossing inside the brain leave it ventrally to form the nervi corporis cardiaci I of Hanström, while the axons of the two lateral groups, taking a simpler course through the brain, form the nervi corporis cardiaci II. These nerves innervate the corpus cardiacum.

In some cases neurosecretory cells have been described in other parts of the nervous system (suboesophageal ganglion and other ganglia, DAY (1940a), B. SCHARRER (1941), ARVY and GABE (1952), BOUNHIOL, GABE and ARVY (1953)).

Already in 1941 HANSTRÖM (1941a) pointed out the analogy between the pars intercerebralis-cardiacum-allatum system of insects and the hypothalamus-hypophysis system of vertebrates. In 1944 B. and E. SCHARRER extended this comparison by adding that neurosecretory granules migrate along the axons from the neurosecretory brain cells to the c. cardiacum in insects and to the neurohypophysis in vertebrates. They further advanced the hypothesis that the neurosecretory cells and the corpus cardiacum should be regarded as one neuro-endocrine complex. At that time neurosecretory granules had only been observed in the axons of two insect species, *Petrobius brevistylis* (described by HANSTRÖM 1940), and the blattid *Leucophaea maderae* studied by BERTA SCHARRER, but some years later CAZAL (1948) made similar observations in the adult *Tipula* and perhaps other insects, and M. THOMSEN (1951) figured neurosecretory granules along the medial (internal) bundle of neurosecretory nerve fibres in the larva of *Tabanus*.

During a stay in the United States in the summer of 1951 the author got hold of a few specimens of the giant digger-wasp *Sphecius speciosus*, in America called "the cicada-killer" as it uses the big cicadas (*Cicada septendecim* and others) as its prey. Two brains were dissected out and fixed in Bouin's fluid. Later study showed that in this insect the neurosecretory material in the brain cells and their axons stands out in an extraordinary clear way, and could be traced down into the c. cardiacum. It was therefore decided to investigate also other species of *Hymenoptera*, preferably large ones, but it proved difficult to obtain suitable material in Denmark. However, through the generous help of Mr. H. STENHOLT CLAUSEN, cand. mag., lecturer of zoology, University College, Ibadan, Nigeria, and Mrs. STENHOLT CLAUSEN, cand. mag., I received an ample collection of African species of *Hymenoptera*, fixed in Bouin's fluid. I am highly indebted to Mr. and Mrs. Clausen for their kind efforts, which proved of extreme value to my studies.

The African and American material has been supplemented by the study of a few Danish species, but so far only representatives of a few families have been considered.

Some of the papers recently published, especially those of STUTINSKY (1952) and ARVY and GABE (1952, 1953), have given results which are similar to those found by me in the *Hymenoptera*. Still I venture to say that among insects the *Hymenoptera* are exceptionally well suited for a histological study of neurosecretion, for in some of the species neurosecretory material occurs in unsurpassed quantity and distinctness.

Material and Technique.

The following species, all belonging to the *Hymenoptera aculeata*, have been studied:

Superfam. *Sphecoidea*. Fam. *Sphecidae*. *Sphecius speciosus* (Drury). From Harvard University, Massachusetts, U. S. A. The genus *Sphecius* is sometimes referred to a special family, *Stizidae*.

Superfam. *Vespoidea*. Fam. *Vespidae*. *Eumenes* sp. Ibadan, Nigeria. Specimens were hatched from a laterit-nest on a stone.

Synagris (*Paragris*) *calida* (L.). Ibadan, Nigeria. Like *Eumenes* a solitary wasp, building laterit-nests.[1]

Belonogaster sp. (probably *junceus* Fabr.). Ibadan, Nigeria. A semi-social species, making paper-nests.

Vespa vulgaris L. Workers. From North Zealand, Denmark.

Superfam. *Apoidea*. Fam. *Megachilidae*. *Megachile* (*Gronoceras*) *cincta* Fabr. Ibadan, Nigeria. Solitary bee, making laterit-nests.

Fam. *Apidae*. *Apis mellifica* L. Workers. Copenhagen, Denmark.

As mentioned above, the African species were collected or hatched from larvae by Mr. and Mrs. STENHOLT CLAUSEN at Ibadan in West Africa. After anaesthetizing the insect by means of cold or chloroform the head was cut off, the mouth parts removed, and the head and body placed in Bouin's fluid, in which the material was shipped to Copenhagen. Here the brains with the adhering endocrine organs were dissected out under the binocular, as the cuticle is too hard to allow sectioning of whole heads. The brains were taken through increasing strengths of alcohol up to 90 per cent. and then through two changes of butylic alcohol into paraffin wax. Sections were cut at 7 μ. The American and Danish material was mostly treated in a similar way, although in some cases the brain was partly or totally dissected out before fixation. This method is rather difficult owing to the fragility of the brain tissue, and fixation before dissection is preferred and as a rule gives a satisfactory fixation of the brain, etc.

Allen's modification of Bouin's fluid and Helly's fluid were used in some cases.

Most of the material was stained with Gomori's chrome-hematoxylin-phloxin method (see BARGMANN 1949). A few series were stained with Masson's trichrome stain.

The photographs were taken with a Zeiss "Phoku" camera and a Zeiss "Lumipan" microscope, using Perutz "Silbereosin" plates (orthochromatic) and an orange filter. In a few cases a red filter gave better results and—contrary to expectation—it

[1] The specimens when received were labelled *Synagris negusi*, and this name was used in a short earlier publication (M. THOMSEN 1954). Some material was later sent to Mr. I. H. H. YARROW, British Museum, London, who determined it as belonging to *S. calida* (L). Mr. Yarrow also checked the determinations of *Belonogaster junceus* and *Megachile cincta*. I am very much indebted to Mr. Yarrow for his valuable help.

did not prolong the exposure unreasonably (fig. 2 – 40 seconds, fig. 5 – 4 minutes). All the photographs show sections stained with Gomori's chrome-hematoxylin-phloxin stain. The original photos were not reduced in reproduction.

I am very grateful to Mr. N. HAARLØV, mag. scient., for his assistance with the photographic work, and to Mr. E. RASMUSSEN, mag. scient., for help with the drawings.

Further I want to express my sincere gratitude to the Carlsberg Foundation, which has supported the work financially.

The Morphology of the Endocrine Organs in the Hymenoptera.

The early history of the discovery of the endocrine organs of insects has been recorded by NABERT (1913), CAZAL (1948), and others, and it will not be repeated here. Only it seems appropriate to mention that what is probably the first figure of the corpora allata of a hymenopterous insect was given by MEINERT in his "Bidrag til de danske Myrers Naturhistorie" (Contributions to the Natural History of the Danish Ants) published in the transactions of this society in 1861. He designated them as "gaadefulde Legemer" (enigmatic bodies) or corpora incerta.

Of more recent publications in which conditions in the *Hymenoptera* are considered, reference should first be made to that of NABERT (1913). He gave an extensive description of the anatomy of the corpora allata and c. cardiaca ("Pharyngealganglia") and the topographical relations between these organs and the brain, the aorta, the oesophagus, etc., in several *Hymenoptera* (*Lasius, Vespa, Chalicodoma, Bombus,* and *Apis*). He regarded the c. allata as endocrine glands, which are innervated by nerves coming from the c. cardiaca, while each of these is innervated by a nerve coming from the brain.

NELSON (1915) described the embryological development of the corpora allata and the stomatogastric nerves including the "pharyngeal ganglia" (= corpora cardiaca) in the honey-bee (*Apis*).

Mention should further be made of de LERMA (1937), who studied the innervation and histology of the corpora cardiaca of *Vespa crabo*. REHM (1939) briefly described the stomatogastric nervous system of the bee; and STÄRCKE (1939) gave some information on the c. allata and c. cardiaca in ants, unfortunately containing some misunderstandings.

HANSTRÖM (1941 b) in his survey of the corpora cardiaca and allata of insects recorded his own observations on two species of *Hymenoptera, Apis mellifica* and *Vespa crabo*. He found that each c. cardiacum is innervated by two nerves from the brain, the nervi corporis cardiaci I and II, and he supposes that the n. c. cardiaci I takes its origin from the neurosecretory cells of the pars intercerebralis which had been discovered by WEYER (1935). He further described the histology of the c. allata and cardiaca, mentioning the two sorts of cells in the c. cardiacum.

Observations on the corpora allata of ants have been published by HULTIN (1947), of *Bombus* by PALM (1948), and of *Apis* by PFLUGFELDER (1948).

In his well-known monograph of the retrocerebral endocrine organs of insects CAZAL (1948) has a section on the *Hymenoptera* based on the study of one representative of the *Symphyta* (*Selandria*) and a number of species belonging to the *Apocrita*. His diagram of the topography of the organs in *Selandria* is redrawn in text-fig. 1. It is seen that the corpora cardiaca form parts of the lateral walls of the aorta, while the c. allata are placed more posteriorly and laterally. The nervi corporis allati are very short, almost wanting. CAZAL states that each corpus cardiacum is only innervated by one cardiac nerve, which, however, has two roots inside the brain, an internal and an external one. A ganglion hypocerebrale is said to be present only in the *Symphyta* and the ants.

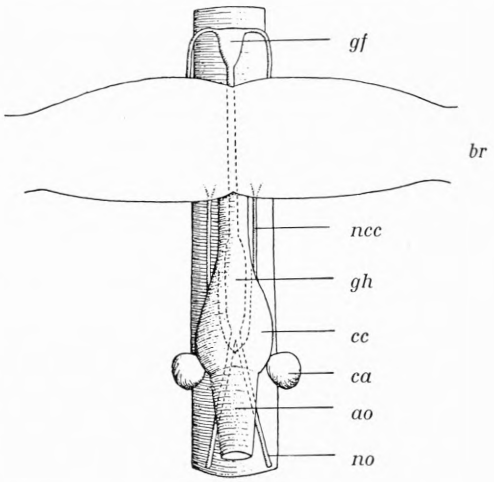

Fig. 1.
Diagram of stomatogastric nervous system and endocrine organs of *Selandria*. *ao* aorta (below this the oesophagus); *br* brain; *ca* corpus allatum; *cc* corpus cardiacum; *gf* ganglion frontale; *gh* ganglion hypocerebrale (on nervus recurrens); *ncc* nervus corporis cardiaci; *no* nervus oesophageus.
(After Cazal).

A short description of the endocrine organs of the larva of the honey-bee was given by SCHALLER (1950). The c. cardiaca are less developed than in the adult bee, while the c. allata of the last stage attain the size found in the imago. The author could not find the two roots of the nervus corporis cardiaci stated by CAZAL to be present.

The same subject was independently treated by L'HÉLIAS in a similar short paper from the same year (1950). Her results, while mainly in accordance with those of SCHALLER, differ from his on certain points. Thus she states very precisely that the single-nervus corporis cardiaci rises from two intracerebral roots, the internal root coming from the large neurosecretory cells of the pars intercerebralis, the external one from "un groupe de grandes cellules analogues aux cellules de la pars intercerebralis, en position latéro-interne par rapport au nid de cellules du futur lobe pédonculé." Outside the brain the n. corporis cardiaci is stated to anastomose with the "nerf stomacal" (= n. oesophageus) of the same side and then go to the c. allatum. The c. cardiacum is faintly developed, consisting of few cells.

In 1952 L'HÉLIAS described the post-cerebral endocrine glands of the larva of *Lophyrus* (*Tenthredinoidea*). Also in this insect she found that the cardiac nerve originates from two roots which show a similar intracerebral course as in the honey-bee larva.

Own observations.

With regard to the topography of the endocrine organs in the adult *Hymenoptera* investigated, my results are in accordance with those of several other recent workers. CAZAL's general diagram is applicable also to the types studied by me, though there are some differences between the species.

The two corpora cardiaca are well-developed organs, which are intimately connected with the lateral walls of the aorta. In *Vespa* they virtually constitute this wall, as already shown in de LERMA's semi-schematic figure (1937, fig. 16); the c. cardiaca meet dorsally for most of their length, but caudally they are separate dorsally, but united ventrally by a narrow bridge. In other types, such as *Eumenes* (Pl. VI, fig. 21) and *Megachile* (Pl. VII, fig. 28), only the dorsal portion of the c. cardiacum forms part of the aortic wall, while the narrower ventral part adjoins the oesophagus. In *Megachile* the two corpora cardiaca are connected ventrally below the oesophagus by a strand of tissue (fig. 28 *vc*); a similar condition has been described by CAZAL (1948) in the bee *Xylocopa*.

The corpora allata are globular or egg-shaped bodies lying below the corpora cardiaca and leaning against the wall of the oesophagus.

Each corpus cardiacum receives only one nervus corporis cardiaci from the brain. In some cases the nerve—i. e. the extracerebral part of the fibre bundle—is extremely short or almost absent (f. inst. *Sphecius*, Pl. II, fig. 8, and *Vespa*, Pl. VII, fig. 26), while in other types it is longer (*Megachile*). The nerve enters the c. cardiacum laterally and in the *Vespidae* it can be followed as a well-defined bundle of nerve fibres inside the c. cardiacum; this is shown in *Synagris* (Pl. IV, fig. 16) and *Eumenes* (Pl. V, fig. 19). But in *Megachile* the fibre bundle can hardly be said to be inside the c. cardiacum; it runs down along the lateral side of this organ, sending fibres into it (Pl. VII, fig. 28 *ncc*).

In all species the fibre bundle continues into the corpus allatum as the nervus corporis allati, but again this nerve differs in length; while it is rather well developed in *Eumenes* (Pl. VI, fig. 21–23) and *Synagris*, it is almost absent in *Sphecius*, where the c. cardiacum and allatum lie very close together.

The nervus recurrens as usual runs along the dorsal side of the oesophagus. In the species investigated the ganglion hypocerebrale is absent or vestigial, i. e. only indicated by a small collection of nerve cells, which can be seen in transverse sections; it is most distinct in *Megachile* (Pl. VII, fig. 28), where there is a slight swelling at the point where these nerve cells occur and the recurrent nerve divides into the two nervi oesophagei. Like HANSTRÖM (1941) and CAZAL (1948) I have not been able to find any nervous connection between the recurrent nerve and the c. cardiaca nor the c. allata.

The Neurosecretory Cells.

The neurosecretory cells observed by me in the brain of the *Hymenoptera* are situated in the anterior and dorsal part of the pars intercerebralis which connects the right and the left halves of the protocerebrum (Pl. I, fig. 1, Pl. III, fig. 9 and Pl. VIII, fig. 29). The cells mostly lie close together around the median plane, virtually forming one large group (Pl. V, fig. 17 and Pl. VII, fig. 27). It is obvious that this group corresponds to the two medial (internal) groups found in most insects, but in the *Hymenoptera* the two groups have practically fused. The cells form several layers, the superficial ones lying just below the perineurium, which is rather thin in this region (Pl. V, fig. 17 and 18). In frontal sections it is seen that the group tapers downward towards the fibre bundle, the greater number of cells lying near the surface.

The region of the brain containing the neurosecretory cells receives two tracheae which penetrate the perineurium and branch inside it. Some of the branches follow the fibre bundle of the neurosecretory cells running between the axons, while others take an oblique course into other parts of the brain.

My search for the lateral groups of neurosecretory cells gave a negative result. It is true that in *Synagris* 5—6 neurosecretory cells may be observed which lie scattered at a distance from the main group between this and the ocellar nerve fibres, i. e. posterior to the medial group. They lie very near the median plane, but may perhaps be said to form two groups. A close scrutiny of the slides revealed, however, that fine axons containing delicate blue granules extend from these cells parallel to the surface of the brain on to the large medial group where they bend downwards joining the main bundle of neurosecretory fibres. So these cells cannot represent the lateral group, but must be regarded as belonging to the medial group.

In the medial group many cells stain dark blue with the chrome-hematoxylin of the Gomori stain. This is due to their content of distinct bluestained granules, which differ somewhat in size and number in various species. They are beautifully seen in *Sphecius, Synagris, Eumenes,* and *Vespa* (cp. fig. 2, 3, 4, 11, 12, 18 and 25), i. e. in the species belonging to the *Vespidae* and *Sphecidae,* while in *Megachile* they are visible, but much less distinctly stained. The same is the case in *Apis* (workers caught and fixed in autumn). My material is not comprehensive enough to decide whether this is indicative of a general difference in the neurosecretory systems of bees and "wasps".

In the single species the granules differ in size from minute particles to distinct, discrete bodies (cp. the photographs). At first it was thought that the larger bodies, which are more or less spheroid, arise by gradual growth of the small granules. But in the best slides (*Synagris*) it could be discerned that more likely the larger inclusions are aggregates of small granules; their surface is not even and smoth, but verrucose or knotty (cp. also E. and M. Thomsen 1954). This does not mean, however, that the small granules are all of the same size; they seem to vary *inter se.*

Among the cells with blue-stained granules there are usually some which only contain a few such granules; and furthermore there are cells—sometimes about half of the cells in the group—without any granules at all, the cytoplasm of these being phloxinophilic (see f. ex. Pl. V, fig. 18). The shape and position of the last-mentioned cells make it highly probable that they, too, are neurosecretory cells, which at the moment of fixation were in a phase of secretion in which no formed granules were present.

In most of the species investigated all granules of the neurosecretory cells appeared blue, being stained by the chrome-hematoxylin, but in *Belonogaster junceus* both blue and red inclusions occurred. The two sorts of inclusions were mostly localized in separate cells which differed somewhat in appearance. The cells with red inclusions were larger and more pear-shaped, while those with blue granules were somewhat smaller and rounded or angular, the blue granules mostly occurring as a cap-like collection above the nucleus. The individual red bodies were larger and fewer than the blue granules and spherular in shape, i. e. they resemble droplets, while the blue inclusions seem to be solid granules (Pl. VIII, fig. 31—32). Sometimes cells were found which contained a number of red spherules beside a majority of blue granules, while the reverse relation was not observed. The red droplets might occur in the thick proximal portion of the axon, which is rather conspicuous in these cells, but they were not observed in the axons farther away from the cell body.

In *Sphecius speciosus* a similar phenomenon was observed. Only a few cells contained red spherules, which were themselves fewer in number, but somewhat larger than in *Belonogaster*, looking very much like droplets.

Apart from my own observations of phloxin-stained neurosecretory cells in the brain of the adult *Calliphora* (M. Thomsen 1954), no other similar cases seem to have been recorded in insects.

Obviously the occurrence of the phloxinophilic inclusions could be explained in two different ways. Either the red material is a second neurosecretory substance, chemically and physiologically different from the blue granules, or it is only another phase in the secretory cycle of the usual blue substance, perhaps representing a liquefaction of the material.

The latter alternative seems the more likely because: (1) red spherules only occur in two of the species; (2) they are found in cells which resemble the "empty" neurosecretory cells of the other species; (3) blue granules and red spherules may occur in the same cell. However, this evidence is only circumstantial and a decision must await further studies.

In the vicinity of the neurosecretory cells or even among them some larger nerve cells occur which are certainly not neurosecretory cells (Pl. V, fig. 18). I have not been able to identify these with any cells described in the papers of Kenyon (1896) or Haller (1905), which deal with the brain of *Apis* and other *Hymenoptera*.

The number of neurosecretory cells in the *Hymenoptera* is very great. In *Eumenes* sp. I have counted the cells with distinct blue granules in four individual brains.

The numbers found were: 120 — 129 — 136 — 142. To avoid counting the same cell twice I have included only cells in which the nucleoli were distinct, so the counts should be rather reliable. On the other hand all cells without unquestionable granules were excluded, as it is difficult to distinguish with certainty the neurosecretory cells in the non-granular phase from other nerve cells. This means that the numbers given above are too low, and presumably they should almost be doubled, so that the total number of neurosecretory cells can roughly be estimated at 200—250 in this species. Some counts from *Synagris calida* gave similar results.

The nuclei of the neurosecretory cells resemble those of other nerve cells. They are rather pale, but contain conspicuous nucleoli which stain red with the phloxin. There are mostly two or more (3—5) nucleoli, which generally lie close together forming an aggregate or more rarely are scattered in the nucleus; they may differ in size in the same nucleus. Such multiplication of the nucleolus is considered to be characteristic of highly active cells.

In *Synagris* 2—3 cells with blue granules (after the Gomori stain) were also observed in the suboesophageal ganglion, but their possible connections with other cells or organs could not be established. In the other species no such cells were seen.

In this connection it should be mentioned that the chrome-hematoxylin of the Gomori stain is not absolutely specific for the neurosecretory material, but also stains some other structures. Thus non-cellular membranes, such as the neural lamella of the brain (cp. B. SCHARRER 1939) and the covering membranes of the corpus cardiacum and allatum, are generally dark blue. Similarly the cuticular wall of tracheae is also stained blue, and this fact sometimes makes it difficult to distinguish between fine tracheae and neurosecretory nerve fibres inside the brain.

In some cases the perineurium, which covers the whole surface of the brain like an epithelium, contained blue structures when stained with chrome-hematoxylin. These inclusions appear as blue granules or fine moniliform filaments which seem to wind between the cells. Especially in *Synagris* they resembled nerve endings in a rather delusive way, but no connection with nerve fibres of the underlying brain tissue could be detected. In one case they seemed to be extensions of the neural lamella, and this is probably the most likely explanation.

Furthermore it should be mentioned that the nuclei should be red in the Gomori-stained slides, but rather often they stain blue. This is the case when the slides remain too long in the hematoxylin, especially when rather fresh hematoxylin is used, and in such cases a prolonged differentiation in acid alcohol may not be able to destain the nuclei before also the blue colour of the neurosecretory material disappears.

The Neurosecretory Nerve Fibres and the Nervi Corporis Cardiaci.

As all insect neurons the neurosecretory cells are unipolar nerve cells. Their axons extend downwards in the brain either directly or after making a more or less conspicuous curve (cp. figures).

The axons from all the neurosecretory cells converge to form a well-defined tract of nerve fibres. Dorsally the fibres still lie somewhat scattered, but they converge more and more, and in the ventral part of the brain they form two distinct cords (Pl. III, fig. 9). *Belonogaster junceus* differs somewhat from the other species, as the neurosecretory nerve fibres dorsally are unusually dispersed and seem to take a rather irregular course. Below the chiasma, however, they concentrate and form two definite bundles.

In some of the types studied, notably *Sphecius*, *Synagris*, and *Eumenes*, axons emerging from neurosecretory cells which contain distinct blue granules, do themselves contain similar blue material in their whole course through the brain and onwards. In such cases the bundle of neurosecretory nerve fibres stands out very clearly in the sections as a blue band on a red background, reminiscent of the tractus hypothalamo-hypophyseus in vertebrates.

Often the proximal portions of the axons are indistinct, but in some cases, especially in *Sphecius* and *Synagris*, also these parts of the axons are well stained (Pl. I, fig. 2—4). The cell tapers conically into the axon which gradually attenuates. The broader part nearest to the pericaryon (the "Zellstiel" of some authors) contains very fine granules, which are sometimes seen to form two convergent or parallel rows, obviously indicating that in reality the granules lie in the superficial layer of an axon cut longitudinally by the microtome knife. This is visible in one of the photographs only (Pl. I, fig. 3), but has repeatedly been observed. Stutinsky (1952) has noticed the same in his material, and Bargmann (1949) has given photographs of similar cases in vertebrates.

At a short distance from the pericaryon the axons appear as delicate filaments where fine blue granules are still visible, but owing to the thinness of the fibre the granules as a rule no longer form two rows, but fill the whole axoplasm. Such fine fibres are seen on some of the photographs of Pl. I and II. Using a high magnification and changing the focus it is sometimes possible to follow a single nerve fibre for a long distance. This is of course difficult to show in a photograph, but Pl. II, fig. 5 pictures rather a long portion of such a fibre, though not one of the thinnest. The diameter of this axon varies, in some parts there is more blue material, which causes the axon to swell, such swellings gradually continuing into extremely thin, thread-like portions.

In the central and lower parts of the protocerebrum swellings become very pronounced and numerous, and therefore this region, especially in sagittal sections, is very conspicuous on account of its dark blue colour (Pl. I, fig. 1 and Pl. III, fig. 9).

There are some differences in detail between the species investigated. In *Sphecius speciosus* the blue fibres are very striking. The single axon is swollen for a shorter or longer distance and then again may get thin and fine. Such elongate thickenings seem to recur several times in the same axon (Pl. II, fig. 6—7). Besides there are also roundish blue lumps or bulbs which occur just around the main tract and probably are connected with this by means of fine filaments which are difficult to trace. Similar

fine fibres, which leave the main bundle and go out into the surrounding brain tissue, were often observed in the other *Hymenoptera* investigated. As they are generally very thin, it is as a rule impossible to decide where they end, but in some cases it seems that they only make a sort of detour into the surrounding tissue and then return to the main route. Such a case is seen in Pl. IV, fig. 13 (*Synagris*), where it could be photographed on account of the bead-like swellings of the fibre. Whether these fine diverging fibres are complete axons or branches of axons could not be decided. I did not succeed in observing any convincing case of branching.

In *Synagris* the swellings are not so long and gradual as in *Sphecius*, but generally appear as short fusiform or sausage-shaped lumps connected by fine filaments. But besides there are round bulbs and also fine moniliform fibres (Pl. IV, fig. 13). In the most successful slides (*Synagris*) it could be distinctly seen that the swellings and bulbs are not uniform, but granular in structure. Thus it seems that they are really formed by accumulations of small granules like those observed in the pericaryon and in the proximal part of the axons. In *Eumenes* and *Vespa* the moniliform fibres predominate, and this also applies to *Apis* and *Megachile*.

In several insects it has been observed that the two fibre bundles which arise from the two medial groups of neurosecretory cells cross in the anterior part of the brain, and this is rightly considered typical. Owing to the fusion of the two medial cell groups in the *Hymenoptera* their axons likewise join to form one median nerve tract, as evident in transversal sections (Pl. V, fig. 17 and Pl. VII, fig. 27). Even so it is possible to observe that the nerve fibres do cross in a similar way as in other insects, though it could not be decided whether all fibres cross. In the above-mentioned photographs (especially Pl. VII, fig. 27) it should be possible to see some evidence of this c h i a s m a in the lower part of the picture. Also other nerve fibres from the right and left parts of the protocerebrum cross in the same region.

Just below the chiasma the fibre tract divides into two, which may remain very close together (as in *Eumenes*) or become more separate (as in *Megachile* and *Apis*). In the antero-ventral region of the brain the fibre tracts curve and proceed in a posterior direction lying very near to the ventral wall of the brain, below the perineurium. This is best seen in sagittal sections (Pl. III, fig. 9 and 10). In the ventral part, which comprises about half of the length of the whole fibre tract, the axons run close together, and no fibres are seen to leave the general course. The swellings show almost the same picture as in the middle of the brain.

Near the posterior surface of the brain the two neurosecretory tracts diverge more, and just before they leave the brain the axons swell considerably. This is very striking in *Eumenes*, *Vespa* (Pl. VII, fig. 26), *Synagris*, and *Sphecius* (Pl. II, fig. 8), where there are big collections of blue material in this place, bigger even in some slides which were not photographed. One cannot help getting an impression that this region forms a mechanical obstruction, which somehow dams up the regular flow of secretory material through the nerve fibres. The swelling of the axons in the central part of the brain might similarly be explained as caused by the curving

of the fibres in the antero-ventral region which slows down the flow of the axoplasm carrying the neurosecretory substance.

In most of the species studied I was unable to observe any lateral (external) root of the nervus corporis cardiaci; only in *Belonogaster*, where I got some obliquely horizontal sections, could this root be found (Pl. VIII, fig. 30). It contained blue, moniliform axons and in some cases also what seemed to be phloxinophilic fibres.

The fibre tracts from the neurosecretory cells extend from the brain as the nervi corporis cardiaci, which, as already mentioned, are short, especially in *Vespa* and *Sphecius*, where the corpora cardiaca almost adhere to the brain. Where the nerves are longer, the chrome-hematoxylin positive axons can be distinctly seen. This is impressively illustrated by the sections of *Synagris* shown on Pl. IV, fig. 14 and 15. In this case the blue, rope-like fibres almost fill the nerve, and one cannot escape the notion of witnessing a copious flow of neurosecretory material from the brain down into the corpus cardiacum.

However, it should be noted that not all axons are blue; some of them are phloxinophilic and mostly thin; perhaps the blue material passes now through some, now through other axons. But it seems that also the red axons may sometimes appear swollen.

The Corpora Cardiaca.

The two corpora cardiaca are oviform or pear-shaped organs lying behind the brain.

The nervus corporis cardiaci, as already mentioned, enters the c. cardiacum laterally, and the axons of the nerve usually form a remarkable blue strand which runs through the c. cardiacum near its lateral surface (Pl. IV, fig. 16 and Pl. V, fig. 19; as to *Megachile* cp. p. 8).

From the fibre bundle ("nerf basal" of CAZAL) the axons diverge, finding their way between the cells of the c. cardiacum and tending—as it seems—towards the surface of the organ. Whether the axons also branch in the c. cardiacum or whether they continue undivided, could not be decided with certainty, though branching was probably observed in a few cases.

Inside the c. cardiacum the axons show many large swellings which are fusiform, ovoid or spheroid in shape. In accordance with STUTINSKY (1952) and ARVY and GABE (1952a and b) it was found that the nerve fibres containing the blue-stained material lie between the cells; though some doubtful cases occurred I could never convince myself that nerve fibres entered cells or connected with them.

In the central part of the c. cardiacum delicate fibres with rather small and regular, bead-like swellings are often seen, but also larger globular or ovoid bulbs (see especially Pl. V, fig. 20). The bulbs somewhat resemble the "Herring-bodies" of the neurohypophysis in vertebrates, and like these they are swellings of nerve fibres caused by local accumulations of neurosecretory material. Although these blue

bulbs may occur almost everywhere in the c. cardiacum they are most numerous near the medial surface, which turns against the aorta and the oesophagus. In some cases this region is literally crammed with blue material. Just as is the case in the brain the bulbs and swellings in the c. cardiacum after suitable differentiation can be seen to consist of smaller elements, which are combined into granular structures.

As found also in other insects the c. cardiacum contains two sorts of cells. The large cells are rounded or polygonal, phloxinophilic cells which vary much in size; the cell borders are distinct. Along the lateral surface they are arranged in a single layer resembling an epithelium (Pl. V, fig. 19); they also make up much of the central and posterior parts of the c. cardiacum, where the cells either occur singly or form roundish clusters between which the blue nerve fibres are seen. They have large spheroid nuclei with one or several conspicuous phloxin-stained nucleoli and small red granules, probably chromatin. I have not been able to detect any cellular processes, so it seems that these cells are not nerve cells.

STUTINSKY (1952) observed a phloxinophilic secretion in the cells of the c. cardiacum of *Carausius*, and ARVY and GABE described a similar phenomenon in *Ephemeroptera* and *Odonata* (1952a and b). These authors therefore regard the large cells as secretory cells. In my material the cytoplasm did not contain definite granules, but in several cases irregular or rounded red masses—one might call it a phloxinophilic colloid—were seen between the cells. It is possible that this "colloid" might represent a secretion produced by the large cells. Such red masses are especially distinct in *Vespa*, where they occur in the region closest to the brain and—what is more surprising—also just inside the brain, but only at the place where the neurosecretory fibres leave (Pl. VII, fig. 26). This observation is a warning not to disregard the alternative possibility that the red colloid might be a product of the brain which, like the blue substance, migrates into the c. cardiacum. In this connection we should remember the occurrence of red droplets in certain neurosecretory cells (p. 10) and the presence of red nerve fibres in the nervus corporis cardiaci (p. 14). Inside the c. cardiacum the red colloid seems to occur intercellularly and not to be confined within the axons. The final decision as to its origin must await further investigation.

The small cells occur in a rather irregular way between the groups of large cells, and besides they almost exclusively form the medial side of the corpus cardiacum, where they are interwoven by the nerve endings containing the blue neurosecretory material (Pl. V, fig. 19—20, Pl. VI, fig. 23—24). Mostly it seems that these cells are almost devoid of cytoplasm, only consisting of a nucleus, somewhat varying in shape and size and containing several small phloxinophilic granules. In other cases, however, the nuclei appear to be situated in vacuolated cytoplasm without definite cell borders, thus forming a sort of syncytium. Several authors have decribed these cells as glia cells, and it is true that they do resemble glia cells, though this designation is perhaps to some degree suggested by the hitherto prevailing concept of the large cells as nerve cells. Furthermore not all small nuclei of the c. cardiacum are of identical nature. Tracheae enter the c. cardiacum from the surface, and there-

fore some of the more elongate nuclei belong to the tracheal cells. And along the nerve fibres of the nervus corporis cardiaci some very small and thin, fusiform nuclei can be found which probably belong to "neurilemma cells" entering the c. cardiacum together with the nerve fibres.

The preceding description of the morphology of the c. cardiacum is mainly based on sections of *Synagris* and *Eumenes*. In the other species studied the appearance of the organ is somewhat different and not quite so clear. In *Megachile* the number of small cells much exceeds that of the large ones, which are mostly confined to the anterior end of the c. cardiacum. In *Sphecius* (Pl. II, fig. 8) and in *Vespa* (Pl. VII, fig. 26) the c. cardiacum looks highly vacuolated and the single cells are difficult to distinguish, but here again the small nuclei seem to predominate in number. The blue neurosecretory material occurs in smaller quantity in the c. cardiaca of these three forms than in *Synagris* and *Eumenes*.

The c. cardiacum of *Apis* is still more peculiar. Most cells are small, highly vacuolated and without distinct borders, only dorsally a few large cells occur with a phloxinophilic, finely granular cytoplasm; these, like the small cells, seem to form a syncytium; the nuclei contain several red granules. Among the cells are found numerous fine, partly moniliform, blue threads, which at first were taken to be nerve fibres with neurosecretory material. A closer study revealed, however, that at least some of these threads are connected with the cuticula-like membrane covering the surface of the organ; in reality the c. cardiacum is subdivided into lobes by fine lamellae descending from the outer covering. Similar blue lamellae are seen to surround the lobes of the c. allatum of *Apis* and the c. cardiacum and c. allatum of *Sphecius*. In this insect unmistakable nerve fibres with neurosecretory material can be observed in the c. cardiacum besides the "cuticular" structures (Pl. II, fig. 8), but this was not the case in the honey-bee. As, however, the intracerebral fibres of the nervus corporis cardiaci in *Apis* show the typical appearance of blue swollen axons, it is possible that the apparent lack of neurosecretory material in the c. cardiacum of the bee only represents a temporary stage, perhaps due to age or season. The specimens sectioned were workers caught in late autumn. No doubt the neurosecretory cells and endocrine organs of the honey-bee deserve a more detailed study.

The Corpus Allatum.

The corpora allata show a much more uniform structure in the *Hymenoptera* investigated than do the c. cardiaca. They are globular or oviform organs connected with the lower or posterior part of the c. cardiacum. They are typically solid organs, but abnormally a small cavity may occur (Pl. VI, fig. 24). The c. allatum consists of rather a restricted number of cells, which vary considerably in size. The size of the nuclei varies still more, the largest ones mostly occurring at the dorsal (anterior) end of the c. allatum. The nucleus generally encloses one big nucleolus and a number

of small granules and threads, probably chromatin. The cytoplasm in the Bouin-fixed sections looks vacuolated or reticular and stains red with the phloxin; as in most other insects the cells of the c. allatum do not show any morphological signs of being secretory, though such a function must be assumed to occur.

The dorsal or anterior end, nearest to the c. cardiacum, has a hilus, through which the nervus corporis allati enters the c. allatum. This nerve is a direct continuation of the nervus corporis cardiaci, of which not all the fibres end in the c. cardiacum, but some continue through the whole length of this organ, keeping laterally, and leave the c. cardiacum ventrally (or posteriorly) as the nervus corporis allati.

It is of some importance to decide whether neurosecretory material is transported along these nerve fibres on to the c. allatum. This was stated to occur in blattids and *Gryllus* by STUTINSKY (1952), and in *Bombyx* by ARVY, BOUNHIOL and GABE (1953).

In *Synagris* and *Eumenes* the existence of blue secretory material in the nervus corporis allati could be observed with great clearness. Transversal sections like those shown in the photographs on Pl. VI are best adapted for demonstrating the connection between the c. cardiaca and allata. The free portion of the nervus corporis allati is very short; the nerve winds somewhat, but perhaps this appearance is augmented by the shrinkage caused by the Bouin fixation. The segment of the nerve inside the c. cardiacum—as repeatedly mentioned—is conspicuous on account of the abundant neurosecretory material present in the axons. Bulbs and swellings are also seen in the axons just leaving the c. cardiacum (Pl. VI, fig. 24), and they continue down into the c. allatum (Pl. VI, fig. 22—23). In the actual sections it is seen better than in the photographs that the blue material is contained inside axons of the nervus corporis allati, which at intervals are dilated by the substance, although the swellings are much smaller than many seen in the c. cardiacum. In the c. allatum the nerve divides into branches which ramify between the cells, the finer branches being difficult to follow. Occasionally a few blue granules could be observed among the cells of the c. allatum, but on the whole the neurosecretory material somehow seems to disappear in the c. allatum.

In the other *Hymenoptera* studied the c. allatum lies so close to the c. cardiacum that practically no free nerve can be found between them. No secretory material was observed in the c. allatum of these species.

Discussion.

The preceding description shows the existence in the *Hymenoptera* of a typical neurosecretory pathway which agrees in all essentials with the diagram set forth by B. and E. SCHARRER (1944 and later). Neurosecretory cells, localized in the pars intercerebralis of the brain, contain stained granules which can be traced

also in the whole course of the fibre bundle comprising the axons of these cells and innervating the corpus cardiacum.

In 1944 such an idea might seem a rather bold generalization as few insects had in fact been studied in this respect, but, as mentioned in the introduction, during the last few years a number of cases have been described which confirm the hypothesis of the Scharrers.

The material presented in this paper seems to show convincingly that such transport occurs, at least as far as stained sections can evince that an active movement takes place. The recent studies of B. SCHARRER (1952a and b) on *Leucophaea* and E. THOMSEN (1954a and b) on *Calliphora* substantiates the hypothesis experimentally, for they found that either by cutting (*Leucophaea*) or ligaturing (*Calliphora*) the nervous connection between the brain and the corpus cardiacum, could the flow of neurosecretory material be blocked. Of course the crucial proof would be the direct observation of moving particles in living nerve fibres, as made by CARLISLE (1953) in preparations of the X-organ connective of the crustaceans *Lysmata* and *Dromia*, but so far this has not been possible in insects.

The original diagram of B. and E. SCHARRER can be amended by adding that neurosecretory material also reaches the corpus allatum, as clearly seen in *Eumenes* and *Synagris*. Probably this occurs in many (perhaps all) insects, for it has been observed also in the living nervi corporis allati of the fly *Calliphora* (E. THOMSEN 1954) and in stained sections of other insects (cp. p. 17). These results suggest the possibility that the c. allatum is activated by means of neurosecretory material produced in the pars intercerebralis. The experiments of E. THOMSEN (1952) on the adult *Calliphora* have already indicated that the c. allatum is activated from the medial neurosecretory cells of the brain.

The corpus cardiacum in the *Hymenoptera*, when stained with chrome-hematoxylin-phloxin, presents a striking picture described on the preceding pages. There is no doubt that a copious amount of neurosecretory material is drained down into the c. cardiacum through the nervus corporis cardiaci. This material seems to be stored for some time in the c. cardiacum, probably still remaining inside the nerve fibres, and finally to be discharged through the surface of the organ into the blood stream. Most of the neurosecretory material collects along the medial surface of the c. cardiacum, from where it may ooze out into the aorta. Here it is at once diluted by the blood so that it is no more possible to show its presence by staining methods.

In the experiments of E. THOMSEN (1952) referred to above it was shown that the c. cardiacum could to some extent be substituted for the neurosecretory brain cells and vice versa. This can be explained by the storing of neurosecretory material in the c. cardiacum.

It is likely, however, that the c. cardiacum is not exclusively a storage organ for a substance produced in the brain. During the last few years morphological evidence has been presented that the large cells of the c. cardiacum do themselves function as secretory cells (STUTINSKY 1952, ARVY and GABE 1952). The phloxinophilic colloid

found between the cells in some of the *Hymenoptera* is perhaps a secretory product of the cells, but so far the possibility cannot be excluded that this substance is also produced by neurosecretory cells of the brain and transported down into the c. cardiacum.

The physiological role of the small cells of the c. cardiacum is unknown. As already mentioned, they have often been spoken of as glia cells, but this designation does not convey much information about their real significance.

The concept of the structure of the c. cardiacum commonly held for some years was introduced by PFLUGFELDER (1937) and further elaborated by CAZAL (1948). According to these authors the c. cardiacum consists of chromophile and chromophobe cells. The chromophile cells—corresponding to our large cells—were described by CAZAL as provided with pseudopodia-like prolongations, often ramified and of considerable length, and besides he found so-called "formations chromophiles", closely resembling the prolongations, but not connected with cells.

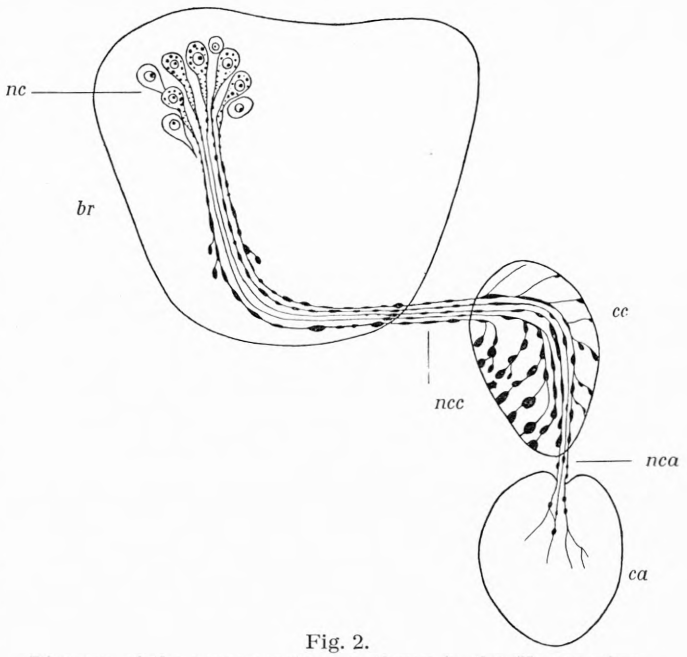

Fig. 2.
Diagram of the neurosecretory pathway in the *Hymenoptera*. *br* brain; *ca* corpus allatum; *cc* corpus cardiacum; *nc* neurosecretory cells; *nca* nervus corporis allati; *ncc* nervus corporis cardiaci.

There is hardly any doubt that the osmic acid impregnation used has led to a misconception of the structure. The "prolongements chromophiles" and the "formations chromophiles" are in all probability the same elements, viz. nerve fibres more or less dilated by neurosecretory material which forms local swellings and bulbs. In the *Hymenoptera* it is clear that there is no connection between these structures and the cells of the c. cardiacum, and no prolongations of the cells were ever observed. STUTINSKY (1952) and ARVY and GABE (1952a and b) came to a similar conclusion. Thus, although the c. cardiaca may have originated as ganglia (HANSTRÖM 1940), it seems that in present-day insects the cells have no axons or other processes and thus lack the typical characteristic of nerve cells.[1]

[1] In an earlier publication (M. THOMSEN 1951) I have described "axonlike processes" from cells of the c. cardiacum of the *Ptychoptera* larva. This observation is open to the same objections as those of CAZAL, as I used the same technique, and the material ought to be reinvestigated.

The revised concept of the neurosecretory pathway according to the preceding discussion is schematically illustrated in text-figure 2, which is modelled after a figure in B. and E. SCHARRER's paper from 1944.

The secretory material included in the neurosecretory cells of various animals is generally described as granular, but sometimes cells occur which in addition contain a homogeneous colloid often staining differently (cp. B. SCHARRER 1941 and other papers). The neurosecretory cells of the *Hymenoptera* mostly contain small discrete granules which may combine into bigger aggregations; they stain blue with the hematoxylin of the Gomori stain. In two species also phloxinophilic inclusions were observed, which seem to be droplets; they are thought to represent another stage in the secretory cycle of the same material, but this has not been proved.

In the nerve fibres the same structure of the blue neurosecretory material can be demonstrated. The swellings, bulbs, etc., are not homogeneous, but, at least in the sections best fixed and stained, show a granular structure indicating that they are composed of particles. In the thinner regions of the axons the material consists of separate granules lying in a single row. In the proximal, thicker part of the axon the granules form a superficial layer.

These observations suggest that in the *Hymenoptera* the neurosecretory material is mostly in a solid state and forms discrete granules. It is possible, that such granules may occasionally be subdivided into still smaller particles, thereby assuming colloid properties, and this may be connected with the change in staining properties from blue to red (cp. CARLISLE 1953 and PASSANO 1954). S. W. SMITH regards similar minute granules in various vertebrates as "relatively dehydrated, very viscous coacervate particles," which may coalesce due to hydration so that hyaline masses are formed. This explanation only applies to the blue-stained material; the phloxinophilic inclusions sometimes present in the neurosecretory cells he provisionally regards as "qualitatively distinct from the CHP-positive type." In the *Crustacea* studied by CARLISLE and PASSANO there is good evidence that the blue and red staining material is qualitatively identical.

Summary.

1. The neurosecretory cells and the retrocerebral endocrine organs have been studied in several species of *Hymenoptera aculeata*, in most cases on sections stained with Gomori's chrome-hematoxylin-phloxin stain.

2. The medial neurosecretory cells mostly contain dark blue granules which form aggregates of varying size. In *Belonogaster* and *Sphecius* also phloxinophilic droplets occurred.

3. The axons of the medial neurosecretory cells contain blue-stained material which in some of the species is very abundant, forming swellings, moniliform strings or lumps. The fibre bundle is very distinct in these species.

4. Lateral neurosecretory cells were not localized; the lateral root of the nervus

corporis cardiaci was only observed with certainty in *Belonogaster*, but probably occurs in the others, too.

5. The nervus corporis cardiaci contains blue axons, which continue into the corpus cardiacum, where most of them deviate from the main bundle (the "nerf basal"), tending towards the surface. Both in the free part of the nerve and inside the c. cardiacum the nerve fibres show more or less conspicuous swellings and bulbs, which in the most developed cases convincingly demonstrate the flow of abundant neurosecretory material from the brain into the c. cardiacum.

6. In several cases the c. cardiacum also contained a phloxinophilic colloid, which may be a secretion of the large cells of the c. cardiacum, although the possibility of its cerebral origin could not be excluded.

7. Some of the nerve fibres of the nervus corporis cardiaci pass through the c. cardiacum and form the short nervus corporis allati. Blue neurosecretory granules occur in the axons of this nerve, but are very rare inside the c. allatum.

8. The results of the present study are in full accordance with the diagram of B. and E. Scharrer (1944) which can be amplified by adding that not only the corpus cardiacum, but also the c. allatum receives neurosecretory material. This substance is produced by definite cells of the brain and transported in the axons of these cells to the organs mentioned.

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Færdig fra trykkeriet den 1. sept. 1954.

PLATES

PLATE I

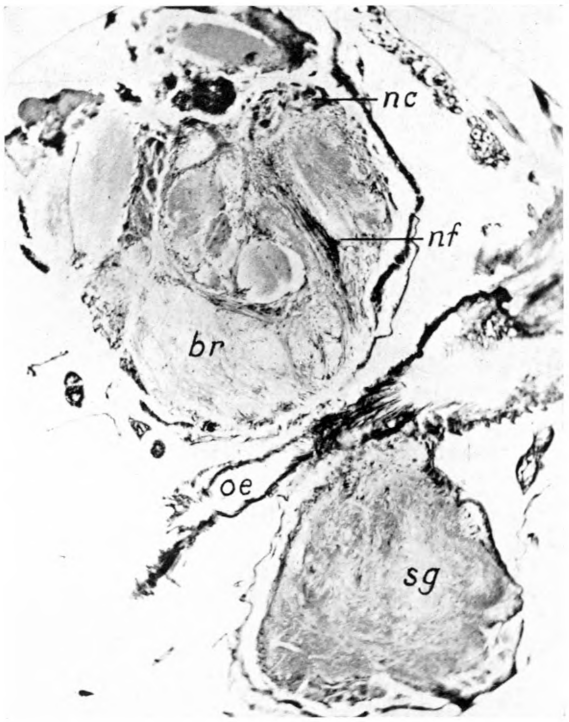
Sphecius speciosus.

Fig. 1. Sagittal section through brain (*br*) and suboesophageal ganglion (*sg*), anterior part to the right in the picture. *nc* group of neurosecretory cells; *nf* fibre bundle consisting of axons from neurosecretory cells containing abundant neurosecretory material, the ventral and posterior portion of the bundle not seen in this section; *oe* oesophagus; *sg* suboesophageal ganglion 60 ×.

Fig. 2. The same group of neurosecretory cells as shown in fig. 1. Note the dark-blue granules, abundantly present in many cells, and the thin axons. Red filter. 300 ×.

Fig. 3. Neurosecretory cells highly magnified. *na* proximal part of axon with granules at surface appearing as two rows. Other axons faintly seen. 720 ×.

Fig. 4. Neurosecretory cells, one of them showing axon. 540 ×.



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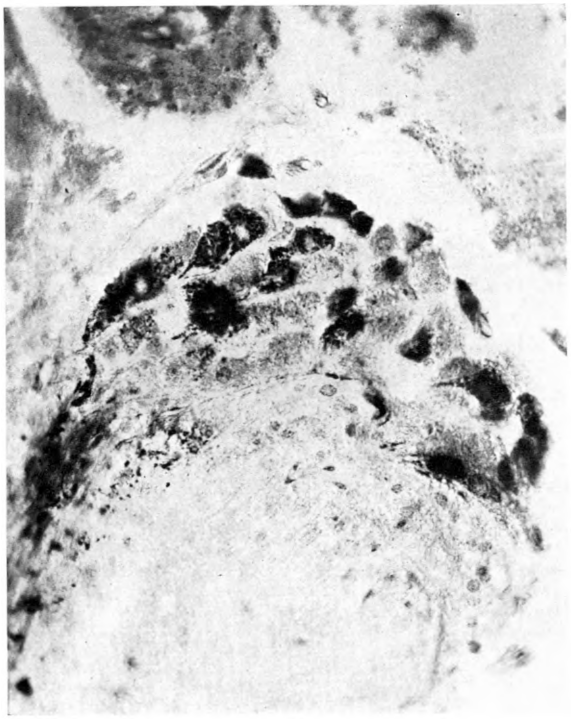

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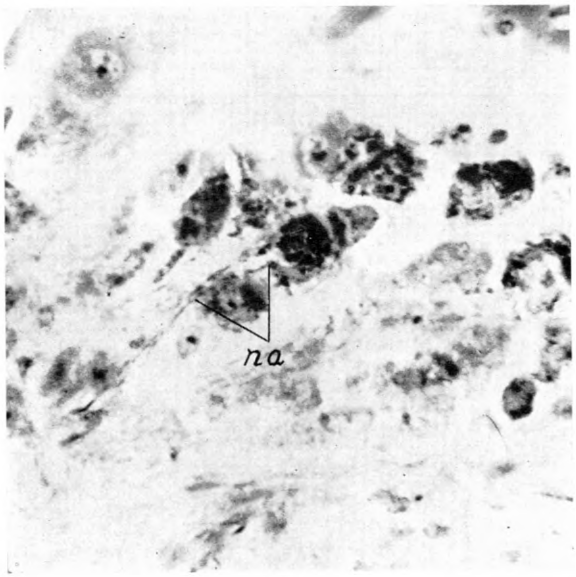

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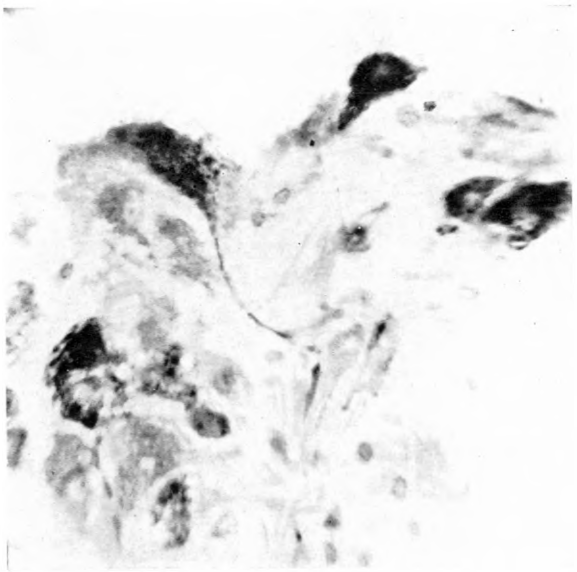

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PLATE II

Sphecius speciosus.

Fig. 5. Single axon with neurosecretory material from dorsal part of brain, showing elongate swellings connected by delicate filaments. On the right other axons are visible. Red filter. 900 ×.

Fig. 6. Portion of intracerebral fibre bundle formed by the axons from the neurosecretory cells. Some axons are swollen and contain abundant blue material, others appear as fine filaments with bead-like thickenings. 500 ×.

Fig. 7. The fibre bundle, coming from above, curves backwards when approaching the ventral wall of the brain seen on the lower margin of the picture. Note the swellings of the single axons. *nl* neural lamella; *pe* perineurium cell; *tr* trachea, around which the fibre bundle bends. 500 ×.

Fig. 8. The corpus allatum (*ca*) and the corpus cardiacum (*cc*) lying behind the brain (*br*, the letters being placed in an artificial break of the section). *ncc* nervus corporis cardiaci, which is very short in this species; *sm* secretory material in highly swollen axons of the nervus corporis cardiaci just before it leaves the brain. Some few blue axons are visible in the nervus corporis cardiaci, and blue droplets in the corpus cardiacum proper. Sagittal section. 300 ×.

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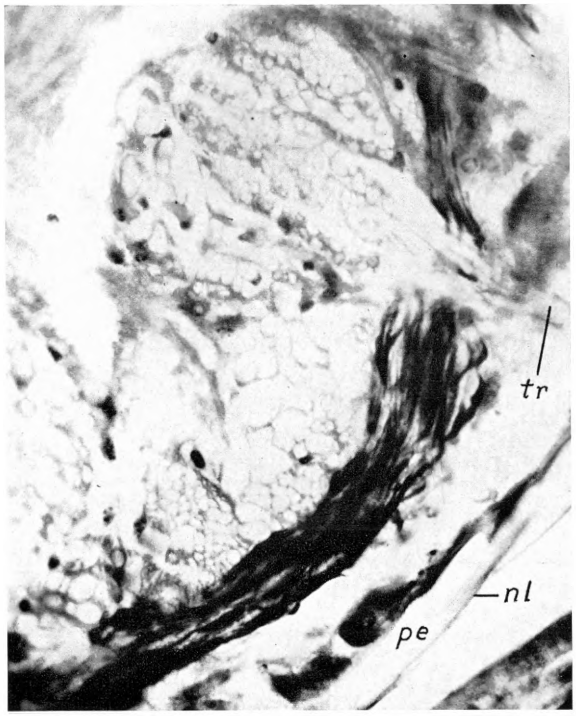

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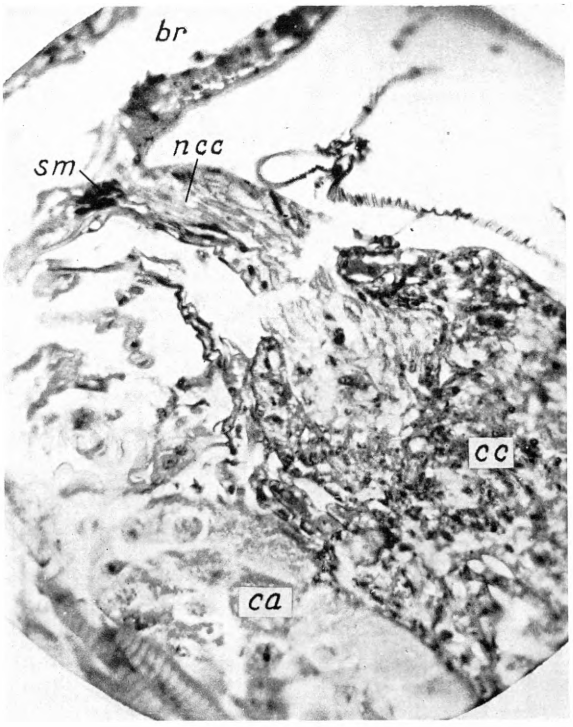

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PLATE III

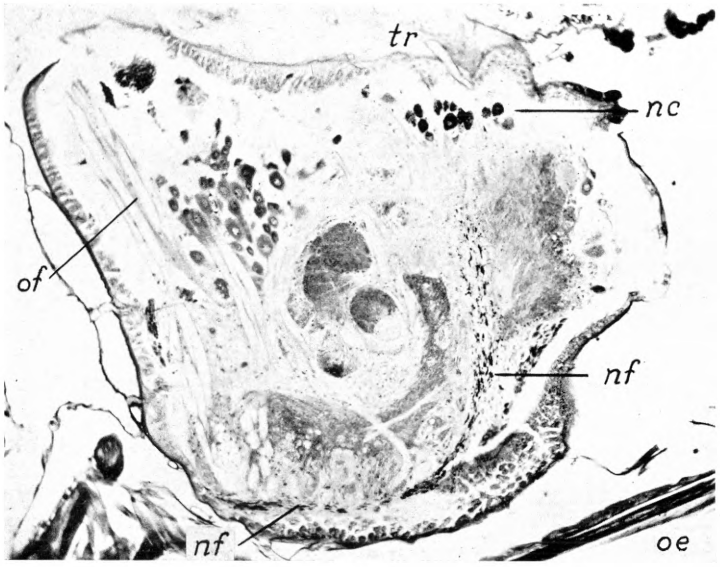
Synagris calida.

Fig. 9. Sagittal section through the pars intercerebralis of the brain; anterior part on the right in the picture. *nc* group of neurosecretory cells; *nf* fibre bundle formed of axons from neurosecretory cells, containing blue material; *oe* oesophagus; *of* fibres from median ocellus; *tr* trachea entering brain. 100 ×.

Fig. 10. Portion of neurosecretory fibre bundle near ventral wall of brain, from another section of the brain shown in fig. 9. Axons with definite swellings caused by the great amount of neurosecretory material. *nr* nervus recurrens; *vb* ventral wall of brain. 540 ×.

Fig. 11. Group of neurosecretory cells from the pars intercerebralis. *nf* axons with neurosecretory material. 300 ×.

Fig. 12. Neurosecretory cells with distinct granules. 540 ×.



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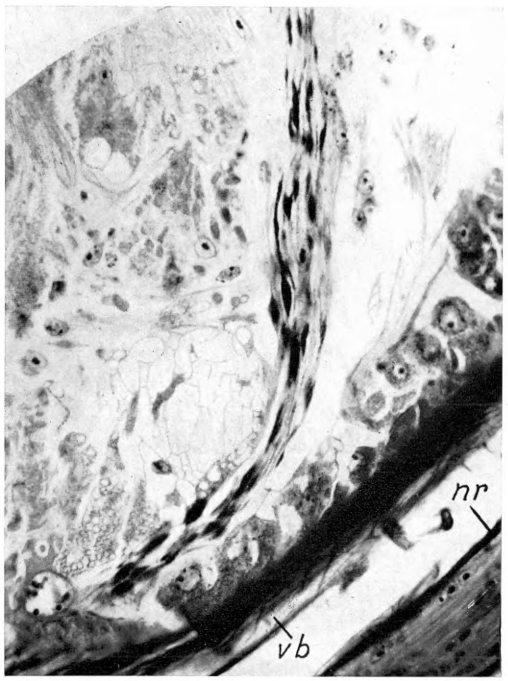

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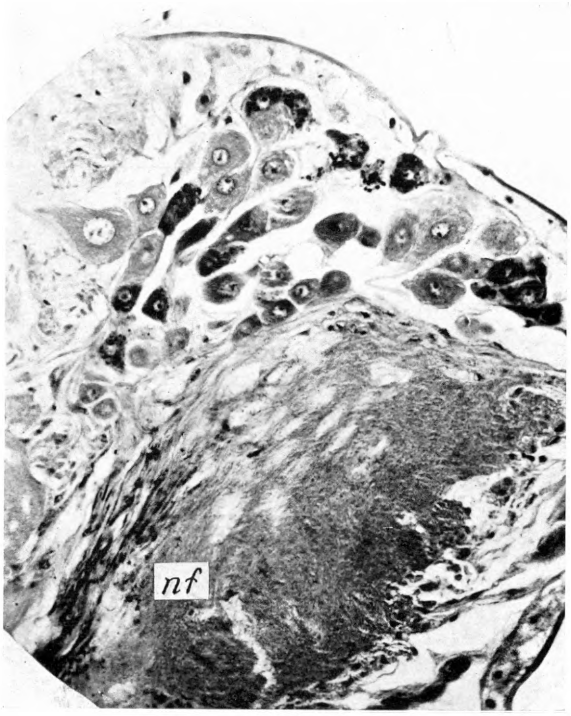

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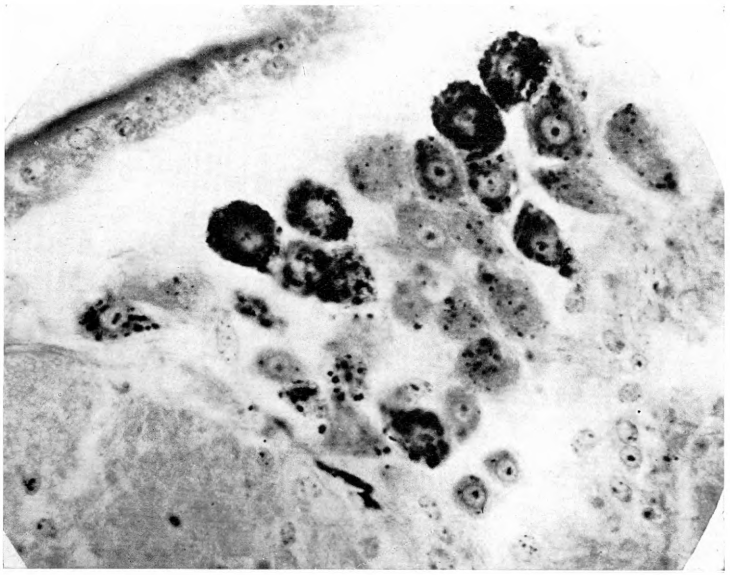

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PLATE IV

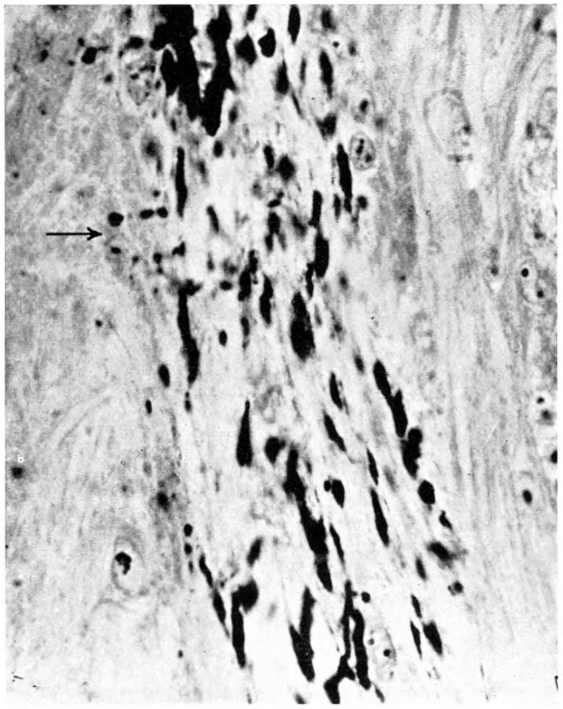
Synagris calida.

Fig. 13. Small portion of the neurosecretory fibre bundle inside the brain, numerous axons with swellings are seen; the arrow on the left points to a moniliform fibre making a loop. 900 ×.

Fig. 14. The nervus corporis cardiaci (*ncc*) leaving the brain (*b*); the nerve has been slightly torn where the letters *ncc* are placed; *cc* corpus cardiacum. The heavily stained and swollen axons are distinctly seen. Sagittal section 300 ×.

Fig. 15. Neighbouring section at higher magnification. The axons of the nervus corporis cardiaci (*ncc*) contain a substantial quantity of neurosecretory material which is flowing down into the corpus cardiacum (*cc*). 540 ×.

Fig. 16. The second corpus cardiacum of the same specimen as shown in figs. 14—15. The axons coming from the neurosecretory brain cells form a well-defined bundle with numerous swellings and bulbs. Note also the large rounded cells of the c. cardiacum. *ncc* nervus corporis cardiaci. 300 ×.



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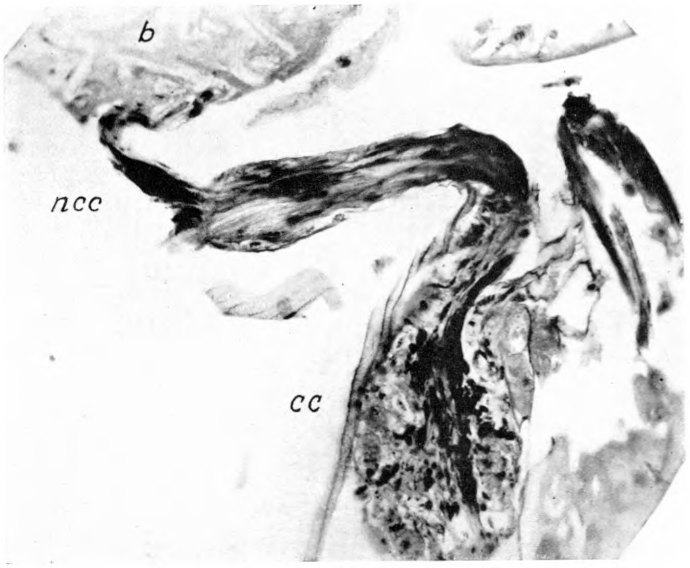

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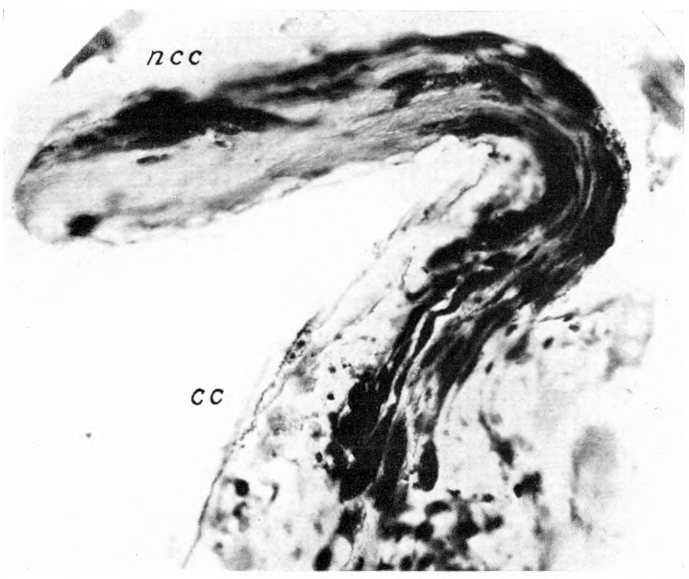

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PLATE V

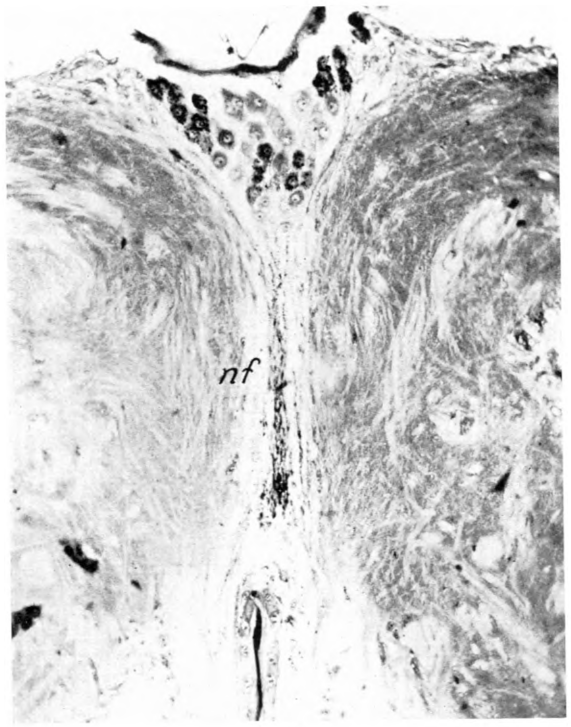
Eumenes sp.

Fig. 17. Transversal section of brain showing dorsal part of the pars intercerebralis with the neurosecretory cells constituting one medial group; the blue stained axons (*nf*) run towards the ventral part of the brain. Section no. 86 of the series. 200 ×.

Fig. 18. Neurosecretory cells from a sagittal section of the brain. The light medium-sized cells between those with dark granules are probably phloxinophilic neurosecretory cells in another phase of secretion. Below and on the right two large nerve cells. 900 ×.

Fig. 19. Section of the corpus cardiacum with large cells in the upper and central parts and small cells at bottom. The axons of the nervus corporis cardiaci continue inside the organ near its latero-caudal side (right in picture) and fan out between the cells. Abundant neurosecretory material near antero-medial surface. 540 ×.

Fig. 20. Posterior part of corpus cardiacum with abundant neurosecretory material. In upper and central part of picture large corpus cardiacum cells and between these moniliform axons 900 ×.



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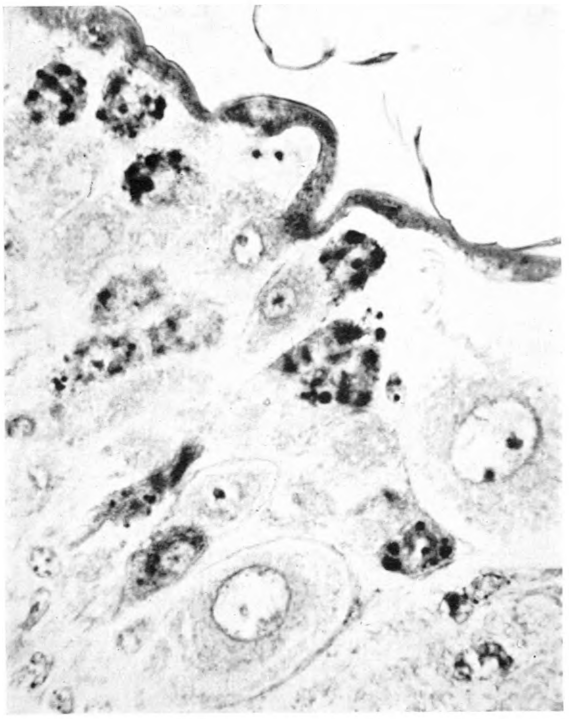

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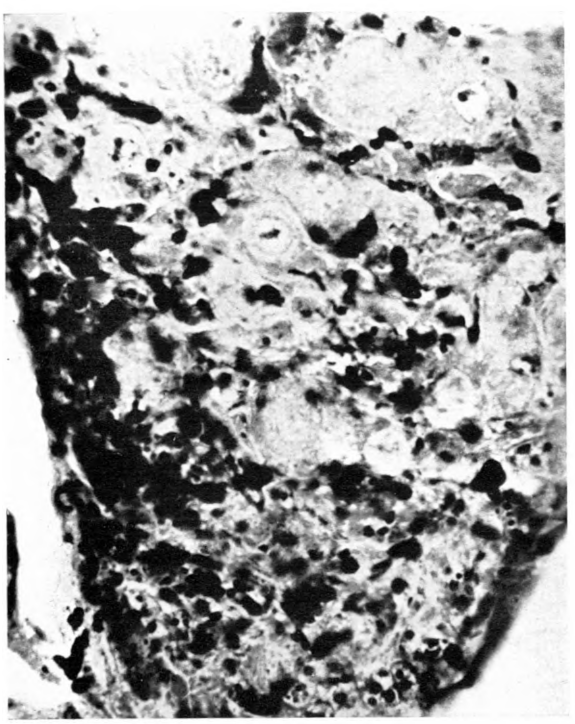

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PLATE VI

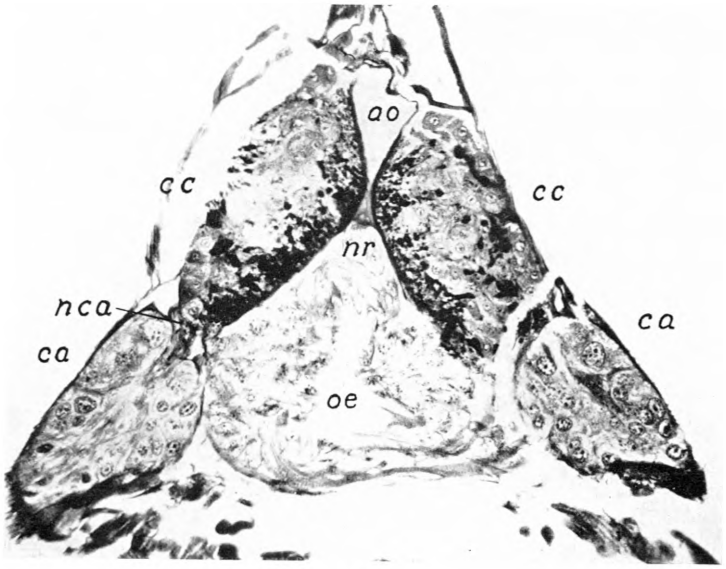
Eumenes sp.

Fig. 21. Transversal section of the retrocerebral endocrine organs (section no. 21 from the same series as fig. 17). The neurosecretory material in the corpora cardiaca is mostly collected at the mediad surface. *ao* aorta, probably the lumen has contracted somewhat due to the fixation; *ca* corpus allatum; *cc* corpus cardiacum; *nca* nervus corporis allati, only cut on the left side; *nr* nervus recurrens; *oe* oesophagus. 200 ×.

Fig. 22. Left side of the section shown in fig. 21, at higher magnification. *ca* corpus allatum; *cc* corpus cardiacum; *nca* nervus corporis allati containing blue material; *oe* oesophagus. 500 ×.

Fig. 23. The connection between the corpus cardiacum and the c. allatum on the right side. Same series, section no. 23. *ao* aorta; *ca* corpus allatum; *cc* corpus cardiacum; *nca* nervus corporis allati; *oe* oesophagus. Note the neurosecretory material in the nervus corporis allati. 500 ×.

Fig. 24. Section no. 19 of the same series. *fb* the fibre bundle inside the corpus cardiacum which continues as the nervus corporis allati (cp. fig. 22). Other letters as in preceding figures. 540 ×.



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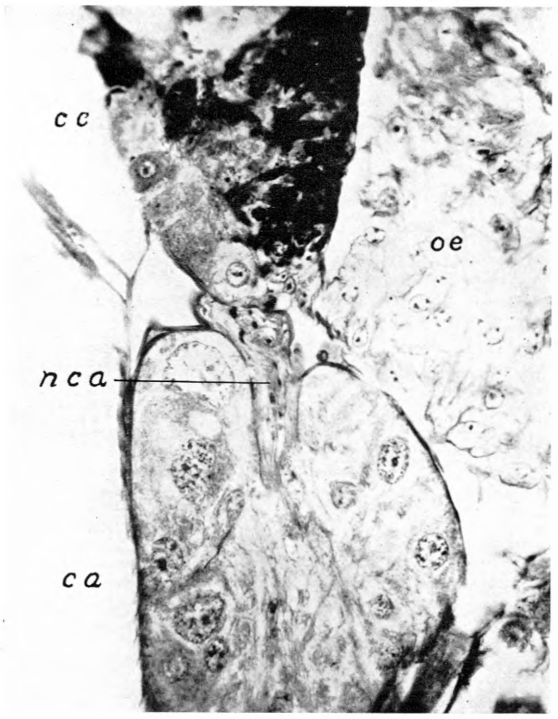

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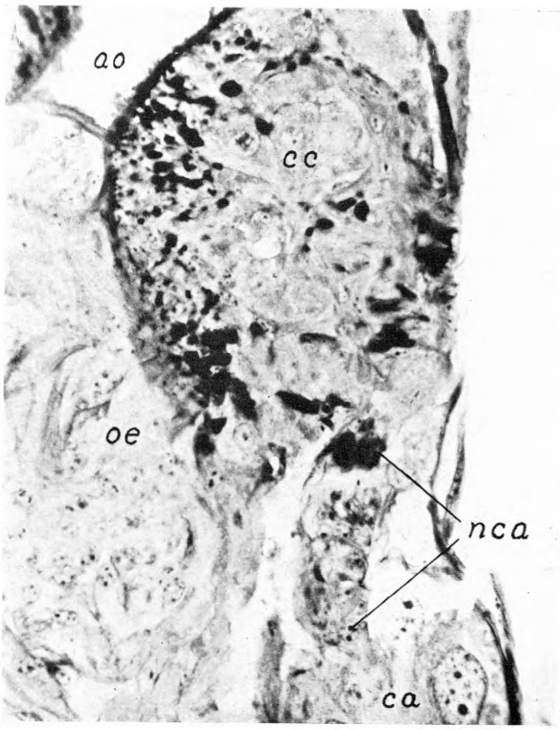

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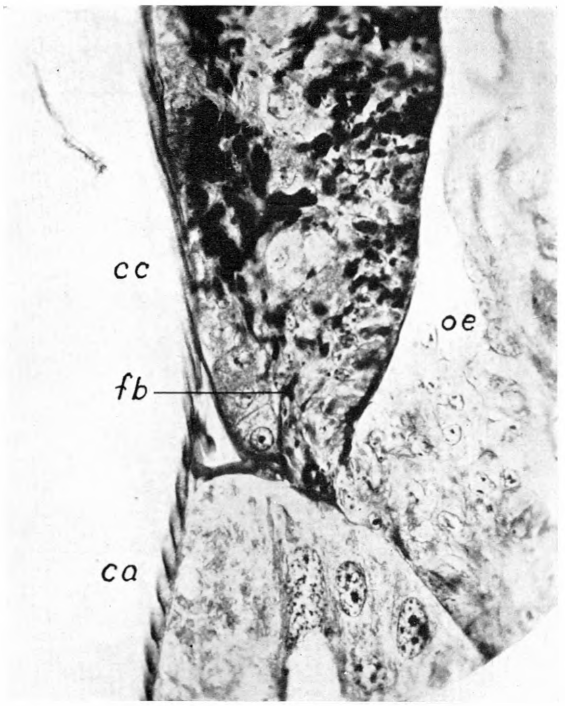

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PLATE VII

Vespa vulgaris.

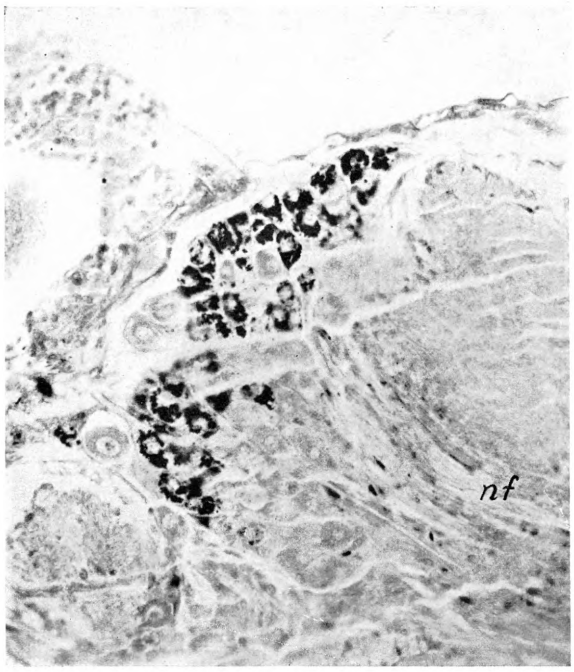
Fig. 25. Neurosecretory cells from the pars intercerebralis; sagittal section. *nf* axons. A few tracheae are visible. 300 ×.

Fig. 26. The connection between the brain and the corpus cardiacum (*cc*); sagittal section. *na* blue stained axon in c. cardiacum; *sb* collection of blue and red secretory substance in the brain; *sc* blue axons and red colloid in the c. cardiacum. The blue parts appear black in the photograph, the red ones grey. 500 ×.

Megachile cincta.

Fig. 27. Transversal section of the brain showing the group of neurosecretory cells (below *nc*). *cp* corpus pedunculatum (calix internus); *nf* crossing axons from the neurosecretory cells. 200 ×.

Fig. 28. Transversal section of the retrocerebral endocrine organs of another specimen. *ao* aorta; *ca* corpus allatum; *cc* corpus cardiacum; *ha* hypocerebral ganglion; *mu* muscles; *ncc* nervus corporis cardiaci; *oe* oesophagus; *vc* ventral bridge connecting the two corpora cardiaca. 200 ×.



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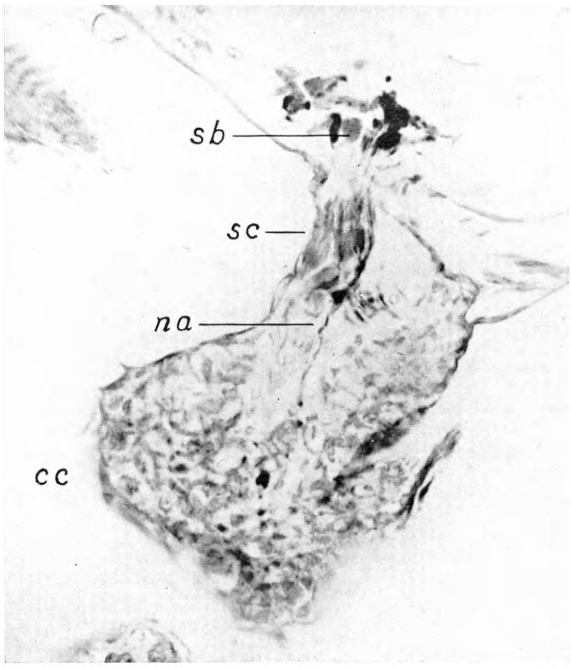

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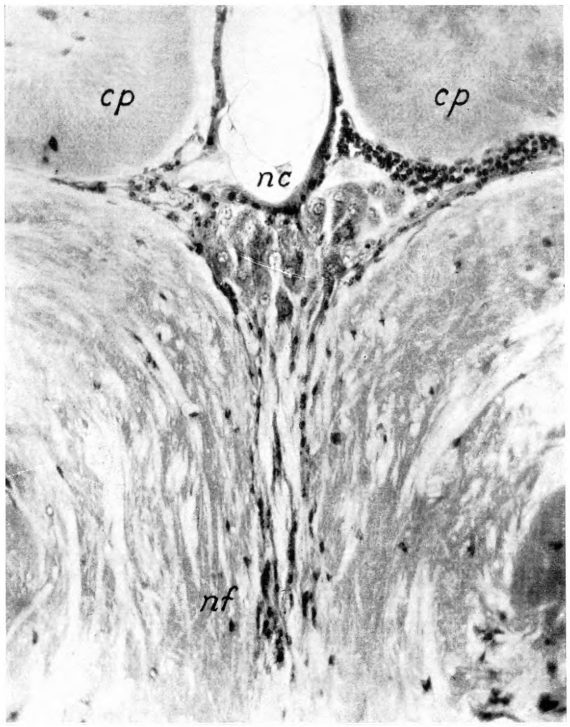

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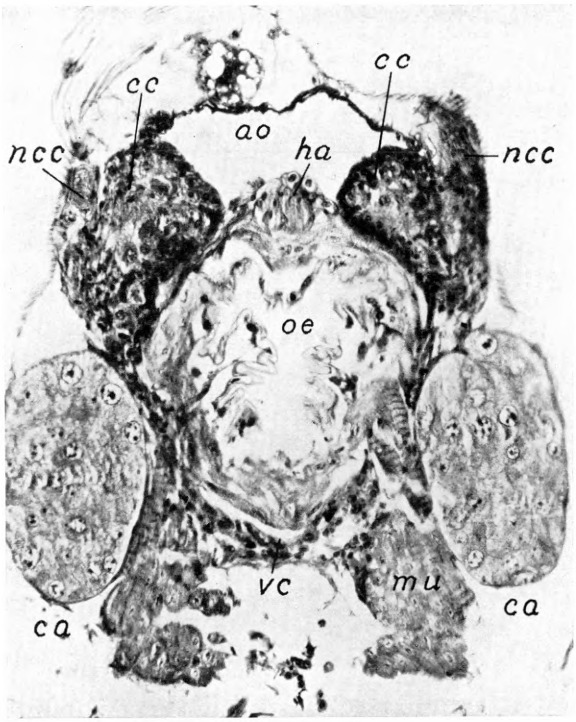

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PLATE VIII

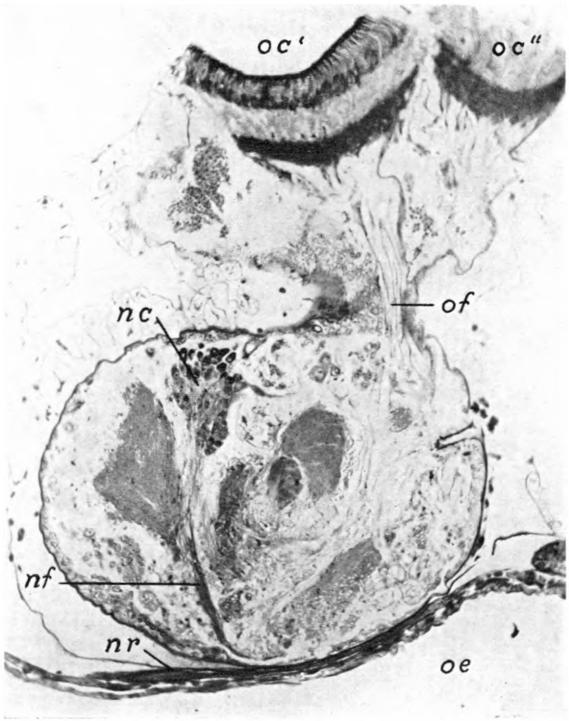
Belonogaster junceus.

Fig. 29. Sagittal section through the pars intercerebralis of the brain; anterior part left in picture. *nc* group of neurosecretory cells; *nf* fibre bundle constituted of the axons from these cells; *nr* nervus recurrens; *oc*' median ocellus; *oc*" lateral ocellus; *oe* oesophagus; *of* nerve fibres from ocellus. 100 ×.

Fig. 30. Obliquely horizontal section through the postero-ventral part of the brain (*br*). *ao* aorta; *cc* corpus cardiacum; *mu* muscle; *nr* nervus recurrens; *oe* oesophagus; *rl* lateral root of nervus corporis cardiaci; *rm* medial root of same. 200 ×.

Fig. 31. Group of neurosecretory cells from the pars intercerebralis, sagittal section. Smaller cells with blue granules (black in the photograph), and larger cells with red spherules (grey in the photograph), cp. the text p. 10. Red filter. 500 ×.

Fig. 32. Part of same group highly magnified. The red spherules are best seen in cells marked with arrows. The blue granules mostly form cap-like accumulations above the nuclei. Red filter. 1000 ×.



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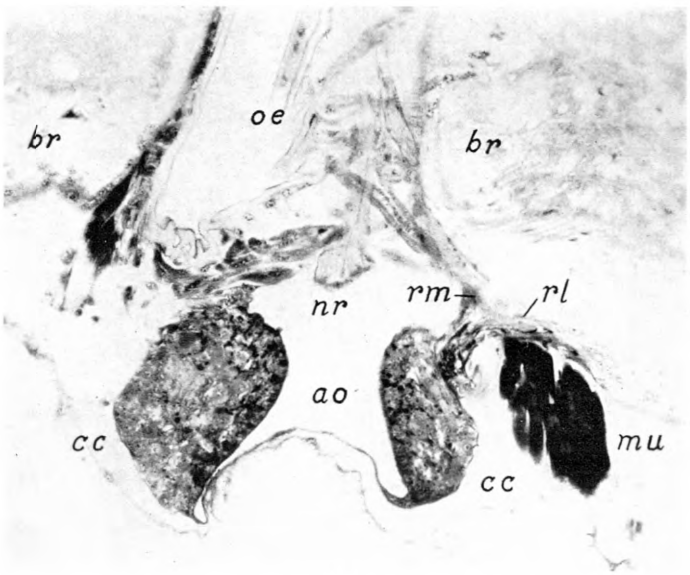

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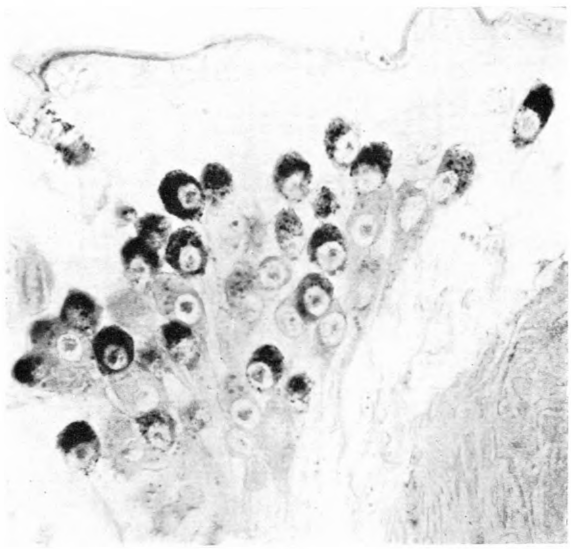

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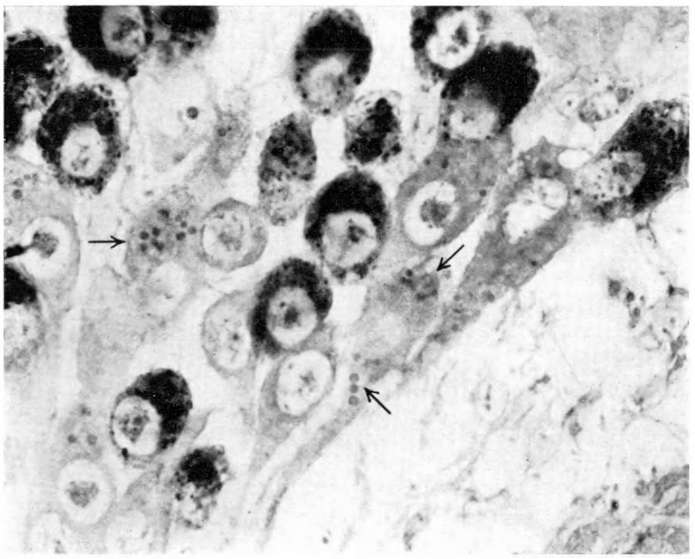

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Det Kongelige Danske Videnskabernes Selskab

Biologiske Skrifter

Dan. Biol. Skr.

Bind **3** (kr. 60.50)

kr. ø.

1. Olsen, Sigurd: Danish Charophyta. Chorological, Ecological and Biological Investigations. 1944 ..... 22.00
2. Jessen, Knud, and Helbæk, Hans: Cereals in Great Britain and Ireland in Prehistoric and Early Historic Times. 1944 ..... 8.50
3. Gram, K., Jørgensen, C. A., og Køie, M.: De jydske Egekrat og deres Flora. 1944 26.00
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BY

E. FJERDINGSTAD

København 1954
i kommission hos Ejnar Munksgaard

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I. Introduction.

The dried-up Bølling Sø, from which pollen diagrams have been published by IVERSEN (1941, 1942, and 1947), is situated in the centre of Jutland at the boundary of the large Karup heath flat and is surrounded on all sides by sandy soil. According to IVERSEN (1941), the greater part of the rather shallow basin is filled with late-glacial sediments. "The post-glacial gyttja is much compressed; at the deepest point the whole Atlantic, sub-boreal, and sub-Atlantic period constitutes less than 1 m. This is connected with the very slow sedimentation in this oligotrophic area. The samples are very rich in pollen, and there are no gaps in the pollen diagram." (Translated from Danish).

IVERSEN (1945, pp. 41—43, and 1947, p. 69) mentions the immense value of which the microflora may be for the elucidation of the climatic variations in late-glacial times. Furthermore, it is pointed out that in certain cases the microflora reacts more readily than the higher vegetation. "Periods with a cold climate are characterised by cold-water diatoms and, in a few cases, Desmidiaceae, while periods with a mild climate are characterised by an abundance of Chlorophyceae and Cyanophyceae." (Translated). It is also pointed out "that the microflora will depend to a very great extent on local conditions, notably on the shape of the lake basin, and in many cases it will be essentially the same throughout the whole late-glacial period, but that a sudden change frequently occurs in the Allerød period, sometimes already at the first, but often not till the second deviation in the birch curve, which in this way, too, is seen to represent the climatic optimum of the period. In the younger Dryas the microflora as a rule reverts just as suddenly to the original cold-water diatomaceous flora, which persists until the beginning of the post-glacial period." (Translated from Danish).

From these considerations JOHS. IVERSEN, Ph. D., State Geologist, in 1944 asked the author to examine the microflora of some samples taken in Bølling Sø in 1939, after which it was intended to carry out a more thorough examination of the changes in the composition of the microflora on the basis of a series of samples taken in 1946. The pollen analysis, however, revealed some disturbances in the post-glacial part of the series of strata, and this unfortunately rendered a treatment of the post-glacial strata on the basis of the 1946-material impossible; the treatment of an essential part of these strata was therefore based on the 1939-material only.

The author considered it necessary that limnological points of view should be taken into account to the greatest possible extent in the treatment of the results. Hence it was necessary to draw parallels with present-day Danish lakes, and recent spectra from a number of Danish lakes are therefore given in tables IV, V, and VII.

The material as well as information of the place of the samples in pollen zones, etc., were kindly placed at my disposal by Dr. JOHS. IVERSEN; for this as well as for many interesting conversations about Bølling Sø I express my most cordial thanks.

The organisms figured on pl. V, which are characteristic components of the micro-communities of the late-glacial Bølling Sø, were drawn by the author from material derived from the lake, the fair drawings, however, were done by Miss Ingeborg Frederiksen. The translation into English was done by Miss E. Gleerup.

II. Methods.

In preparing the special slides of the diatoms on which the calculation of the percentage occurrence of the diatoms is based, the material was treated with 30 % hydrogen peroxide in accordance with the method described by BRANDER (1936, p. 135) and used by HUSTEDT as well (1948, p. 183).

To obtain the special preparations of Chlorophyceae and Cyanophyceae the material was treated with 10 % sodium hydroxide. As for the 1939-material, the frequencies were calculated on the basis of a number of individuals of 1850—1950, with the exception, however, of samples 97/39 and 108/39, for which the frequencies, owing to their small content of organisms, had to be calculated from a number of 1393 and 296, respectively.

The procedure used in counting was to count all the organisms found in the particular preparation.

Of samples 97/39 and 108/39 five slides were made owing to the small number of diatoms which they contain. The count represents the total number of all the five preparations. The percentage frequency is only indicated for species and varieties present in at least five specimens; as to the rest, their presence is indicated by a +.

In the 1939-material the Chlorophyceae and the Cyanophyceae were only counted in preparation no. 66/39; the frequency was here computed on the basis of a number of individuals of 478. As for the numerical treatment of the species of *Pediastrum*, fragments were counted as numbers of cells and then converted into individuals, 25 cells being regarded as the equivalent of one individual.

In the 1946-material the total number of micro-organisms in all the samples was taken into consideration in the numerical treatment. For that purpose a general preparation of material in suspension in water was first made for each sample. In this preparation the interrelation between diatoms, Chlorophyceae, and Cyanophyceae was determined, and then preparations for the further determination were made in the way described above. In these special preparations the frequency of the individual

species was determined, the mutual relation between the various groups of organisms being taken into consideration.

For the 1946-material it was attempted in some measure to take the degree of covering into consideration, an ocular micrometer having been used for the counting. Every time one of its division lines "hit" an organism, the presence of the particular species was noted as 1. The distance between the lines with the magnification used (1000 ×) was 0.97 μ. By this procedure it was ensured that larger diatoms, notably of the genera *Cymbella* and *Pinnularia*, which, as a rule, are represented in these samples by a few specimens only, were to a less extent "suppressed" by the small species, rich in individuals, of the genus *Fragilaria*.

A complete computation of the degree of covering must, at any rate as regards the benthic algae, require a computation of the area for each individual species, for plankton forms of the cubic content, a procedure which must seem quite overwhelming in practice, not least if the organism in question has no mathemathical shape; cf. also NYGAARD (1950, p. 5), who for the solution of this problem, as far as the plankton organisms are concerned, proposes a computation of the weight.

HUSTEDT (1948, p. 187), however, maintains that in the analysis of the diatoms, in contrast to the pollen analysis, one may abandon the quantitative analysis, but that the qualitative analysis should be carried out all the more carefully. Of decisive importance, according to HUSTEDT, is only the presence of this or that species. The author, however, does not entirely share this view, but is of opinion that the composition of the micro-communities must be considered of paramount importance, and that it is the composition of the communities which should alone form the basis of the geological as well as the limnological conclusions that are drawn (cf. p. 14).

III. The Microflora.

The late-glacial strata (Tables I and II).

a. *Earliest Dryas.*

The micro-organisms from this period, belonging to pollen zone I a and characterised by a cold climate, according to MILTHERS (1935, p. 163) with a July temperature of probably 8—10° C., are exclusively diatoms. In the 1939-material, sample 108, the community-forming organisms are *Fragilaria construens, F. construens* var. *venter*, and *F. pinnata*. Of the other species present the following should be mentioned: *Amphora ovalis, Cyclotella comta, Cymbella ventricosa, Diatoma vulgaris, Epithemia sorex, E. zebra, Gyrosigma attenuatum*, and *Synedra ulna*. The total number of species and varieties is 23.

b. *The Bølling oscillation.*

According to IVERSEN (1947, p. 73), the Bølling oscillation is an older heat oscillation of a similar character, though of less extent, to the Allerød oscillation.

It manifests itself stratigraphically as a layer of diatomaceous gyttja in the middle of the older Dryas clay, and in the pollen diagram a sharply defined maximum of *Betula* pollen is seen there.

From this layer, termed pollen zone I b, a sample is at hand from 1939, and two samples from the 1946-material.

Sample 97/1939 shows a very great frequency of *Fragilaria construens* and *F. construens* var. *venter*, while *Fragilaria pinnata* constitutes 3.1 % only. A similar fall in frequency is shown by the other diatoms, as e. g. *Amphora ovalis, Gyrosigma attenuatum*, and *Synedra ulna*.

Of diatoms with small frequencies may further be mentioned *Epithemia turgida, Fragilaria construens* var. *binodis, F. lapponica*, and *Melosira arenaria*, cf. Table I.

That the total number of species and varieties in this sample—26—is greater than in the sample from the earliest Dryas, is due to the fact that (besides those included in the numerical treatment) a good many species have been added which according to CLEVE-EULER (1922, p. 51) are markedly "heat-forms", e. g. *Cymbella Ehrenbergi, Navicula oblonga*, and *Surirella Caproni*, cf. p. 13. New-comers are further *Cymatopleura solea, C. elliptica, Cymbella obtuciuscula, Epithemia turgida, Fragilaria construens* var. *binodis, F. lapponica, Navicula menisculus, N. oblonga, N. placentula, N. pupula* var. *rectangularis, N. viridula*, and *Pinnularis gentilis*.

In the 1946-material, sample 637, the microflora consists of such species as *Fragilaria Harrissonii* and *F. pinnata*. The other species and varieties present which were included in the numerical treatment are *Amphora ovalis, Fragilaria construens, F. construens* var. *binodis*, and *F. pinnata* var. *lancettula*. The total number of species and varieties is 14. Sample 635 likewise belongs to the Bølling oscillation. The dominant species there are *Fragilaria Harrissonii* with the variety *dubia* and *F. pinnata*. The total number of species and varieties is 9, cf. Table II.

The dominant species *Fragilaria Harrissonii* occurs in recent waters in bottom mud, especially in stagnant waters, and in an ecological respect it hardly differs from the other dominant species of *Fragilaria* occurring in Bølling Sø; but it is remarkable that *F. Harrissonii* only occurs as a dominant in the samples from the Bølling oscillation and the succeeding sample from pollen zone I c—early Dryas, that is, within the strata from depths 305—335 cm.[1]

c. *Early Dryas.*

In the 1946-material the early Dryas is represented by sample 630. The microcommunity of this sample consists of *Fragilaria construens, F. Harrissonii*, and *F. pinnata*. In this very sandy sample only three community-forming organisms were found. The most characteristic feature of the sample is that *Fragilaria construens* has again attained a frequency which places it as a dominant with the highest percentage.

[1] FOGED (1948) records the species from Odense Aa and Vindinge Aa, both alkaline streams.

d. *Allerød a.*

With the Allerød a period a climatic change to a milder climate with a July temperature of probably ca. 12° C. set in, cf. MILTHERS (1935, p. 163). Sample 86/39 belongs to pollen zone II a, and of dominant species it contains only *Fragilaria construens* and its variety *venter*; cf. Table II. Of the remaining species the following should be mentioned: *Amphora ovalis, Diatoma vulgaris, Diploneis ovalis, D. ovalis* var. *oblonga, Epithemia sorex, E. turgida, E. zebra, Fragilaria construens* var. *binodis, F. pinnata, Melosira arenaria,* and *Neidium iridis.*

The sample thus shows a considerable increase in the number of species as compared with the samples from the Bølling oscillation (1939-material), but of the total number of species, 42, only 12 are included in the numerical treatment.

In the 1946-material the Allerød a is represented by samples 628, 624, 621, and 618. In these samples *Fragilaria construens* and its varieties constitute 65.8, 39.0, 10.2, and 46.1 %, respectively, while *F. Harrissonii* and its varieties exhibit 2.0, 3.6, 8.0, and 0.5 %, and *F. pinnata* and its varieties 7.8, 42.1, 36.4, and 24.9 %, respectively. Together these three species and their varieties constitute 75.4, 84.7, 54.6, and 71.5 %, respectively.

Of diatoms which in the numerical treatment attain frequencies in one or several of the aforementioned samples, the following may be mentioned: *Amphora perpusilla, A. veneta, Cyclotella comta, Cymbella cuspidata, C. ventricosa, Diatoma vulgare, Diploneis ovalis* var. *oblongella, Epithemia argus* (only in sample 275 and there only with 1.8 %), *E. sorex* (only in sample 275 with 2.6 %), *Fragilaria brevistriata* (only in sample 275 with 4.6 %), *Gomphonema constrictum, Melosira granulata* (sample 275 with 1.6 %), *Navicula anglica, N. placentula* (only in sample 275 with 1.1 %), *N. Schönfeldii* (only in sample 295 with 1.3 %), *N. tuscula* forma *minor* (only in sample 265 with 1.1 %), *Rhopalodia gibba* (only in sample 265 with 3.8 %), *R. gibberula* (only in sample 265 with 1.4 %), *Stauroneis phoenicenteron, Stephanodiscus astraea* var. *minutula* (only in sample 265 with 0.6 %), and *Synedra ulna.*

Of more "heat-requiring" species mention may be made of *Cyclotella comta* and *Melosira granulata,* but it should be added that *Cyclotella comta* was also noted in the sample from the earliest Dryas, though with a low frequency (1.8 %), whereas *Melosira granulata* did not appear till in the samples from the Allerød period.

Mention should further be made of *Surirella Caproni* and *Synedra capitata,* which were described by CLEVE-EULER (1922, p. 56) as "heat forms", and which are also present in the sample from the Bølling oscillation.

Finally, the Chlorophyceae appear for the first time in sample 265, represented by such species as *Pediastrum Kawraiskii* (7.2 %) and *Scenedesmus quadricauda* (0.9 %). In view of this fact and owing to the considerable increase in the number of diatom species, the composition of the microflora in the early Allerød period differed essentially from that of the early Dryas. However, as regards Bølling Sø the distinctive change in the composition of the microflora did not set in till the Allerød b period (pollen zone II b); cf. Pl. III.

e. *Allerød b.*

From the Allerød b, which in a climatic respect represents a heat maximum, three samples are at hand from the 1946-material, nos. 608, 610, and 613, and one from the 1939-material, no. 117. Characteristic of these samples is the immense reduction in the number of diatoms, which in the above-mentioned samples attain a frequency of only 1.0, 3.7, and 0 %, respectively, represented by *Fragilaria construens* and *Tabellaria flocculosa*.

The dominant Chlorophyceae in the 1946-material are *Pediastrum Kawraiskii*, which constitutes 53.6 and 71.2 %, respectively, *Pediastrum Boryanum* with 25.4 and 14 %, respectively, and *Tetraedron minimum* with 14.6 and 7.5 %.

In the 1939-sample traces of the Cyanophycea *Gloeothricia* cfr. *echinulata* were also found.

f. *Late Dryas.*

From this period, when the climate deteriorated again, and the July temperature was probably only ca. 10° C., cf. MILTHERS (1935, p. 163), the 1946-material includes a number of samples, and the 1939-material a single sample, no. 130 (pollen zone III).

Already the oldest sample from this zone, no. 608/46, shows a rapid decline for the Chlorophyceae represented by the species *Pediastrum Kawraiskii* and *P. Boryanum*, and a corresponding rapid rise in frequency for the diatoms, which now constitute 61.6 %, of which *Fragilaria pinnata* constitutes the 43.4 %, while the remaining *Fragilaria* species together amount to 16.6 %.

Thus the climatic change is distinctly indicated by the composition of the microflora. The diatom flora of this sample is very poor in species. The following species and varieties were included in the numerical treatment, the majority with very low frequencies: *Achnanthes Oestrupii*, *Fragilaria brevistriata*, *F. construens*, *F. construens* var. *binodis*, *F. construens* var. *venter*, *F. Harrissonii* var. *dubia*, *F. pinnata* var. *lancettula*.

The same relation between the frequencies for Chlorophyceae and diatoms is also found in sample 606/46, where *Pediastrum Boryanum* constitutes 11.1 % and *P. Kawraiskii* 25.6 %. Of the diatoms, *Fragilaria pinnata* is dominant with 12.3 %, while the other diatoms attain frequencies below 10 %.

In sample 658/46 the share in the spectrum taken by the Chlorophyceae has fallen to 4.9 %, and the Chlorophyceae, represented by *Pediastrum Boryanum*, are thus about to disappear. Of the diatoms, *Fragilaria construens* and *F. pinnata* with 26.6 and 40.4 %, respectively, can be regarded as dominants, while the diatoms *F. construens* var. *binodis*, *F. Harrissonii* var. *dubia*, *Navicula Schönfeldii*, and *Neidium iridis* each only attains frequencies of less than 10 %. Outside the numerical treatment *Epithemia sorex* and *E. zebra* were noted.

Samples 655/46 and 651/46 contain only diatoms, of which *Fragilaria construens* attains frequencies of 32 and 26 %, respectively, and *F. pinnata* of 17 and

35.8 %, respectively. Altogether no very material changes in the composition of the diatom flora have taken place.

In sample 590/46 *Fragilaria* attains a frequency of 33.5 % and *Synedra ulna* a frequency of 30.0 %. Of species included in the numerical treatment the following should be mentioned: *Amphora ovalis, Cocconeis placentula, Cyclotella comta, Cymbella ventricosa, Epithemia sorex, Eucocconeis flexella* var. *alpestris, Fragilaria construens, F. construens* var. *semibinodis, F. construens* var. *venter, F. Harrissonii, F. Harrissonii* var. *dubia, Nitzschia stagnorum, Synedra capitata,* and *Tabellaria fenestrata.*

In the 1939-material the late Dryas is represented by sample 130. The dominant diatoms, which together attain a frequency of 82.3 %, are *Fragilaria construens* (48.5 %), *F. construens* var. *venter* (19.9 %), and *F. Harrissonii* (13.9 %). The numerical treatment further comprises: *Amphora ovalis, Cocconeis placentula, Cyclotella comta, Cymatopleura solea, Cymbella Ehrenbergi, C. prostrata, C. ventricosa, Epithemia sorex, E. turgida, E. zebra, E. zebra* var. *saxonica, Eucocconeis flexella, Fragilaria pinnata, Melosira arenaria, M. granulata, Navicula cryptocephala, Rhoicosphenia curvata, Synedra affinis, S. capitata, S. ulna,* and *Tabellaria flocculosa.*

It is a considerable number of species that are present in this sample — 61 —, of all the samples the richest in species. The following twenty were seen for the first time in the sample from the late Dryas: *Achnanthes minutissima, Cocconeis pediculus, Cyclotella antiquae, C. lanceolata, C. prostrata, Diatoma elongatum, Epithemia zebra* var. *porcellus, Eucocconeis flexella, Eunotia faba, E. gracilis, Gomphonema acuminatum* var. *Brebissoni, G. constrictum, G. gracile, G. intricatum, Meridion circulare, Navicula dicephala, Nitzschia paleacea, Pinnularia subcapitata, Stauroneis anceps,* and *Tabellaria flocculosa.* The presence of *Amphora coffaeformis* and *Caloneis silicula* var. *truncatula* is probably quite casual, so they must be left out of account.

If the late-glacial samples are considered *en bloc*, it will be seen that the community-forming organisms, apart from the Allerød period, consist exclusively of species and varieties belonging to the diatom genus *Fragilaria,* especially *Fragilaria construens* and its variety *venter.*

In the sample from the earliest Dryas *Fragilaria construens* with var. *venter* is dominant, while *F. pinnata* is subdominant. In the samples from the Bølling oscillation however, the communities are composed of either *F. construens* var. *venter* or of *F. pinnata* and *F. Harrissonii.* In the samples from the early Dryas the communities are formed of either *Fragilaria Harrissonii* and *F. pinnata* or of *F. construens* var. *venter* and *F. pinnata.* In the Allerød a samples the community-forming organisms are either *Fragilaria construens* var. *venter* or *F. construens* and *F. pinnata.* The late Dryas had communities formed by *Fragilaria construens* and *F. pinnata* with *F. Harrissonii* as subdominant.

Noteworthy is the large number of diatoms which the earliest Dryas has in common with the samples from the other late-glacial strata, thus 12 with the Bølling oscillation, 20 with the Allerød a, and 17 with the late Dryas.

The post-glacial strata.

1. *The pre-boreal strata (Tables I and II).*

In this period, which belongs to pollen zone IV (birch-pine time), the July temperature rose to 12—14° C., cf. MILTHERS (1935, p. 163). The oldest sample from this zone is represented in the 1946-material as sample 585. This sample shows no decrease in frequency for *Fragilaria construens* incl. its varieties (22.8 %), but a considerable decline in frequency for *F. pinnata* (from 33.5 to 14.1 %) and for *F. Harrissonii* including its varieties a small rise in frequency (from 6.3 to 9.6 %). Together these *Fragilaria* components constitute 46.5 %.

The following diatoms jointly attain to a total frequency of 44.0 %: *Cyclotella comta, Cymbella gracilis, C. sinuata, C. ventricosa, Epithemia zebra, Fragilaria capucina* var. *lanceolata, F. virescens, Navicula cryptocephala, N. dicephala, Synedra capitata,* and *S. ulna.*

The most remarkable feature of the sample is that the Chlorophyceae, which are not present in the upper layers of the late Dryas, now appear again, represented by *Pediastrum Boryanum,* which, it is true, is only present in small numbers, frequency 1.6 %.

In the following sample, no. 580, the Chlorophyceae entirely dominate the spectrum, constituting together 85.3 %, distributed as follows: *Pediastrum Boryanum* 31.7 %, *P. Kawraiskii* 35.4 %, *Scenedesmus arcuatus* 10.3 %, and *Tetraedron minimum* 7.9 %. The Cyanophyceae together constitute 9.5 %, and are represented by spores of *Anabaena* cfr. *flos-aquae* (5.5 %) and spores of *Gloeothricia* (4.0 %). Thus the diatoms form only 5.2 % and are represented by the species *Cocconeis placentula* (0.6 %), *Fragilaria construens* (2.5 %), and *F. Harrissonii* (1.8 %).

Similarly, the Chlorophyceae with 84.9 % dominate the spectrum for sample 575, but *Scenedesmus arcuata* has now been replaced by typical *S. quadricauda* (10.2 %). The frequency for the Cyanophyceae proves to have been halved (4.8 %), still spores of *Gloeothricia* constitute 4.5 %, *Anabaena* cfr. *flos-aquae* is absent, but cells of *Microcystis* sp. occur (0.3 %). A Chrysomonade sp., probably *Tracelomonas volvocina,* attains 1.0 %.

Thus the somewhat milder climate in the pre-boreal time is manifested by a Chlorophycea maximum, corresponding in some degree to conditions in the Allerød b period. The diatoms constitute 9.3 %, which is a slight increase as compared with the preceding sample, and the sample also exhibits a greater abundance of species.

The following diatoms are present: *Amphora Normani, Cocconeis placentula, Cymatopleura solea, Cymbella prostrata, C. lanceolata, C. ventricosa, Eucocconeis flexella, Eunotia monodon, Fragilaria construens, F. construens* var. *binodis, F. construens* var. *venter, F. Harrissonii, F. Harrissonii* var. *dubia, F. pinnata, Gomphonema constrictum, Navicula helvetica, N. laterostrata, Rhopalodia gibba, R. gibberula, Synedra capitata, S. ulna,* and *Tabellaria flocculosa.*

From the 1939-material sample 66 from a depth of 160 cm is available. The dominant diatom is *Fragilaria construens,* which constitutes 49.5 %, and its variety

venter 24.6 %, together 74.1 % of all the diatoms. The other species present, which were included in the numerical treatment, each have a frequency of less than 10 %.

The predominance of *Fragilaria construens* and its variety *venter* in the late-glacial strata (with the exception of Allerød b) has now come to an end, the Chlorophyceae in the 1946-material, as in the samples mentioned above, now being predominant, while in the 1939-material it is *Tetraedron minimum*[1] which attains to the greatest frequency (45 %), *Pediastrum Boryanum* 29.5 %, and *P. Kawraiskii* 2.9 %.

2. *The boreal strata (Table I).*

In sample 49/39 from the pine-hazel period, belonging to pollen zone V, *Melosira granulata* including the variety *angustissima* is the only dominant diatom. It constitutes 81.9 % of all the individuals, while it is remarkable that *Fragilaria construens* attains only 0.3 %.

Of the remaining species, *Cyclotella stelligera* attains 7 %, while the following species exhibit quite inconsiderable frequencies: *Achnantes exigua, Amphora ovalis, Eucocconeis flexella, Fragilaria Harrissonii, Navicula cryptocephala, N. cryptocephala* forma *minuta, N. dicephala, N. radiosa, Neidium iridis, Synedra ulna,* and *Tabellaria fenestrata.* The total number of species amounts to 33.

The species *Achnantes exigua, Cyclotella stelligera, Fragilaria Harrissonii* var. *rhomboides, Navicula radiosa, N. rhynchocephala, Pinnularia appendiculata,* and *P. Legumen* are new. In this sample, also, spores of *Gloeothricia echinulata* and specimens of the Desmidiacea *Cosmarium Botrytis* were found.

The Atlantic strata (Table I).

3. *Sub-Atlantic Period (Table I).*

This is a period with a humid climate and a July temperature of probably ca. 17° C.; cf. Iversen (1944) and Milthers (1935, p. 163). The great role played by *Melosira granulata* (incl. var. *angustissima*) in the boreal layers is continued in sample 34/39 from the early Atlantic period, pollen zone VII, where with a frequency of 82.9 % it is also the only dominant species. As a subdominant *Cyclotella stelligera* attains only 7.0 %. *Amphora ovalis, Fragilaria construens, F. construens* var. *venter, Melosira arenaria, Navicula cryptocephala, Pinnularia viridis, Synedra affinis,* and *S. ulna* together constitute the remaining 10.1 %. The total number of diatoms is 43.

Cymbella aspera and *Pinnularia interrupta* are new-comers. The sample in addition contains a number of Chlorophyceae represented by *Pediastrum Boryanum* and *P. Kawraiskii,* which, however, have not been subjected to numerical treatment.

4. *Sub-Atlantic Period (Table I).*

In sample 4/39 from this climatic period, the beech period, pollen zone IX, the predominance of *Melosira granulata* (incl. var. *angustissima*) in boreal and Atlantic

[1] The frequency was calculated for Chlorophyceae only.

periods has ceased, its frequency having fallen to 7.5 %, while *Fragilaria construens* with var. *venter* has re-captured its great frequency of former periods, totalling 80.6 % or 55.3 and 25.3 %, respectively.

Of the other types, *Melosira islandica* subsp. *helvetica* constitutes 7.9 %, while *Fragilaria construens* var. *binodis*, *F. pinnata*, *Nitzschia paleacea*, and *Pinnularia subcapitata* are only present in small numbers.

Melosira islandica subsp. *helvetica*, *Nitzschia amphibia*, and *N. commutata* are new species. The sample is rather poor in species as far as diatoms are concerned (total: 23 species), but like the other samples from the post-glacial layers, it contains a number of Chlorophyceae (*Pediastrum Boryanum*) and in addition some Cyanophyceae, thus spores of *Aphanothece* sp., *Chroococcus* sp., and cells of *Microcystis* sp.

Comments.

As appears from what precedes, the microflora, without determination as to species, solely on the basis of the various algal groups, diatoms, Chlorophyceae (Desmidiaceae), and Cyanophyceae, can to some extent be used for the determination of the age of the sediments in Bølling Sø, cf. Pls. II and V.

In the early Dryas period (including the Bølling oscillation) and the late Dryas (with the exception of the earliest layer in which the Chlorophyceae are disappearing) the microflora exclusively consists of diatoms. The early and the late Dryas can be separated on the basis of the number of species, this being 2—3 times larger in the younger than in the older Dryas.

The Allerød b is characterised by its abundance of Chlorophyceae with a small element of Cyanophyceae and diatoms, while the pre-boreal climatic period is characterised by an abundance of Chlorophyceae with a larger element of Cyanophyceae than is the case in the Allerød b, cf. pl. V.

There is some indication that the remaining post-glacial climatic periods may perhaps be differentiated to some extent by means of the proportional representation of the four algal groups, but further investigations in that respect will be required before it will be possible to come to any decision.

It is a characteristic feature of the diatomaceous vegetation in the various layers that new species, dependent to a greater or less extent on alterations of the climate and possibly other conditions as well, seem to have difficulty in establishing themselves; in consequence these species attain to very low frequencies only, often they will not even manifest themselves in the numerical treatment, as is clearly revealed in Tables I and II.

Hustedt (1948, p. 186) arrived at the same result by investigation of the diatom flora of diluvial deposits, and states that this is especially true when the local species are eurytopic. It will therefore be of importance, thinks Hustedt, to attach weight to the appearance of new species as well as to study the question of species common to different layers.

"Heat forms" — "cold forms" (diatoms).

The classification of the diatoms into "heat forms" and "cold forms" played a great role especially in former times, cf. BACHMANN & CLEVE-EULER (1922). It is especially such species as *Anomoeoneis spaerophora, Cymbella Ehrenbergi, Fragilaria construens* with var. *trigona, Navicula cuspidata, N. oblonga, N. radians* var. *suecica, N. radiosa, Nitzschia sigmoidea, Cymatopleura elliptica* var. *turicensis, C. solea* var. *gracilis, Fragilaria pinnata* var. *intercedens, Gomphonema spicatum, Surirella Caproni,* and *Synedra capitata* which have been regarded as "heat forms". CLEVE-EULER (1922, p. 45) in this connection points out that we are here concerned with bottom- or littoral diatoms which in the present day occur in eutrophic waters and apart from this are more or less rare.

LUNDQVIST (1927) as well as HUSTEDT (1939, 1944, and 1948), however, strongly oppose the decisive importance which in this respect has been one-sidedly attached to the diatoms as indicators of, respectively, warm and cold climatic periods.

Drawing a comparison with Bølling Sø, we shall find that it is only an inconsiderable number of these "heat forms" that have been found in the material from this lake. It is chiefly *Fragilaria construens,* which, as mentioned above, should probably especially be characterised as dominant in periods with colder climates, but otherwise seems to be rather indifferent to the temperature fluctuations that may come into question here. *Cymbella Ehrenbergi* is present in small numbers in the 1939-samples from the Bølling oscillation, the late Dryas, and pre-boreal periods, *Navicula cuspidata* in small numbers in the 1939-samples from the Allerød a and the late Dryas. *Navicula oblonga* occurs in a few specimens from the Bølling oscillation (1939-material), *Navicula radiosa* in small numbers in the 1939-sample from the boreal period, as well as in the 1946-samples from the late Dryas, the Allerød a, and the Bølling oscillation. *Synedra capitata* is present in inconsiderable numbers in the 1939-samples from the Allerød a, the late Dryas, and the early Atlantic periods, while in the 1946-material it is found in a sample from the pre-boreal period and the late Dryas. According to HUSTEDT (1948, p. 196) they are Northern types, whose temperature requirements place them as meso-eurythermic forms in the lower part of the meso-thermic stage.

Thus, apparently, the occurrence of the aforementioned species in the Bølling Sø material should afford no basis for rightly considering them as "heat forms", as the appearance of *Cymbella Ehrenbergi, Navicula oblonga,* and *N. radiosa* in the Bølling oscillation, which is regarded as a heat period, though to a less extent than the Allerød period, will be in accordance with the placing of the species as meso-eurythermic. On the other hand, it should be pointed out that their immigration during this period can probably hardly be due to other causes than the prevailing rise of temperature at that time. Neither the pH, the alkalinity, nor the halobion spectra express any demonstrable change in the chemical conditions, cf. Tables III, VI, and VII. Nothing except the nature of the sediment, a diatomaceous gyttja a few centimetres

thick in the middle of the clay gyttja from the early Dryas, indicates a change of the environmental conditions, and from the pollen analysis we know that a rise of the temperature has taken place.[1] There is, however, a close connection between the temperature and the chemical conditions, for the degree of solubility of the nutritive substances found in the water depends on the temperature, and the circulation in nature is accordingly furthered by a rise of temperature. Moreover, some organisms require certain minimum temperatures to be able to develop. Hence it may be difficult to decide whether the main stress should be laid on the temperature itself or on the greater or smaller alteration of the chemical conditions which it produces (see further p. 26). As mentioned above, neither the pH-, the alkalinity-, nor the halobion-spectra furnish evidence of a change of the chemical conditions during this period, which is called the Bølling oscillation, nor do the spectra for the Allerød a period indicate a decisive change of the chemical conditions as far as these factors are concerned. I cannot, therefore, entirely join LUNDQVIST (1924, pp. 48—50) in his categorical rejection of the temperature rise as a cause of alterations in the composition of the microflora (for further details, cf. p. 27).

In estimating the value of a species as indicator of climatic changes, we must, according to HUSTEDT (1944), attach decisive importance to its first appearance, but in this connection less importance to its frequency. In that case the aforementioned species *Cymbella Ehrenbergi*, *Navicula oblonga*, and *N. radiosa* must be regarded as the character species of the Bølling oscillation and accordingly, in spite of all, as a kind of "heat indicators", though in a somewhat different sense from that in which the term was used by CLEVE-EULER (1922).

The author, however, agrees with IVERSEN (verbal information) in the view that no decisive significance should be attached to the presence of species occurring in small numbers only, as the ascertainment of their occurrence must to some extent be due to chance, so it may give rise to erroneous conclusions if they are included in the estimation of the material.

As to "cold-water forms" it may be mentioned that a number of species occurring in arctic areas are, it is true, present, but they are largely species with a fairly cosmopolitan distribution. A single exception is perhaps *Eunotia monodon*, which was characterised by KRASSKE (1938, p. 523) as Northern-alpine; in Bølling Sø it was found in a sample of the 1946-material, though from the preboreal period (frequency 0.1 %).

It has long been customary in works on diatoms to make comparisons with other areas as regards common species. The result of such comparisons is, as a rule, converted into percentages and thus actually suggests an accuracy which can in no way be said to be present, and by no means when the comparison is made with regions as to which our knowledge of the diatom flora is only based on a small number of samples, often taken in quite random places and as to the ecological conditions

[1] White birch occurred, whose pollen exceeds in number that of dwarf birch, cf. IVERSEN (1942, p. 143).

of which there is sometimes no information available. Localities with entirely dissimilar ecological conditions may thus come to form the basis of a comparison on which conclusions of far-reaching significance are often based. Hence no synopsis of species which this region has in common with other floral areas is given here.

Benthic species — planktonic species.

In an investigation of recent waters it is very difficult to obtain even a tolerably reliable picture of the relation between benthic and planktonic species. It is true that by investigations of oligotrophic waters we shall get an immediate impression that a low production of plankton is not necessarily accompanied by a low production of benthic types, in most cases the contrary will seem to be the case.

A drilled sample containing subfossil algae, however, should in some measure provide a truer basis for an estimation of this fact. But here it must be realised that the siliceous skeleton of the euplanktonic types is less solidly built than that of the benthic types, and that accordingly it will more easily be destroyed, which may mean a source of error. On the other hand, with drilled samples taken in or near the centre of the lake there may be a possibility of an overdimensioning of the planktonic organisms in relation to the more benthically marked organisms, notably the epiphytic shore forms. Moreover, the vegetation period of the planktonic organisms is for some species relatively short, while the benthic forms often have a vegetation period lasting from the beginning of spring till well into the autumn. Thus, there will be no inconsiderable sources of error on either side, and even if it may perhaps be assumed that these will in some degree counterbalance each other, this must be taken into consideration in a valuation of the relation between the planktonic and the benthic diatoms, as appears from the representation given in Table I (cf. Plate I). The tendency, however, which appears so distinctly from the figure, can probably be regarded as definite.

The figure shows that the benthic species played a very important role both in the early Dryas and in the late Dryas as well as in the earliest part of the Allerød layer, but also the species which must be denoted as tychoplanktonic constitute a considerable part of the total number of individuals, while the euplanktonic diatoms in the said portions of the late-glacial layers constitute only a small proportion of the number of individuals. In this younger part of the Allerød layer, however, the euplanktonic Chlorophyceae (notably *Pediastrum Boryanum* and *P. Kawraiskii*) constitute almost 100 %.

IV. Some environmental factors in Bølling Sø, judged from the relation of recent diatoms to these factors.

In recent years a great deal of work has been done by various research workers, e. g. KOLBE, KRASSKE, HUSTEDT, BOYE PETERSEN, etc., for the purpose of elucidating the relation of recent diatoms to some ecological factors, and with these investigations are associated, especially as regards Danish waters, works by BOYE PETERSEN (1943), FOGED (1948, 1950), JØRGENSEN (1948, 1950), and MØLLER (1950). In this way we have obtained knowledge of certain aspects of the ecology of recent diatoms, a knowledge which it will be natural to try to utilize for the elucidation of the environmental conditions of Bølling Sø during the late-glacial and post-glacial periods.

a. *Halobion spectra.*

As regards the ecology of the diatoms, the relation to the chloride content of the water is that which is best known. KOLBE's fundamental division of the diatoms into ecological groups according to their relation to the chloride content still remains the basis of the setting-up of halobion spectra. The works of later authors chiefly aimed at extending our knowledge of the placing of the individual species in the system, as also employing the system in ecological investigations of recent diatoms; cf. BOYE PETERSEN.

The halophobous diatoms are, according to KOLBE (1927), confined to peat bogs, mountain lakes, and similar waters. Later, however, KOLBE (1932) pointed out that the halophobous species form no natural community and are, no doubt, to a greater extent associated with other environmental factors (pH, content of organic matter, etc.) than with the content of chloride.

JØRGENSEN (1948) in this connection rightly pointed out that many acidotrophic waters have not always a lower NaCl-content than basic waters.

In Bølling Sø, as appears from Table III, the indifferent diatoms are predominant in the late-glacial as well as the post-glacial layers, the maximum and minimum being 100 % and 90.6 %, respectively, of the number of individuals, and 95.9 and 68.0 % respectively, of the number of species and varieties. This apparent contrast is due, i. a., to the circumstance that in the latter calculation were also included species of such rare occurrence that they are only indicated by a + in Tables I and II; cf. p. 4. The halophobous diatoms are represented in the late Dryas by, respectively, 0.4 % (number of individuals) and 11.0 % (number of species and varieties), in the boreal period by 2.0 % and 15 %, respectively, in the Atlantic period by 0.0 % and 11.0 %, respectively, and in the sub-Atlantic period by 7.9 % and 4.0 %, respectively. The other ecological types are not represented in the calculation on the basis of the percentage number of individuals, still in the calculation based on the

number of species and varieties the halophilous types attain to low frequencies, thus in the early Dryas: 7.0 %, the Bølling oscillation: 4.1 %, the Allerød a: 1.1 %, the late Dryas: 1.5 %, and in the sub-Atlantic period 4.0 %.

Thus the lake, as might be expected, was a purely fresh-water lake during all the periods of time.

b. *pH spectra.*

Recent investigations have shown that the diatoms depend upon the pH factor, or, as expressed by JØRGENSEN (1948), "the various diatoms have their optima within different pH limits, whether this be due to the pH value itself or to factors varying parallel with this factor."

The grouping of the recent diatoms in relation to the pH follows the system employed by HUSTEDT (1938—39), who distinguishes between

alkalibiontic, occurring at pH values above 7;
alkaliphilous, occurring at pH about 7 and with the greatest distribution at pH above 7;[1]
indifferent, equable occurrence at pH about 7;
acidophilous, occurrence at pH about 7, but with the greatest distribution at pH below 7;
acidobiontic, occurrence at pH values below 7, widest distribution at pH values of 5.5 and lower values.

On the basis of material from the Sunda Islands, HUSTEDT (1938—39) has characterised the different pH intervals as follows:

pH > 7: species occurring in quantity consist almost exclusively of alkalibiontic and alkaliphilous species in addition to indifferent species.
pH = 6—7: chiefly alkaliphilous species which are beginning to decrease within this range. The indifferent species are more frequent, while almost 30 % are represented by acidophilous species (cf. JØRGENSEN 1948, p. 45).
pH = 5—6: alkaliphilous and indifferent species are less numerous, while the acidophilous and acidobiontic species constitute up to 75 %.
pH = 4—5: no alkaliphilous species occur, the indifferent species consitute only ca. 21 % of the most frequent species, while 80 % are acidophilous, sometimes acidobiontic.
pH < 4: a very small number of species, exclusively acidobiontic.[2]

To this HUSTEDT adds that a marked acidotrophy thus does not on the whole appear till a pH interval of 5—6 is reached, and that accordingly the diatom analysis agrees with the views put forward by NAUMANN and THIENEMANN regarding the delimitation of the acidotrophic type of lake with a pH of ca. 5.6 (THIENEMANN 1932, p. 211). But HUSTEDT goes on to say that "in this connection the fact should not

[1] It should be pointed out that the alkaliphilous species thus also occur at pH values below 7 (up to ca. 6), similarly the acidophilous species may be found at pH values above 7. The terms alkaliphilous and acidophilous may therefore easily be misleading for all others than specialists in diatom ecology. It will probably be more correct to call the alkaliphilous species alkaliclinic, and the acidophilous species acidoclinic species, since actually they have their distribution around the neutral point, but with their main distribution at, respectively, the alkaline and the acid side of the neutral point. Since, however, HUSTEDT's designations have long been established and are now generally employed, I shall not cause confusion by the introduction of new terms.

[2] See, however, Bøllemosen and Lille Øksø (Table IV).

be underrated that the influence of acidotrophy is ascertainable up to a pH of 7, since for many diatoms this value means a limit that cannot be surpassed'' (translated).

On the basis of investigations in the preserved area ''Heiliges Meer'' in western Germany, BUDDE (1944, p. 273) has adopted HUSTEDT's division, and JØRGENSEN (1948, p. 45) states that his investigations of Danish lakes and ponds revealed a somewhat similar distribution.

In JØRGENSEN's work information is given of the relation of Danish diatoms to the pH; no spectra are set up for the individual waters, but coupled with BOYE PETERSEN's work (1943) it furnishes an exceedingly valuable material for the preparation of spectra. The author therefore studied the fresh waters treated in these works, and in Table IV has set up spectra for each individual lake or pond both as regards the percentages of the number of individuals and the percentages of the species and varieties. With a few exceptions the two methods of calculation give largely the same result as to dominance.

In cases where JØRGENSEN's view as to the place in the pH-system differed from those of HUSTEDT or BUDDE, the spectra were, as a rule, set up on the basis of JØRGENSEN's view. In assessing the result, importance was especially attached to spectra set up on the basis of percentage numbers of individuals.

IVERSEN (1929) has shown that the pH-value in patches of vegetation differs from that found in open water. BUDDE (1944, p. 268) mentions, as the cause of this, that at the boundary between the surface of the plants and the surrounding medium, conditions will develop that exert an essential influence on the micro-vegetation. During the process of assimilation the bicarbonate is extracted from the carbon dioxide with formation of $CaCO_3$, from which, again, OH ions, which alkalinise the border layer, are liberated by hydrolysis. In waters containing demonstrable quantities of bicarbonate, the pH value will therefore be greater at the surface of assimilating plants than in the surrounding open water.

Sphagnum (cf. BUDDE) is said to be capable of absorbing the bases from the resolved salts through the cell membrane, thus liberating acid.

The importance of the above-mentioned conditions for the pH spectra will also appear distinctly from the examples, given in Table V, of changes in the spectra from different patches of vegetation (+ bottom samples) within the same body of water. The greatest and most decisive difference is shown by the sample from Hampen Sø, where a sample from *Heleocharis* exhibits dominance for the alkaliphilous individuals with 53 %, while in the bottom sample the acidophilous individuals dominate with 42.5 %. The samples from Store Gribsø and Agersø also show remarkable changes, according to the substratum from which the material is derived. As the bottom samples will probably give the most constant spectra, and they must be regarded as the best basis of comparison for the geological samples, decisive importance was attached to these samples during the treatment of the material. However, in this connection it should be mentioned that the pH decreases with the depth of the water,

so in normal recent waters the pH will be somewhat lower at the bottom than at the surface of the water.

IVERSEN (1929, p. 283) has classified the larger Danish lakes according to pH conditions, and distinguishes between various types, which are in the main described below. The reader is also referred to the characterisation of Danish ponds made by NYGAARD (1938, p. 543).

It is obvious that these methods of division, though they take only one single factor into consideration, are nevertheless based on a condition, the pH variations, which is of fundamental significance for the distribution of the organisms. Hence it will be of much greater value, not least for employment in the service of geology, to characterise the diatom spectra according to these modes of division than to characterise them according to the pH intervals alone.

By means of the pH spectra it will be possible to distinguish between the following types of Danish waters mentioned in Table IV:

I. Constantly acid waters, in which the percentages for the acidophilous and acidobiontic individuals combined constitute 70 % or more; with two exceptions it is exclusively acidophilous individuals which attain dominance; the number of indifferent individuals may vary from 0.0 to 33.9 %. Alkaliphilous individuals occur in few acid waters, and if so, in inconsiderable numbers. It seems impossible, however, to distinguish between the strongly acid and the alternately strongly acid—slightly acid waters. The reason is that the acidobiontic species even in the strongly acid waters—with a single exception, viz. Bøndernes Mose (pH < 4)—are of less importance in the spectrum than might be expected.

II. Alternately acid and alkaline waters can be divided into two groups:
(a) Largely acid waters, in which the acidobiontic individuals are almost absent, while the acidophilous individuals constitute ca. 60 % (minimum 42.5 %, maximum 70.7 %) and the indifferent individuals 20—33 %; the alkaliphilous individuals are likewise more numerous, which is especially reflected in the spectrum for percentage number of species.

Hampen Sø, which belongs to this group, is in a way a transitional type, as appears distinctly in the percentages: for the alkaliphilous individuals 35.3 % for the indifferent ones 20.7 %, and for the acidophilous individuals 42.5 %. This is even more distinct if we look at the spectrum for percentage numbers of species, for it shows a dominance for the alkaliphilous species of 43.2 %.
(b) Largely neutral-alkaline waters. This group is readily distinguishable from the others, the indifferent and the acidophilous individuals together constituting high percentages, 23.5—50.1 %, while the alkaliphilous individuals constitute 44—67 %.

III. Constantly alkaline waters, in which the alkalibiontic and the alkaliphilous individuals together constitute ca. 90 %. But the alkalibiontic individuals do not

generally present the distribution that might be expected,[1] and in one lake only, Frederiksborg Slotssø (pH 7.2—9.7), the alkalibiontic individuals attain to predominance. It does not seem possible, therefore, solely on the basis of the diatoms to distinguish between slightly alkaline waters with a maximum pH value < 9.0 and highly alkaline waters with a maximum pH value > 9.0 or $= 9.0$.

Thus, on comparing the pH spectra from the subfossil material from Bølling Sø with spectra from recent samples (especially bottom samples) it will be possible to decide to which pH type the lake belonged during the various climatic periods, as we may distinguish between the aforementioned types: I, II a, II b, and III.

In Bølling Sø the alkaliphilous species, judging from the total number of individuals in the different layers (Table VI), constitute between 89.0 % (minimum) in sample 108 from the earliest Dryas, and 98.0 % (maximum) in sample 130 from the late Dryas. The alkalibiontic species attain the greatest frequency, 7.9 %, in sample 4 from the beech period, while the indifferent species have their greatest frequency, 8.1 %, in sample 66 from the birch-pine period. The acidophilous and acidobiontic species are represented in very small numbers only (< 1 %) and are entirely lacking in most of the samples.

Computed from the number of species and varieties, the pH spectra show a predominance, traceable through all the samples, for the alkaliphilous species, corresponding to the spectra based on the total number of individuals, though with a somewhat lower frequency, the minimum being 51.0 % in sample 49 from the pine-hazel period, and the maximum 65 % in sample 108 from the earliest Dryas. The alkalibiontic species in these spectra constitute from 0—13 %, with the maximum in sample 4 from the beech period, while the indifferent species constitute 0—20 %, with the maximum in sample 97 from the Bølling oscillation.

A comparison of the spectra for Bølling Sø with those for the recent lakes and ponds which must be referred to the group of constantly alkaline waters, will show such good agreement that there can be no doubt that Bølling Sø during the whole sequence of strata from the earliest Dryas to the beech period had a pH value above 7.0, and thus belonged to the type of lake which is characterised as constantly alkaline.

This is further confirmed by the fact that the dominant species *Fragilaria construens* and its variety *venter*, which together in the Bølling Sø material from 1939 attain the following percentages: sample no. 108, 65.5 %; no. 97, 92.0 %; no. 86, 89.6 %; no. 130, 68.4 %; no. 66, 74.1 %; no. 49, 4.3 %; no. 34, 4.1 %; no. 4, 80.6 %, are precisely dominant in bottom samples from eutrophic ponds and lakes, thus in Arresø (15.1 %), Skanderborg Sø (var. *venter*: 22.6 %), Sorø Sø (29.0 %), Sjælsø (30.3 %), Bagsværd Sø (29.3 %), Lyngby Sø (62.5 %, var. *venter*: 21.2 %), forest lake north of Mørkedam (var. *venter*: 16.4 %), Karlssø (12.0 %), Funkedam (11.6 %,

[1] In a single case, Badstuedam, which has a pH value of 7.4—9.0, the alkalibiontic species are not represented at all in the spectrum set up on the basis of percentages of individuals.

var. *venter*: 32.5 %), Badstuedam (42.0 %, var. *venter*: 28.3 %), Kongekilde Mølledam (var. *venter*: 22.3 %), and Løgsø (24.5 %).

Of these waters, the forest lake north of Mørkedam is referred to the neutral-alkaline waters, while the rest all belong to the group of constantly alkaline waters.

In samples 49 from the pine-hazel period and 34 from the early Atlantic period *Fragilaria construens* (+ var. *venter*) shows an exceedingly marked decline, and is replaced as a dominant by *Melosira granulata* + var. *angustissima*, both dominant in Tystrup Sø (46.0 %), Kongekilde Mølledam (13.3 %), Badstue-Ødam (10.1 %), and Frederiksborg Slotssø (47.0 %), all of which are constantly alkaline lakes.

c. *Alkalinity spectra.*

Hustedt (1938—39) divided the diatoms according to their relation to alkalinity, setting up four groups, of which the calciphobous group especially comprises species which as to pH are characterised as acidobiontic and acidophilous, while the indifferent group especially includes species which as to pH are indifferent, alkaliphilous, or alkalibiontic.

Hustedt (p. 291) states that the majority of diatoms within rather wide limits appear to be indifferent to alkalinity. It is further pointed out that the alkalinity within the intermediate range and the lower values of its influence on the diatom flora seems to be of subordinate importance as compared with factors such as pH and temperature, even though in a quantitative as well as a qualitative respect it influences the composition of the diatom flora.

In order to obtain a basis for an estimation of the relation of the Danish diatoms to alkalinity, I studied the Danish literature on recent diatoms (Boye Petersen, Jørgensen, and Foged). The results of this study, supplemented by my own experiences, were utilised in the preparation of Table VII. Judging by the Danish material, the limits drawn by Hustedt for the indifferent as well as the calciphilous species seem to be somewhat too narrow. It seems reasonable to regard the indifferent species as species whose optimal occurrence extends from the lowest alkalinity values to ca. (3—)4.5, and the calciphilous species as species whose optimal development falls within the range 1—4.5.

On this view the following diatoms should be termed indifferent:

Achnanthes exigua, *A. minutissima*, *Amphora ovalis*, *Asterionella gracillima*, *Caloneis silicula* var. *truncatula*, *Campylodiscus noricus* var. *hibernicus*, *Cocconeis placentula*, *C. placentula* var. *lineatus*, *C. pediculus*, *Cyclotella comta*, *C. stelligera*, *Cymbella helvetica*, *C. prostrata*, *C. obtuciuscula*, *Diploneis ovalis*, *D. ovalis* var. *oblonga*, *Epithemia argus*, *E. intermedia*, *E. turgida*, *Eunotia faba*, *Fragilaria construens* var. *binodis*, *F. construens* var. *exigua*, *F. construens* var. *venter*, *F. lapponica*, *F. virescens*, *Gomphonema acuminatum*, *G. constrictum*, *G. gracile*, *Meridion circulare*, *Melosira granulata* incl. var. *angusstissima*, *Navicula cryptocephala*, *N. dicephala*, *N. placentula*, *N. popula* var. *rectangularis*, *N. radiosa*, *N. rhynchocephala*, *N. viridula*, *Neidium iridis*, *Pinnularia Legumen*, *P. maior*, *P. molaris*, *P. subcapitata*, *P. viridis*, *Rhoicosphenia curvata*, *Rhopalodia gibba*, *R. gibberula*, *Stauroneis anceps*, *Surirella Caproni*, *Tabellaria flocculosa*, and *T. fenestrata*.

The following species can be regarded as calciphilous:

Achnanthes Oestrupii, *Cymatopleura solea*, *C. elliptica*, *Cymbella affinis*, *C. amphicephala*, *C. lanceolata*, *C. ventricosa*, *Diatoma vulgaris*, *Epithemia sorex*, *E. zebra* incl. var. *saxonica* and *porcellus*, *Fragilaria pinnata*, *Gomphonema acuminatum* var. *Brebissoni*, *G. intricatum*, *Navicula anglica*, *N. cuspidata*, *N. menisculus*, *N. Schönfeldii*, *Nitzschia angustata*, *N. amphibia*, *N. paleacea*, *N. thermalis*, and *Synedra capitata*.

It is possible, however, that some of the calciphilous species on closer examination must be referred to the group of indifferent species.

As calciphilous species we must regard *Coscinodiscus Rothii* var. *subsalsa*, *Eunotia gracilis*, *Gomphonema acuminatum* car. *coronata*, *Navicula oblonga*, *Pinnularia appendiculata*, *P. gentilis*, *P. gracillima*, *P. microstauron* var. *Brebissoni*, and *Surirella elegans*.

In Bølling Sø, throughout the whole sequence of strata (1939-material), only those indifferent species occur in quantity for which the minimum, computed from the number of individuals, is 74.5 % from the early Dryas and the maximum 99.3 % from the pine-hazel period.

In the early Dryas the calciphilous species constitute 22.6 % which is the maximum, cf. Table VII. It must be considered of great significance that the calciphobous species are not represented in the spectra, and since the optimal development of these species, as mentioned above, falls within the range of alkalinity 0—0.8 mvl., from this alone it may be inferred that the alkalinity of the lake even during the early Dryas exceeded 0.8 mvl., which corresponds to a CaO-content of not less than 22.4 mg/l. If the alkalinity had ranged around 0.8 mvl., the calciphobous species might be expected to constitute a greater or smaller part of the spectrum. Since, however, these species are not at all represented in the spectra, it is probably justifiable to infer that the alkalinity was materially higher, especially when it is taken into consideration that the calciphobous species in a number of recent lakes even with an alkalinity exceeding 2.0, are represented in the alkalinity spectra, though, as a rule, with comparatively low frequencies.

Thus the Badstuedam with an alkalinity of 2.3 mvl. has 0.9 % calciphobous species, Sjælsø with 1.98 mvl. has 1.0 % calciphobous species, Brabrand Sø with 3.81 mvl. has 0.3 % calciphobous species, Karlssø with 2.1 mvl. has 7.3 % calciphobous species, Funkedam with 2.04 mvl. has 2.2 % calciphobous species, and even Kongekilde Mølledam with 4.52 mvl. has 0.9 % calciphobous species.

If we further compare with the lakes and ponds in which *Fragilaria construens* and (or) its var. *venter* occurs as dominant in recent samples, we shall find the following values for the alkalinity (JØRGENSEN's analyses): Arresø 2.19; Karlssø 2.10; Skanderborg Sø 2.99; Sorø Sø 2.21; Bagsværd Sø 1.14; Lyngby Sø 1.99; (forest lake north of Mørkedam 1.14); Kongekilde Mølledam 4.52; Badstuedam 2.30; Brabrand Sø 3.81; Funkedam 2.04; Sjælsø 1.98; (Løgsø 0.69).

Melosira granulata incl. var. *angustissima*, which is a dominant in samples 49 and 34/39, in recent material occurs as dominant in constantly alkaline waters

with an alkalinity of between 2.64 and 3.79 mvl. (Tystrup Sø 3.79 mvl.; Frederiksborg Slotssø 2.64 mvl.; and Badstue Ødam 2.64 mvl.). As the forest lake north of Mørkedam and Løgsø belong to the alternately acid-alkaline, though chiefly neutral-alkaline waters, they can, considering the above statements as to pH conditions, be left out of consideration, and we may then infer that the alkalinity of Bølling Sø must have ranged between 1.14 and 4.52 mvl.; the probability is that the value ranged between 2 and 3, cf. Table VII, as the period, the early Dryas, in which we should expect to find the lowest alkalinity value, has a spectrum consisting of 74.5 % of indifferent and 22.6 % of calciphilous species, totalling 97.1 %. Comparing this with recent material from a lake with a fairly similar spectrum, viz. Arresø, which has 73.6 % of indifferent and 18.9 % of calciphilous species, totalling 92.5 %, we shall find an alkalinity value of 2.19 mvl., and hence we must assume that Bølling Sø in the early Dryas period had an alkalinity of ca. 2.0 mvl.

In the late Dryas we find a spectrum composed of 77.8 % of indifferent and 6.3 % of calciphilous species, and comparing this with the recent lake Sjælsø, which has 78.6 % of indifferent and 7.7 % of calciphilous species, totalling 86.3 %, and an alkalinity of 1.98 mvl., we must assume that Bølling Sø in the late Dryas likewise had an alkalinity of ca. 2.0 mvl.

If we consider the alkalinity spectra set up on the basis of the percentage numbers of species, we find for Bølling Sø likewise a dominance of the indifferent species, and considerable frequencies for the calciphilous species, while with a single exception the calciphobous and the calcibiontic species are not represented in the spectra. At the same time, however, we find high frequencies for such species whose place must still be left open. But in the face of this it should be mentioned that we are here largely concerned with species which either attain to quite an insignificant frequency, or—mostly—are present in such small numbers that they are not included in the numerical treatment, which appears from the spectra set up on the basis of percentage numbers of individuals, cf. Table VII. Moreover, by far the greater number of this group should, no doubt, be regarded as indifferent, and no small number of the rest as calciphilous; there remain, then, low frequencies of calciphobous (and calcibiontic?) species.[1] The conclusions as to the alkalinity of Bølling Sø drawn from the spectra for percentage numbers of individuals accordingly are not altered by considering the spectra set up on the basis of the numbers of species.

Sørensen (1948, p. 27), cf. also Olsen (1950, p. 12), used the following division for an alkalinity spectrum:

oligo range	< 0.5 mvl.
β meso range	0.5—2.5 —
α meso range	2.0—4.5 —
poly range	> 4.5 —

[1] The correctness of this view is confirmed by the fact that the species in question in regard to the pH are indifferent or alkaliphilous.

According to this method of division we can say that the probability is that Bølling Sø down through the ages belonged to the β meso range, which corresponds to a content of CaO of between 28 and 70 mg/l; thus, during the whole period the lake belonged to the water-bodies fairly rich in lime.

d. *Trophic conditions — type of lake — type of sediment.*

What is stated in the preceding section as to the place of the lake in regard to pH and alkalinity, naturally leads to the question of trophic conditions and lake type.

The concept lake type originates from Teiling (1916) and has been further extended by Naumann (1917, 1932). It is based on a characterisation of the lakes by means of the nutritive-biological conditions. The plankton and the littoral production depend in some degree on the same factors. The shape, the cubic content, and the depth of the lake basin influence the concentration of nutrition and the circulation of the nutritive substances.

However, several of the lake types set up by Naumann on the basis of such conditions have been challenged from various quarters, so it is largely only his eutrophic, oligotrophic, and dystrophic types of lakes with the appurtenant subphases that have been fully accepted.

Nygaard (1950, p. 14) thus distinguishes between oligotrophic lakes of the dystrophic phase—oligotrophic lakes of the acidotrophic phase—approximately oligotrophic lakes—intermediate (mesotrophic) lakes—slightly eutrophic lakes—moderately eutrophic lakes—more eutrophic lakes—eutrophic lakes of the mixotrophic phase. Thienemann (1928) characterised the types of lakes according to the occurrence of the bottom animals, but also used the relation between the oxygen content of the hypolimnion and the epilimnion as a measure for the degree of trophism. That this measure is not usable under all conditions appears from the work of Lohammer (1938, p. 237), who points out that it is the plankton production that is the decisive factor.

As the most important distinguishing character of the following three types of lakes may, according to Thienemann, be mentioned (1) the oligotrophic lake: usually deep lakes (Thienemann estimates the depth at 18.5 m), the hypolimnion constituting a greater part of the volume of water than the epilimnion, high degree of transparency, paucity of N, P, and humus, while the calcium content may be varying, sparseness of plankton; (2) the eutrophic type of lake: slight depth of water, the hypolimnion constituting a smaller part of the volume of water than the epilimnion, transparency inconsiderable, richness in N and P, Ca usually present in large quantity, rich plankton production; (3) the dystrophic type of lake: variable depth, slight transparency, inconsiderable content of N and P as well as Ca, abundance of humus, slight plankton production.

Hustedt (1939, p. 43) states that subalpine lakes and many recent oligotrophic northern lakes are characterised by a vigorous *Cyclotella* vegetation in the plankton,

so that a pure *Cyclotella* mud occurs as a sediment. As a characteristic peculiarity of oligotrophic lakes in the temperate zone he mentions: (1) *Melosira granulata* is rare, in most cases it is entirely absent; (2) abundant development of the genus *Cyclotella* in the plankton, as also of *Melosira distans*; (3) in the littoral and upper profundal zone an abundant *Eunotia-Pinnularia* vegetation, but, HUSTEDT adds, not all three characteristics need be present at the same time.

If we make a comparison with Bølling Sø, we shall see that species of *Fragilaria* or *Melosira granulata*,[1] respectively, are dominants, that *Cyclotella* is exceedingly sparsely represented (*Melosira distans* is entirely absent), and that the species of *Eunotia* and *Pinnularia* are also extremely sparsely present.

However, it is not only *Fragilaria construens* and its varieties and *Melosira granulata* (incl. var. *angustissima*) which indicate an abundance of nutritive matter (cf. JØRGENSEN 1948, pp. 46—48), but the great majority of the species which can be characterised as accompanying species are representatives of eutrophic waters.

Thus a number of conditions characteristic of eutrophic waters are met with. Since, however, eutrophy is primarily a production concept, it is, of course, only justifiable to draw a conclusion of such far-reaching importance on the basis of the diatomaceous sediments, only, if we are concerned with mass occurrence, which is typical of eutrophic waters.

It is not only the diatom flora of Bølling Sø that is indicative of eutrophy; also the presence of Cyanophyceae and an abundance of Chlorophyceae during the periods of warm climate, coupled with a lack of Desmidiaceae, are characteristic features found in recent eutrophic alkaline lakes rich in lime. HUSTEDT (1939, p. 45), however, points out that all not too shallow-watered eutrophic lakes in the temperate zone contain a sediment of which the greater part by far is made up of pelagic species, so that high production of planktonic diatoms is thereby proved. In the oligotrophic lakes, however, the littoral species, owing to the low production of plankton, occupy a "wider" space in the sediment when the shore vegetation has become eutrophied on account of an abundantly developed belt of vegetation; this can be observed in many recent oligotrophic lakes. The preponderance of the littoral species in the bottom mud simultaneously with a decline in number of the pelagic species suggests that the plankton production is diminutive and accordingly that the lake has a relatively oligotrophic character. This fact is of exceedingly great importance in the estimation of trophic conditions during the late-glacial climatic periods in Bølling Sø.

As no euplanktonic diatoms, cf. Tables I and II and Plate 1, are found in the samples from the earliest Dryas, the Bølling oscillation, and the early Dryas (pollen zones I a, I b, and I c), and the only algae present are benthic diatoms in small numbers and quantity, we must infer, considering the statements of HUSTEDT, and irrespectively of the eutrophic character of the dominant benthic diatoms, that

[1] It also appears from JØRGENSEN's material that *Melosira granulata* attains only a low frequency in the oligotrophic Danish lakes, and NYGAARD (1949, p. 18) likewise writes that it must be regarded as a fact that the euplanktonic species of *Melosira* are characteristic of eutrophic waters. HUSTEDT (1939, p. 42) regards it as a guiding species for eutrophic waters.

during these periods the lake, as far as the production is concerned, was of an oligotrophic type.

The alkalinity spectrum for the earliest Dryas, the Bølling oscillation, and the early Dryas, cf. Table VII, shows that in this respect indifferent and calciphilous species come into question, for which reason it must be justifiable to conclude that the lake belonged to the oligotrophic lakes fairly rich in lime.

During the Allerød a period (pollen zone II a) the lake must also have belonged to this type; but in the Allerød b period a distinct change in the composition of the microflora took place. The diatoms decreased in number and were almost entirely replaced by the Chlorophyceae *Pediastrum Boryanum*, and *P. Kawraiski*, *Tetraedron minimum*, and the Cyanophycea *Gloeothricia* cfr. *echinulata*, all of them eutrophic species.

Lundqvist (1927, p. 26) from Bärnarpsjön from the sub-Atlantic period describes a similar case, and regards the high content of *Pediastrum* as a proof of a high degree of pollution due to settlements situated near the lake. In Bølling Sø the above-mentioned Chlorophyceae disappeared again in the late Dryas (1939-material), when the microflora again consisted of diatoms. A pollution, moreover, of the above-mentioned extent, cannot come into question for Bølling Sø, and a distinctive change in the Allerød b period of the chemical conditions, pH, Cl, and alkalinity (cf. Tables III, VI, and VII) must be regarded as little probable, whereas an increase in the content of nutrients which the rise in temperature brings about by furthering the bacteriological decomposition and fermentation processes, seems more likely, cf. p. 14. On this background the great advance of the two algal groups, the Chlorophyceae and the Cyanophyceae, must be viewed. The complex of processes taking place in the water may be roughly divided into three groups: (1) the production in connection with autotrophic plants (algae), (2) the consumption, and (3) the reduction due to the activity of the bacteria.

The production depends on factors such as light, temperature, and nutrients, and it is considered a fact that a rising temperature will cause an increased production of algae. In this connection reference need only be made to the great abundance of algae in our eutrophic lakes during the summer months. Even though it can thus be demonstrated that the plankton content of a lake increases with a rising temperature, and that in winter it is chiefly the diatoms which characterize the plankton, while in the summer months it is especially the Chlorophyceae and Cyanophyceae, notably the latter, which constitute the main volume of the plankton, it has been maintained from various quarters that it is by no means the temperature alone which is the most important factor for the development of the plankton organisms. The importance of the temperature, however, for the quantity of available nutrients, is certain, and it can therefore be established that changes in temperature, at any rate for this indirect reason, are of great importance for the phytoplankton.

As regards chemical conditions, it has been found that the Cyanophyceae attain their highest maximum when the water is rich in decomposed organic matter, but

they can subsist on insignificant quantities of such substances as nitrate and phosphate, while the diatoms seem to attain to their greatest distribution when the water is richest in nitrate, phosphate, and silicon. MARGALEF (1949, p. 275), investigating North Spanish waters, found that the algal flora in oligotrophic waters was dominated by diatoms. JUDAY (1942), however, in manuring experiments has shown that inorganic fertilisers are of no importance for the plankton production, and CHANDLER & WEEKS (1945) regard turbidity and the temperature of the water as the most essential causes of alterations in the plankton content with regard to the varying spring and autumn pulses, and they also state that phosphorus and nitrogen have a very limited effect, only, on the amount of the plankton production. NYGAARD (1945, p. 14) mentions that in large eutrophic lakes (which normally have formation of water bloom in summer) the water temperature, in cold summers, may not rise above 16° C., and a result of this may be a remarkably slight formation of water bloom in those years.

This explains the sudden change in the composition of the microflora in the Allerød b period, and it also shows that the chemical conditions alone cannot give rise to a mass production of these organisms (Chlorophyceae and Cyanophyceae), but that a certain minimum temperature is also required. When once the large quantities of plankton have been produced, the temperature of the water during the summer months may be considerably above the air temperature. Thus WESENBERG-LUND (1930) has demonstrated that ponds containing large quantities of plankton, especially Cyanophyceae plankton, may on calm days have a temperature which ranges 4—5° above that found in ponds with a low plankton content; this is due to the fact that the plankton absorbs heat more rapidly than the surrounding water, after which the organisms give off heat again to the surrounding water—a phenomenon which has probably been left unnoticed by those who deny the existence of any kind of influence of the temperature on the composition of the micro-communities. The geologist must therefore regard the temperature as the primary cause, and is confirmed in this view by the fact that in the period with the colder climate, the late Dryas, the microflora again became a pure diatom flora as in the early Dryas, which can be explained by the reduced decomposition of organic matter caused by the fall of temperature. Hence it is fully justifiable to use the microflora (i. e. the ratio between the diatoms on the one hand and the Chlorophyceae and Cyanophyceae on the other hand) as an indicator of the changing climatic periods, whereas the author agrees with HUSTEDT, LUNDQVIST, and others, in the view that among the diatoms we cannot distinguish between actual cold forms and heat forms, but that as to the latter we are concerned with more eutrophic species.

Considering what is stated above as to the importance of the temperature, it cannot be correct, as maintained by LUNDQVIST (1927) and other authors, that the Cyanophycean stage is exclusively an indication showing that the lake in its development with an increasing content of lime has reached the eutrophic phase, for, as pointed out above, the large-scale development of the Cyanophyceae depends on the presence of the minimum temperature. It will be more correct, therefore, to express

it as follows: that a lake which in its development has reached a stage with a fairly considerable content of organic matter will, when the conditions—temperatures—required for it are present, pass into the Cyanophycean stage, but it will only remain at this stage as long as the temperature requirements are fulfilled, cf. the Allerød and the late Dryas, respectively, in Bølling Sø.

Of the Chlorophyceae mentioned in Tables I and II, *Pediastrum Kawraiskii* is euplanktonic, while *P. Boryanum* and *Tetraedron minimum* must rather be regarded as facultative planktonic organisms.

Considering the large production of euplanktonic organisms, the lake in the Allerød b period must be referred to the eutrophic type of lake, as is further confirmed by the circumstance that the algal gyttjas are formed in water rich in nutrients, more especially in lime.

As mentioned above, the euplanktonic Chlorophyceae and Cyanophyceae disappeared in the late Dryas (pollen zone III), and the benthic and facultative species of diatoms were again predominant; accordingly, during this climatic period the lake must in regard to production have belonged to the oligotrophic type. The decreasing eutrophication must be due to the fall of temperature and the accompanying decomposition of matter which took place during this period.

The birch-pine period (pollen zone IV), which means another rise in temperature, exhibits a considerable advance, again, of the aforementioned eutrophic Chlorophyceae and Cyanophyceae, which shows that a distinct eutrophication along with the rise of temperature again took place.

The samples from the pine-hazel period (pollen zone V) and the early Atlantic period (pollen zone VI) are dominated by the eutrophic diatom *Melosira granulata* incl. var. *angustissima*, which shows that the eutrophication of the lake was far advanced, cf. p. 25.

The circumstance that *Melosira granulata* almost disappeared again in the samples from the beech period (pollen zone IX), and the benthic species of *Fragilaria* dominated again, cannot be taken as proof that the abundance of nutrients was about to disappear, and that oligotrophy was setting in again. The cause must be looked for in the advancing overgrowing of the lake, owing to which the level of the water gradually became so low that conditions for the existence of the euplanktonic diatoms were no longer present. However, there can be no doubt about the eutrophic condition of the lake during this period.

Thus Bølling Sø is a typical example of the development of a lake from an oligotrophic stage via the eutrophic stage to the extinction due to overgrowing. That the whole post-glacial gyttja measures only ca. 1 m, cf. Iversen (1941, p. 63), must be due to the fact that the lake is situated in a region where the adjacent areas are poor in nutrients. Lundqvist (1927) points out the importance of employing the sediments in the characterisation of lakes. The oldest layers in Bølling Sø were formed by clayey gyttja often intermixed with stripes of sand. During these climatic periods

the lake must have belonged to the type, mentioned by LUNDQVIST (1927), with clayey sediments (Tongyttjassen), which may be poor as well as rich in nutrients (cf. 1927, p. 104). Later strata are made up of algal gyttja, which according to LUNDQVIST is formed in clear and shallow water (depth estimated at 2—3 m) rich in nutrients, notably lime, and LUNDQVIST states that the stage in the development of an inland lake when the algal gyttja is formed must probably be ascribed to a warm and dry climate.

WESENBERG-LUND (1909) mentions that the algal gyttjas imply a high production of Cyanophyceae, in which are found "enormous masses of diatoms, but that these in the course of time are decomposed" (translated). Such a process of decomposition of the siliceous skeleton of the diatoms must then, according to HUSTEDT (1934, p. 24), be ascribed to the content of $CaCO_3$ in the water or mud. WESENBERG-LUND's view as to the "enormous masses of diatoms" which are decomposed, is hardly of general validity. As regards Bølling Sø, the small number of diatoms that have been found in the algal gyttja from the Allerød b period, show no traces of disintegration, and CEDERCREUTZ (1937, p. 328) states about recent algal gyttja-lakes from Åland that "Das wichtigste Algenelement stellen hier die Cyanophyceae dar, unter ihnen finden sich aber Protococcacéen und Diatoméen mehr oder weniger reichlich eingestreut, ausserdem einzelne Desmidiacéen."

Summary.

IVERSEN (1941, 1942, 1947) has published some preliminary notes on a pollen-analytical investigation of the dried-up Bølling Sø, which is situated on the border of the large Karup heath-flat in central Jutland. The great value of which the microflora may be for the elucidation of the climatic variations in late-glacial time is pointed out by IVERSEN (1945, pp. 41—43, and 1947, p. 69).

In the present paper the microflora of Bølling Sø is treated on the basis of the drilled samples taken by IVERSEN in 1939 and 1946. The author has endeavoured to the greatest possible extent to allow for limnological points of view in the interpretation of the results, for which reason diatom spectra from a number of recent Danish waters are inserted in the tables for comparison.

The preparations of diatoms were cleaned by means of 30 % hydrogen peroxide, cf. BRANDER (1936, p. 135), while the special preparations of Chlorophyceae and Cyanophyceae were treated with 10 % sodium hydroxide.

In the 1939-material, the number of individuals were counted, while in the 1946-material it was endeavoured to some extent to take the degree of covering into consideration. For this purpose an ocular micrometer was used. Whenever one of its division lines "hit" an organism, the presence of that particular organism was

noted as 1. The distance between the division lines at the magnification employed (1000 × 10) was 0.97 μ. This procedure prevents big diatoms, especially of the genera *Cymbella* and *Pinnularia*, from being suppressed by the small species rich in individuals of the genus *Fragilaria*.

In the earliest Dryas period the microflora consisted exclusively of diatoms, with *Fragilaria construens* and *F. pinnata* as community-forming organisms.

According to IVERSEN (1947, p. 73), the Bølling Sø oscillation is an ancient heat oscillation of a similar character though of less extent than the Allerød oscillation. During this period the microflora also consisted exclusively of diatoms with (the 1939-sample) *Fragilaria construens* and *F. pinnata* as community-forming organisms. Some species, such as *Cymbella Ehrenbergi*, *Navicula oblonga*, and *Surirella Caproni*, which were characterised by CLEVE-EULER (1922, p. 51) as "heat forms", immigrated during this period, cf. p. 13.

The early Dryas (the 1946-material) is represented by a very sandy sample with a micro-community formed by *Fragilaria construens*, *F. Harrissonii*, and *F. pinnata*

The 1939-sample from the Allerød a period is still a pure diatom sample with *Fragularia construens* and its var. *venter* as community-forming organisms, but in sample 618/46 the Chlorophyceae appear for the first time, though with low frequencies only, thus *Pediastrum Kawraiskii* with 7.2 % and *Tetraedron minimum* with 0.9 % in a microcommunity which is otherwise composed of diatoms with *Fragilaria construens* and its var. *venter* and *F. pinnata* as dominant species.

The Allerød b period, which represents the heat maximum, is characterised by an excessive decline of the diatoms, while the Chlorophyceae such as *Pediastrum Kawraiskii*, *P. Boryanum*, and *Tetraedron minimum* entirely characterise the spectrum.

With the colder climate during the late Dryas period the microflora was again transformed into a diatom flora with an element of Chlorophyceae, which in the oldest sample constitute 38.4 %, but decrease to 4.9 % in sample 658/46 and in the 1939-sample even to 0.

The most remarkable feature of the samples from the pre-boreal layers (zone IV) is the presence of Chlorophyceae represented by *Pediastrum Boryanum*, even in the last sample, though with a low frequency only, 1.6 % (sample 585/46). In the next sample, 580/46, the spectrum was entirely dominated by Chlorophyceae, which attain to a total frequency of 85.3 %, while the Cyanophyceae constitute 9.5 %, and the diatoms 5.2 %. Thus the somewhat milder climate during this period is manifested by a maximum of Chlorophyceae, corresponding in some degree to the conditions in the Allerød b period.

In sample 49/39 from the boreal layers the diatom *Melosira granulata* incl. var. *angustissima* with a frequency of 81.9 % is the only dominant species.

In the sample from the early Atlantic period, sample 34/39, *Melosira granulata* incl. var. *angustissima* is also dominant, but in addition the sample contains a great many Chlorophyceae.

In the sub-Atlantic time the dominance of *Melosira granulata* ceased, *Fragularia*

construens incl. var. *venter* now being dominant. Similarly to the other samples from the post-glacial layers, this layer, too, contains a great many Chlorophyceae.

CLEVE-EULER (1922) introduced the concept "heat-forms". LUNDQVIST (1927) and HUSTEDT (1939, 1944, 1948), however, strongly opposed the application of this concept to the diatoms, cf. p. 13, and the author agrees with them in their view that it is impossible to distinguish between actual "cold forms" and "heat forms" among the diatoms, but that as to the latter we are concerned with more eutrophic species.

It appears from Plate 1 that the benthic diatoms play a very important role during the early and the late Dryas as well as in the earliest part of the Allerød layer; but also the species which must be regarded as tychoplanktonic, constitute a considerable part of the total number of individuals, while the euplanktonic species in these parts of the late-glacial layer constitute only a small part of the number of individuals.

As an attempt at estimating the environmental factors in Bølling Sø during the different climatic periods, spectra were set up on the basis of the relation of recent diatoms to factors such as Cl, pH, and alkalinity.

The setting-up of halobion spectra is based on the division of diatoms, proposed by KOLBE (1932), according to their relation to the content of Cl in the water. Table III shows that the indifferent species, that is, such as are considered purely freshwater species, mark the spectra throughout the whole sequence of strata.

Table VI, which follows HUSTEDT (1938—39), shows that the spectra for the pH during all the climatic periods have been marked by the alkaliphilous species, which constitute the greater part, while the alkalibiontic and the indifferent species are of slight importance; corresponding conditions apply to the same extent to the acidophilous and the acidobiontic species. HUSTEDT designates such species as alkaliphilous whose occurrence ranges around a pH value of 7, and whose maximum occurrence is at a pH value > 7.

On the basis of ecological investigations of recent diatoms in Danish waters, preferably JØRGENSEN's work (1948), the spectra shown in Tables IV and V were set up. In Table IV these spectra are distributed over IVERSEN's division (1929) of Danish lakes according to pH conditions, cf. also NYGAARD (1938). It is here apparent that it is possible to distinguish between the following types of water: I. constantly acid waters, where acidophilous and acidobiontic species form a total of 70 % or more; II. alternately acid and alkaline waters, which can be subdivided into (a) predominantly acid waters, in which the acidobiontic species are almost absent, while the acidophilous species constitute ca. 60 % (minimum 42.5 %, maximum 70.7 %), the indifferent species 20—33 %, and (b) chiefly neutral-alkaline waters, which are readily distinguishable from the others, as the indifferent and acidophilous species together represent high percentages, 23.5—50.1 %, while the alkaliphilous species constitute 44—67 %. III. constantly alkaline waters, in which the alkalibiontic and the alkaliphilous species combined constitute ca. 90 %; but the

alkalibiontic species generally do not attain to the distribution that might be expected, cf. p. 20.

On a comparison with the recent Danish lakes so good agreement was found between the spectra for Bølling Sø and the constantly alkaline waters that there can be no doubt that Bølling Sø during all the climatic periods belonged to the constantly alkaline lakes.

In Table VII alkalinity spectra (cf. HUSTEDT 1938—39) are set up for Bølling Sø and for some recent Danish lakes. The indifferent species, that is, species whose occurrence ranges from the lowest alkalinity values to ca. 2—3 mvl., entirely dominate the spectra. Calciphobous species are lacking in the spectrum for Bølling Sø, to which great importance must be ascribed, as the optimum development of these species falls within the alkalinity range 0—0.8 mvl.; from this we may infer that the alkalinity of the lake even during the earliest Dryas was above 0.8 mvl. Probability suggests a much higher alkalinity, 2.0 mvl. or more, cf. p. 23.

NYGAARD (1945, p. 14) states that in larger eutrophic lakes the water temperature in cold summers may not rise above 16° C., and in consequence the formation of water colouring may be remarkably slight (cf. CHANDLER & WEEKS, 1945). This explains the sudden change in the composition of the microflora in the Allerød b and the late Dryas, and it also shows that chemical conditions alone cannot give rise to mass production of these organisms, but that a certain minimum temperature is required. Hence it is fully justifiable to use the microflora (i. e. the proportion of the diatoms on the one hand and the Cyanophyceae and the Chlorophyceae on the other hand) as an indicator of the changing climatic periods, cf. p. 27.

As mentioned by CLEVE-EULER (1932, p. 204), *Fragilaria construens* cannot be regarded as an indicator of "the concentration of nutrients and organic products of destruction occurring in association with an overgrowing" (translated), but it must be regarded as a species which is not absolutely linked up with these conditions, though it must be considered highly tolerant of pollution by organic matter.

Bølling Sø can be regarded as a typical example of the development of a lake from an oligotrophic stage via the eutrophic stage to extinction by overgrowth.

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TABLES

Table I. Synopsis of orga-

Sample no.	4	34	49	66
Depth below surface	12.5 cm.	85 cm.	120 cm.	160 cm.
Climatic periods	Beech time	Heat optimum Early Atlantic time	Pine-hazel time	Birch-pine time Allerød climate
	Sub-Atlantic	Atlantic	Boreal	Pre-boreal
Pollen zone	IX	VII	VI	IV
	%	%	%	%
Diatomaceae				
Achnanthes exigua Grun.	+	..	0.7	..
— minutissima Kütz.	..	+	..	..
— Oestrupii (A. Cl.) Hustedt	..	..	..	+
Amphora coffaeformis Ag.	..	..	..	..
— ovalis Kütz.	+	1.3	0.5	1.8
Asterionella gracillima (Hantzsch.) Heiberg	..	+	..	+
Caloneis silicula var. truncatula (?) Grun	..	..	..	..
Campylodiscus noricus var. hibernicus (Ehrbg.) Grun.	..	+	..	+
Cocconeis placentula Ehrbg.	+	0.3	+	..
— — var. lineatus (Ehrbg.) Cleve	..	..	..	..
— pediculus Ehrbg.	..	..	..	0.4
Coscinodiscus Rothii var. subsalsa (Juhl-Dannk.) Hust.	..	..	..	..
Cyclotella antiquae W. Smith	..	..	..	..
— comta (Ehrbg.) Kütz.	..	0.8	..	2.7
— stelligera Cl. et. Grun.	..	4.5	7.0	..
Cymatopleura solea (Bréb.) W. Smith	..	+	..	0.3
— elliptica (Bréb.) W. Smith	..	..	..	..
Cymbella aequalis W. Smith	..	..	..	..
— affinis Kütz.	..	..	..	..
— amphicephala Naegeli	..	..	..	0.3
— aspera (Ehrbg.) Cl.	..	+	..	..
— Ehrenbergii Kütz.	..	..	..	0.3
— helvetica Kütz.	..	+	..	..
— lanceolata (Ehrbg.) v. Heurck	..	3.5	+	+
— prostrata Cleve	..	+	..	..
— obtuciuscula (Kütz.) Grun.	..	..	..	..
— ventricosa Kütz.	..	+	+	..
— sp.	..	+	..	..
Diatoma elongatum Ag.	..	..	..	..
— vulgaris Bory	+	+	..	0.3
Diploneis ovalis (Hilse) Cl.	..	..	..	+
— — var. oblonga (Naegeli) Cl.	..	..	..	+
Epithemia argus Kütz.	..	..	..	..
— intermedia Fricke	..	..	..	..
— sorex Kütz.	+	..	+	0.5

nisms in the 1939-material.

130	117	86	97	108	Ecology		
210 cm.	275 cm.	307.5 cm.	345 cm.	367.5 cm.			
late Dryas	Heat maximum Allerød b.	Allerød a.	Bølling oscillation	Tundra time earliest Dryas	Cl-affinity	pH	Alkalinity
Late-glacial							
III	II b	II a	I b	I a			
%	%	%	%	%			
..	..	..	..	..	indifferent	alkaliphilous	indifferent
+	..	..	..	..	—	indifferent	—
..	..	..	..	..	—	—	?
+	..	..	..	..	mesohalobous	?	?
0.7	..	0.5	0.9	2.6	indifferent	alkaliphilous	indifferent
+	..	+	..	+	—	—	—
+	..	..	..	..	—	—	—
..	..	..	..	..	—	—	—
0.7	..	+	..	..	—	—	—
..	..	..	+	+	—	—	—
+	..	..	..	..	—	—	—
..	..	+	+	+	halophilous	?	?
+	..	..	..	..	?	acidophilous	?
1.3	..	+	..	1.8	indifferent	alkaliphilous	indifferent
..	..	..	..	..	—	?	—
0.3	..	+	+	..	—	alkaliphilous	calciphilous (?)
..	..	..	+	..	—	—	—
..	..	+	..	..	—	?	?
..	..	+	..	..	—	alkalibiontic	calciphilous
..	..	..	..	..	—	indifferent	—
..	..	..	..	..	—	alkaliphilous	indifferent
0.3	..	..	+	..	—	—	calciphilous
..	..	+	+	..	—	—	?
+	..	..	..	..	—	—	?
0.4	..	..	..	..	—	—	indifferent
+	..	..	+	..	—	indifferent	—
0.9	..	+	..	2.0	—	—	calciphilous
0.1	..	..	..	+	..	..	..
+	..	..	..	..	halophobous	—	—
+	..	0.6	..	3.6	indifferent	alkalibiontic	—
..	..	0.5	+	+	—	alkaliphilous	—
..	..	+	..	..	—	—	indifferent
+	..	..	..	..	—	—	—
+	..	..	..	..	—	indifferent	—
0.6	..	0.7	..	3.1	—	alkaliphilous	calciphilous

(To be continued)

Table I. (Continued)

Sample no.	4	34	49	66
Depth below surface	12.5 cm.	85 cm.	120 cm.	160 cm.
Climatic periods	Beech time	Heat optimum Early Atlantic time	Pine-hazel time	Birch-pine time Allerød climate
	Sub-Atlantic	Atlantic	Boreal	Pre-boreal
Pollen zone	IX	VII	VI	IV
	%	%	%	%
Epithemia turgida (Ehrbg.) Kütz.	..	+	..	0.7
— zebra (Ehrbg.) Kütz.	..	+	..	..
— — var. saxonica (Kütz.) Grun.	..	..	..	..
— — var. porcellus (?) (Kütz.) Grun.	..	..	..	..
— sp. (scraps)	..	+	+	..
Eucocconeis flexella Kütz.	..	+	0.5	..
— sp. (scraps)	..	..	+	..
Eunotia faba (Ehrbg.) Grun.	..	..	..	..
— gracilis (Ehrbg.) Rabenh.	..	+	..	..
— sp.	..	..	..	..
Fragilaria construens (Ehrbg.) Grun.	55.3	3.2	3.4	49.5
— — var. binodis (Ehrbg.) Grun.	1.4	..	..	5.0
— — var. exigua (W. Smith) Schulz	+	..	..	..
— — var. venter (Ehrbg.) Grun.	25.3	0.9	0.9	24.6
— Harrissonii W. Smith	..	+	0.7	..
— — var. dubia Grun.	..	..	..	..
— — var. rhomboides Grun.	..	..	+	..
— lapponica Grun.	..	..	..	..
— pinnata Ehrbg.	0.6	..	..	0.9
— virescens Ralfs.	..	..	..	..
Gomphonema acuminatum Ehrbg.	..	..	..	+
— — var. Brébissoni (Kütz.) Cl.	..	..	..	..
— — var. coronata (Ehrbg.) W. Smith	..	..	..	..
— constrictum Ehrbg.	..	+	..	+
— gracile Ehrbg.	..	..	..	..
— intricatum Kütz.	..	..	..	..
Gyrosigma attenuatum (Kütz.) Rabh.	..	..	..	0.4
Meridion circulare Ag.	..	..	..	..
Melosira arenaria Moore	..	0.3	+	7.4
— granulata + var. angustissima Müll.	7.5	82.3	81.9	+
— islandica subsp. helvetica Müll.	7.9	..	..	..
Navicula anglica Ralfs.	..	..	..	0.4
— cuspidata Kütz.	..	+	..	..
— cryptocephala Kütz.	..	0.5	1.3	0.3
— — forma minuta	..	+	0.4	..
— dicephala (?) (Ehrbg.) W. Smith	..	..	0.8	..

130	117	86	97	108	Ecology		
210 cm.	275 cm.	307.5 cm.	345 cm.	367.5 cm.			
Late Dryas	Heat maximum Allerød b.	Allerød a.	Bølling oscillation	Tundra time Earliest Dryas	Cl-affinity	pH	Alkalinity
Late-glacial							
III	II b	II a	I b	I a			
%	%	%	%	%			
0.3	..	0.3	0.6	..	indifferent	alkaliphilous	calciphilous
0.5	..	0.5	..	2.9		—	—
0.3	..	..	..	..	—	—	—
+	..	..	..	..	—	—	—
..	..	..	..	..	..	..	..
0.9	..	..	..	..	halophobous	indifferent	indifferent
..	..	..	..	..	..	..	..
+	..	..	..	..	halophobous	acidophilous	calciphobous
0.3	..	..	..	..	—	alkaliphilous	—
..	..	+	..	+	..	..	..
48.5	..	59.7	57.2	35.8	indifferent	—	indifferent
+	..	2.3	0.6	..	—	—	—
..	..	+	..	+	—	—	—
19.9	..	29.9	34.8	29.7	—	—	—
13.9	..	..	..	..	halophobous	—	—
+	..	..	..	..	—	—	—
..	..	..	..	..	—	—	—
+	..	+	0.5	..	indifferent	indifferent	—
3.4	..	3.5	3.1	11.0	—	alkaliphilous	—
+	..	..	..	..	halophobous	indifferent	—
..	..	..	..	..	indifferent	alkaliphilous	—
+	..	..	..	..	—	—	—
+	..	..	..	..	—	indifferent	calciphobous
+	..	..	..	..	—	alkaliphilous	indifferent
+	..	..	..	..	—	indifferent	—
+	..	..	..	..	—	alkaliphilous	—
..	..	+	0.8	2.9	—	alkalibiontic	?
+	..	..	..	..	—	alkaliphilous	calciphilous
1.2	..	0.6	1.1	+	—	indifferent	?
0.9	..	..	..	..	—	alkaliphilous	indifferent
..	..	..	..	..	—	alkalibiontic	?
..	..	+	..	..	—	alkaliphilous	?
+	..	+	..	..	—	—	indifferent
0.8	..	+	..	..	—	—	—
+	..	+	..	..	—	—	—
+	..	..	..	..	—	—	calciphilous

(To be continued)

Table I.

Sample no.	4	34	49	66
Depth below surface	12.5 cm.	85 cm.	120 cm.	160 cm.
Climatic periods	Beech time	Heat optimum Early Atlantic time	Pine-hazel time	Birch-pine time Allerød climate
	Sub-Atlantic	Atlantic	Boreal	Pre-boreal
Pollen zone	IX	VII	VI	IV
	%	%	%	%
Navicula menisculus Schum.	..	..	..	..
— oblonga Kütz.	..	..	..	..
— placentula (Ehrbg.) Grun.	..	..	..	..
— — var. rostrata A. Mayer	..	..	..	..
— pseudoscutiformis Hust.	..	..	..	+
— pupula var. rectangularis (Greg.) Grun.	..	..	..	0.7
— radiosa Kütz.	..	..	0.5	..
— rhynchocephala Kütz.	..	..	+	..
— Schönfeldii Hust.	..	..	..	..
— viridula Kütz.	..	..	..	..
— sp.	+	0.4	0.2	..
Neidium iridis (Ehrbg.) Cl.	+	+	0.3	..
Nitzschia angustata (W. Smith) Grun.	+	..	..	..
— amphibia Grun.	+	..	..	..
— commuta Grun.	+	..	..	..
— hungaria Grun.	+	..	..	..
— paleacea Grun.	0.4	..	..	..
— thermalis Kütz.	..	..	..	0.7
— sp.	0.6	+	..	..
Pinnularia appendiculata (Ag.) Cl.	..	..	+	..
— gentilis (Donkin) Cl.	..	..	..	..
— gracillima Gregory	..	..	..	+
— interrupta W. Smith	..	+	..	..
— Legumen Ehrbg.	..	..	+	..
— maior (Kütz) Cl.	..	+	..	+
— microstauron var. Brébissoni (Kütz.) Cl.	..	..	+	+
— molaris Grun.	+	..	..	..
— subcapitata Greg.	0.4	+	+	..
— viridis (Nitzsch.) Ehrbg.	..	0.3	..	0.4
— sp.	0.3	+	+	..
Rhoicosphenia curvata (Kütz.) Grun.	..	+	..	..
Rhopalodia gibba (Ehrbg.) Müller	..	..	..	..
— gibberula (Ehrbg.) Müller	..	..	+	..
Stauroneis anceps Ehrbg.	..	..	..	..
Surirella Caproni Bréb.	..	..	..	..
— elegans Ehrbg.	..	..	+	+

(Continued)

130	117	86	97	108	Ecology		
210 cm.	275 cm.	307.5 cm.	345 cm.	367.5 cm.			
Late Dryas	Heat maximum Allerød b.	Allerød a.	Bølling oscillation	Tundra time Earliest Dryas	Cl-affinity	pH	Alkalinity
Late-glacial							
III	II b	II a	I b	I a			
%	%	%	%	%			
..	..	..	+	..	indifferent	alkaliphilous	calciphilous
..	..	..	+	..	—	—	indifferent
..	..	+	+	..	—	—	?
+	..	..	..	..	—	—	?
..	..	..	..	+	?	—	?
..	..	..	+	..	indifferent	indifferent	?
..	..	..	..	..	—	—	indifferent
..	..	..	..	..	—	alkaliphilous	—
..	..	+	..	..	..	..	..
..	..	..	+	..	—	—	—
0.2	..	0.6	..	2.4	..	..	..
..	..	..	..	..	halophobous	indifferent	—
+	..	+	..	..	indifferent	alkaliphilous	—
..	..	..	..	..	—	alkalibiontic	—
..	..	..	..	..	halophilous	?	?
..	..	+	..	..	mesohalobous	?	?
+	..	..	..	..	?	alkaliphilous	calcibiontic
..	..	..	..	..	indifferent	?	?
0.2	..	+	+	..	..	..	..
..	..	..	..	..	oligohalobous	indifferent	indifferent
..	..	..	+	..	indifferent	—	—
..	..	..	..	..	..	..	..
..	..	..	..	..	—	acidophilous	—
..	..	..	..	..	?	indifferent	—
..	..	+	..	..	indifferent	acidophilous	—
..	..	..	..	..	—	—	—
..	..	..	..	..	—	indifferent	?
+	..	..	..	..	—	?	?
..	..	..	..	..	—	indifferent	indifferent
+	..	..	..	..	..	..	..
0.4	..	+	..	+	—	alkaliphilous	—
..	..	+	..	..	—	—	—
+	..	..	..	..	?	indifferent	—
+	..	..	..	..	indifferent	—	—
..	..	+	+	+	—	?	?
..	..	..	..	..	—	indifferent	?

(To be continued)

Table 1.

Sample no.	4	34	49	66
Depth below surface	12.5 cm.	85 cm.	120 cm.	160 cm.
Climatic periods	Beech time	Heat optimum Early Atlantic time	Pine-hazel time	Birch-pine time Allerød climate
	Sub-Atlantic	Atlantic	Boreal	Pre-boreal
Pollen zone	IX	VII	VI	IV
	%	%	%	%
Surirella sp.	..	+	..	..
Synedra affinis Kütz.	..	0.4	+	..
— capitata Ehrbg.	..	+	..	..
— ulna (Nitzsch.) Ehrbg.	..	1.2	0.3	2.3
Tabellaria flocculosa (Roth.) Kütz.	..	+	+	..
— fenestrata (Lyngb.) Kütz.	..	..	0.5	..
Dominants and subdominants:	Fragilaria construens / Melosira islandica f. Helvetica + M. granulata	Melosira granulata	Melosira granulata / Cyclotella stelligera + Fragilaria construens	Fragilaria construens / Melosira arenaria
Numbers of species and varieties	23	43	23	35
	%	%	%	%
Cyanophyceae.				
Anabaena spores	..	..	..	3.3
Aphanothece sp.	+	..	..	..
Chroococcus sp.	+	..	..	..
Gloeothricia echinulata spores (J. E. Smith) Richter	..	+	+	10.5
Lyngbya sp. (sheets)	..	..	..	+
Microcystis sp.	+	..	..	..
Chrysophyceae.				
Chrysomonade sp.	..	..	..	2.5
Chlorophyceae.				
Pediastrum Boryanum (Turp.) Meneg.	+	+	..	29.5
— angulosum (Ehrbg.) Meneg.	..	..	..	+
— duplex Meneg.	..	..	..	+
— Kawraiskii Schmidle	..	..	..	2.9
— Tetras (Ehrbg.) Ralfs.	..	..	..	..
Tetraedron minimum Hansg.	..	..	..	45.0
— tumidulum (Reinsch.) Hansg.	..	..	..	+
— muticum Hansg.	..	..	..	+
Scenedesmus sp.	..	..	..	4.3
Desmidiaceae.				
Cosmarium Botrytis Meneg.	..	..	+	+

(Continued)

130	117	86	97	108	Ecology		
210 cm.	275 cm.	307.5 cm.	345 cm.	367.5 cm.			
Late Dryas	Heat maximum Allerød b.	Allerød a	Bølling oscillation	Tundra time Earliest Dryas	Cl-affinity	pH	Alkalinity
Late-glacial							
III	II b	II a	I b	I a			
%	%	%	%	%			
..	..	..	..	..	..	..	..
0.3	..	+	..	..	?	?	?
0.3	..	+	..	..	indifferent	alkaliphilous	?
1.5	..	+	0.4	2.1	—	—	?
0.6	..	..	..	..	halophobous	indifferent	indifferent
..	..	..	..	..	..	..	..
Fragilaria construens — F. Harrissonii + F. pinnata		Fragilaria construens — F. construens var. venter	Fragilaria construens — F. pinnata	Fragilaria construens — F. pinnata			
61		42	26	23			
%	%	%	%	%			
..	..	..	..	..			
..	..	..	..	..			
..	..	..	..	..			
..	+	..	..	..			
..	..	..	..	..			
..	..	..	..	..			
..	..	..	..	..			
..	+	..	..	..			
..	+	..	..	..			
..	..	..	..	..			
..	+	..	..	..			
..	+	..	..	..			
..	+	..	..	..			
..	..	..	..	..			
..	..	..	..	..			
..	..	..	..	..			
..	..	..	..	..			

Table II. Synopsis of orga-

Climatic periods	Pre-boreal			Late Dryas				
Pollen zones	IV			III				
Sample no.	575	580	585	590	651	655	658	606
Depth in cm.	154	164	174	184	194	205	215	225
Diatomaceae.	%	%	%	%	%	%	%	%
Achnantes Oestrupii A. Cl.	..	..	..	..	2.1	..	..	..
Amphora Normani Rabh.	0.6	..	..	..	..	..	..	..
— ovalis Kütz.	..	..	..	0.6	..	..	..	..
— perpusilla Grun.	..	..	..	..	..	..	..	..
— veneta Kütz.	..	..	..	..	..	..	..	..
Cocconeis placentula Ehrbg.	0.1	0.6	..	0.4	12.6	..	..	..
— — var. euglypta (Ehrbg.) Cl.	..	..	..	..	..	..	..	..
Cyclotella comta (Ehrbg.) Kütz.	..	..	0.9	1.2	2.5	..	..	..
Cymatopleura elliptica (Bréb.) W. Smith	..	..	..	..	..	..	..	..
— solea (Bréb.) W. Smith	+	..	..	..	..	..	..	..
Cymbella cistula var. maculata (Kütz.) v. Heurck	..	..	+	..	..	..	..	..
— cuspidata Kütz.	..	..	..	..	..	..	..	..
— gracilis (Rabh.) Cl.	..	..	3.6	..	..	..	..	..
— lanceolata (Ehrb.) v. Heurck	+	..	..	+	..	..	..	..
— prostrata Cl.	+	..	..	+	..	..	..	..
— sinuata Gregory	..	..	1.4	..	..	..	..	..
— ventricosa Kütz.	0.3	..	8.0	2.2	..	..	..	..
— sp.	..	..	1.8	..	..	..	..	..
— scraps	..	..	0.6	..	..	..	..	..
Diatoma vulgare Bory	..	..	+	..	..	..	..	..
Diploneis ovalis (Hilse) Cl.	..	..	..	..	..	..	..	..
— — var. oblongella (Nägeli) Cl.	+	..	..	..	..	..	..	..
Epithemia argus Kütz.	..	..	..	..	..	..	..	..
— — var. longicornus Grun.	..	..	..	..	..	..	..	..
— intermedia Fricke	..	..	..	..	..	..	..	..
— sorex Kütz.	+	..	..	1.2	..	..	+	..
— turgida (Ehrbg.) Kütz.	..	..	..	..	..	..	..	..
— zebra (Ehrbg.) Kütz.	+	..	2.4	..	..	..	+	..
— — var. saxonica (Kütz.) Grun.	..	..	..	..	..	..	..	..
— scraps	0.1	..	1.7	..	..	..	..	8.3
Eucocconeis flexella Kütz.	+	..	..	..	..	..	..	..
— — var. alpestris Brun	..	..	..	1.2	..	..	..	..
Eunotia arcus var. bidens Grun.	..	..	..	..	..	..	+	..
— gracilis (Ehrbg.) Rabenh.	..	..	..	+	..	..	..	..
— monodon Ehrbg.	0.1	..	..	..	..	..	..	..
Fragilaria brevistriata Grun.	..	..	..	..	..	..	..	..
— — var. inflata (Pant.) Hust.	..	..	..	..	..	..	..	..
— capucina var. lanceolata Grun.	..	..	2.0	..	..	..	..	..

nisms in the 1946-material.

Allerød							Earlier Dryas		Bølling oscillation	Ecology		
II b			II a				I c		I b			
608	610	613	618	621	624	628	630	635	637	Cl-affinity	pH	Alkalinity
235	245	255	265	275	285	295	305	315	335			
%	%	%	%	%	%	%	%	%	%			
0.8	..	..	..	..	..	..	..	..	..	indifferent	?	?
..	..	..	..	..	..	..	..	..	..	halophobous	?	?
..	..	..	..	..	..	..	..	..	1.4	indifferent	alkaliphilous	indifferent
..	..	..	3.0	..	1.7	0.7	..	..	+	—	?	?
..	..	..	2.8	..	..	..	..	..	..	—	?	?
..	..	..	..	..	..	..	..	..	..	—	alkaliphilous	indifferent
..	..	..	..	..	..	..	..	..	+	—	—	?
+	..	..	1.3	..	+	2.3	..	..	..	—	—	indifferent
..	..	..	..	..	..	+	..	..	..	—	—	calciphilous
..	..	..	..	+	..	..	..	4.9	..	—	—	—
..	..	..	..	..	..	..	..	..	..	—	?	?
..	..	..	..	..	1.3	..	..	..	..	—	?	indifferent
..	..	..	..	..	..	..	..	..	..	—	acidophilous	..
..	..	..	..	..	..	..	..	..	..	—	alkaliphilous	?
..	..	..	..	..	..	..	..	..	..	—	—	..
..	..	..	..	..	....	..	..	..	..	—	indifferent	..
..	..	..	+	5.0	..	+	..	..	..	—	—	calciphilous
..	..	..	..	..	..	2.6	..	..	..	..	..	..
..	..	..	..	..	..	2.6	..	..	..	..	..	..
..	..	..	..	1.6	..	..	..	..	+	—	alkalibiontic	—
..	..	..	+	..	..	..	..	..	..	—	alkaliphilous	—
..	..	..	+	6.7	..	+	..	..	..	—	—	indifferent
..	..	..	..	1.8	..	..	..	2.4	..	—	—	—
..	..	..	+	..	..	..	..	..	..	—	—	—
..	..	..	+	..	..	..	..	..	..	—	indifferent	—
+	..	..	2.8	..	4.6	..	..	..	..	—	alkaliphilous	calciphilous
..	..	..	..	2.6	..	..	..	..	..	—	—	—
+	..	..	..	+	3.2	2.6	..	3.4	..	—	—	—
..	..	..	+	..	..	..	..	..	..	—	—	—
..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	halophobous	indifferent	indifferent
..	..	..	..	..	..	..	..	..	..	—	—	—
..	..	..	..	..	..	..	..	..	..	indifferent	alkaliphilous	—
..	..	..	..	..	..	..	..	..	..	halophobous	—	calciphobous
..	..	..	..	..	..	..	..	..	..	?	acidophilous	—
0.9	..	..	..	4.9	..	..	..	..	+	indifferent	alkaliphilous	indifferent
+	..	..	..	..	..	..	..	..	..	?	?	?
..	..	..	..	..	..	..	..	..	..	halophobous	?	indifferent

(To be continued)

Table II.

Climatic periods	Pre-boreal			Late Dryas				
Pollen zones	IV			III				
Sample no.	575	580	585	590	651	655	658	606
Depth in cm.	154	164	174	184	194	205	215	225
	%	%	%	%	%	%	%	%
Fragilaria construens (Ehrbg.) Grun.	1.6	2.5	9.1	6.2	26.0	32.0	26.6	9.1
— — var. binodis (Ehrbg.) Grun.	0.1	..	..	..	..	..	5.3	1.3
— — var. semibinodis Østrup	..	..	..	0.7	..	..	..	..
— — var. venter (Ehrbg.) Grun.	1.2	..	13.7	9.0	2.0	..	..	..
— Harrissonii W. Smith	0.8	1.8	6.8	4.5	12.8	8.0	9.0	5.8
— — var. dubia Grun.	2.3	..	2.8	1.8	..	..	5.4	4.6
— pinnata Ehrbg.	+	..	14.1	33.5	35.8	17.0	40.4	12.3
— — var. bicapitata A. Mayer	..	..	..	..	..	..	..	..
— — var. lancettula (Schum.) Hust.	..	..	..	..	..	..	..	1.9
— virescens Ralfs.	..	..	1.8	..	..	..	..	..
— sp.	..	..	..	..	1.3	..	..	..
Gomphonema constrictum Ehrbg.	+	..	0.9	..	..	..	..	..
Gyrosigma acuminatum (Kütz.) Rabenh.	..	..	..	..	..	..	..	..
— scraps	..	..	..	..	..	..	..	..
Melosira granulata (Ehrbg.) Ralfs	..	..	..	..	..	15.0	..	4.6
Navicula anglica Ralfs.	..	..	..	..	..	..	..	..
— cryptocephala Kütz.	..	..	4.8	..	..	..	..	..
— dicephala (Ehrbg.) W. Smith	..	..	3.0	..	..	..	..	..
— helvetica Brun	+	..	..	..	..	..	..	..
— laterostrata Hust.	+	..	..	..	..	..	..	..
— minuscula Grun.	..	..	..	..	..	..	..	..
— placentula (Ehrbg.) Grun.	..	..	..	..	..	..	..	..
— — var. rostrata A. Mayer	..	..	..	..	..	..	..	..
— Schönfeldii Hust.	..	..	..	+	2.5	..	5.3	6.3
— tuscula forma minor Hust.	..	..	..	..	..	..	..	..
— scraps	0.2	..	2.8	..	..	..	..	..
— sp.	..	..	..	..	2.3	..	..	..
Neidium affine var. amphirhynchus (Ehrbg.) Cl.	+	..	..	..	..	..	..	..
— iridis (Ehrbg.) Cl.	..	..	..	..	..	..	3.1	..
— — forma vernalis Reichelt	..	..	..	..	..	..	..	..
— sp.	..	..	..	..	..	..	..	..
Nitzschia stagnorum Rabenh.	..	..	..	0.8	..	..	..	..
— tryblionella var. levidensis (W. Smith) Grun	..	..	..	..	..	..	..	..
— sp.	..	..	..	1.5	..	..	..	..
Pinnularia gentilis (Donkin) Cl.	..	..	..	..	..	..	..	..
— scraps	+	..	..	+	..	..	..	..
Pleurosigma sp. (scraps)	..	..	..	..	..	..	..	..
Rhopalodia gibba (Ehrbg.) O. Müller	+	..	..	+	..	..	..	..
— gibberula (Ehrbrg.) O. Müller	+	..	..	..	..	..	..	..

(Continued)

Allerød							Earlier Dryas		Bølling oscillation	Ecology		
II b			II a				I c		I b			
608	610	613	618	621	624	628	630	635	637	Cl-affinity	pH	Alkalinity
235	245	255	265	275	285	295	305	315	335			
%	%	%	%	%	%	%	%	%	%			
4.7	0.5	1.5	32.2	5.3	24.0	9.0	39.0	..	4.8	indifferent	alkaliphilous	indifferent
0.9	..	..	..	1.4	7.0	10.5	..	2.9	5.0	—	—	—
..	..	..	..	..	..	..	..	..	..	—	—	—
1.5	..	..	13.9	3.5	8.0	46.3	..	2.4	..	—	—	—
2.5	..	..	..	8.0	2.5	2.0	25.0	28.3	25.0	halophobous	—	—
0.7	..	..	0.5	..	..	1.1	..	17.7	..	—	—	—
43.4	..	..	23.3	31.4	34.4	7.6	20.0	35.6	61.0	indifferent	—	—
..	..	..	1.6	..	..	..	..	..	..	?	?	?
5.4	..	..	..	..	5.0	7.7	..	..	2.0	indifferent	alkaliphilous	indifferent
..	..	..	..	..	..	..	..	..	..	halophobous	indifferent	—
..	..	..	..	1.2	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	indifferent	alkaliphilous	—
..	..	..	1.8	..	3.7	..	..	..	..	—	—	—
..	..	..	..	..	..	..	..	..	0.9	..	..	..
..	..	..	..	1.6	..	..	..	..	..	—	—	—
..	..	..	..	1.0	..	+	..	..	..	—	—	?
..	..	..	+	..	..	..	..	..	..	—	—	indifferent
..	..	..	..	..	..	..	..	..	..	—	—	calciphilous
..	..	..	..	..	..	..	..	..	..	?	?	?
..	..	..	+	..	..	..	..	..	..	?	?	?
..	..	..	+	..	..	..	..	..	..	?	indifferent	indifferent
..	..	..	..	3.6	..	..	..	..	..	indifferent	alkaliphilous	?
..	..	..	..	1.1	..	..	..	..	..	—	—	?
..	..	..	..	..	..	1.3	..	..	+	—	—	?
..	..	..	1.1	..	..	..	..	..	..	—	alkalibiontic	?
..	0.5	..	..	4.1	..	..	..	..	..	..	..	..
0.3	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	indifferent	indifferent	?
..	..	..	..	..	..	..	..	..	..	halophobous	—	indifferent
..	..	..	..	..	+	..	..	..	..	—	—	—
..	..	..	+	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	indifferent	?	?
..	..	..	..	..	+	..	..	..	..	halophilous	indifferent	indifferent
..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	+	..	..	..	..	indifferent	—	—
0.4	..	..	1.7	9.5	..	..	..	2.4	+	..	..	..
..	..	..	..	..	+	..	..	..	..	—	—	—
..	..	..	3.8	..	..	..	..	..	..	indifferent	alkaliphilous	—
..	..	..	1.4	..	..	..	..	..	..	—	indifferent	—

(To be continued)

Table II.

Climatic periods	Pre-boreal			Late Dryas				
Pollen zones	IV			III				
Sample no.	575	580	585	590	651	655	658	606
Depth in cm.	154	164	174	184	194	205	215	225
	%	%	%	%	%	%	%	%
Stauroneis anceps Ehrbg.	..	..	+	..	..	..	..	..
— phoenicenteron Ehrbg.	..	..	..	..	+	..	..	..
Stephanodiscus astrea var. minutula (Kütz.) Grun.	..	..	..	..	..	..	..	..
Surirella Capronii Bréb.	..	..	..	..	..	..	..	..
Synedra capitata Ehrbg.	1.3	..	4.0	3.0	..	..	..	..
— ulna (Nitzsch.) Ehrbg.	0.3	..	12.1	30.0	..	..	..	..
— scraps	0.3	..	..	..	..	..	..	..
Tabellaria fenestrata (Lyngb.) Kütz.	..	..	..	1.3	..	..	..	..
— flocculosa (Roth.) Kütz.	+	..	..	..	..	..	..	..
Scraps which cannot be referred to any species or genus	..	0.3	..	..	..	28.0	..	9.0
Numbers of species and varieties	26	3	22	22	11	4	9	8
	%	%	%	%	%	%	%	%
Chlorophyceae.								
Pediastrum Boryanum (Turpin) Menegh.	27.8	31.7	1.7	..	..	..	4.9	11.1
— Kawraiskii Schmidle	38.4	35.4	..	..	..	..	..	25.6
Scenedesmus arcuatus Lemm.	+	10.3	..	..	..	..	..	..
— quadricauda (Turpin) Bréb.	10.2	..	..	..	..	..	..	..
Tetraedron minimum Hansg.	8.5	7.9	..	..	..	..	..	..
Chrysophyceaea.								
Chrysomonade sp.	1.0	..	..	0.9	..	..	..	..
Cyanophyceae.								
Anabaena cfr. flos-aquae	+	5.5	..	..	..	..	..	..
Gloeothricia spores	4.5	4.0	..	..	..	..	..	..
Microcystis sp.	0.3	..	..	..	..	..	..	..

(Continued)

Allerød							Earlier Dryas		Bølling oscillation	Ecology		
II b			II a				I c		I b			
608	610	613	618	621	624	628	630	635	637	Cl-affinity	pH	Alkalinity
235	245	255	265	275	285	295	305	315	335			
%	%	%	%	%	%	%	%	%	%			
..	..	..	..	..	..	..	..	..	..	indifferent	indifferent	indifferent
..	..	..	..	3.1	4.6	..	..	..	..	—	—	—
..	..	..	0.6	..	..	..	..	..	..	—	alkalibiontic	—
..	..	..	+	..	..	..	..	..	..	—	?	?
..	..	..	..	..	..	..	..	..	..	—	alkaliphilous	?
..	..	..	..	2.6	..	3.8	..	..	+	—	—	?
..	..	..	..	..	..	..	..	..	..	..	..	..
..	..	..	..	..	..	..	..	..	..	halophobous	acidophilous	indifferent
..	..	..	..	..	..	..	..	..	..	—	indifferent	—
..	..	2.2	..	..	..	1.7	16.0	..	..	..	..	..
14	2	1	25	20	16	17	3	8	12			
%	%	%	%	%	%	%	%	%	%			
20.9	14.0	25.4	..	..	..	..	..	..	..			
16.3	71.2	53.6	7.2	..	..	..	..	..	..			
..	..	..	..	..	..	..	..	..	..			
..	6.2	0.9	..	..	..	..	..	..	..			
..	7.5	14.6	0.9	..	..	..	..	..	..			
..	..	1.2	..	..	..	..	..	..	..			
..	..	..	..	..	..	..	..	..	..			
1.2	..	0.6	..	..	..	..	..	..	..			
..	..	..	..	..	..	..	..	..	..			

Table III. Halobion spectra for Bølling Sø, diatoms.

Pollen zone	Climatic period	cm. depth	Sample no. (1939)	% of number of individuals					% of numb. of spec. and variet.					Number of individuals	Number of species and varieties
				Halophobous	Indifferent	Halophilous	Mesohalobous	?	Halophobous	Indifferent	Halophilous	Mesohalobous	?		
IX	Sub-Atlantic	12.5	4	7.9	90.6	0.0	0.0	1.5	4.0	68.0	4.0	0.0	24.0	1950	23
VII	Atlantic	85	34	0.0	99.1	0.0	0,0	0.9	11.0	73.0	0.0	0.0	16.0	1950	43
V	Boreal	120	49	2.0	97.9	0.0	0.0	0.2	15.0	70.0	0.0	0.0	15.0	1850	33
IV	Pre-boreal	160	66	0.0	99.9	0.0	0.0	0.1	0.0	99.0	0.0	0.0	1.0	1950	35
III	Late Dryas	210	130	0.4	98.9	0.0	0,0	0.7	11.0	76.0	1.5	1.5	9.0	1850	61
II b	Allerød b	275	117	diatoms absent.											
II a	Allerød a	307.5	86	0.0	98.9	0.0	0.0	1.1	0.0	90.0	1.0	0.0	9.0	1850	42
I b	Bølling oscillation	345	97	0.0	100[1]	0.0	0.0	0.0	0.0	95.9	4.1	0.0	0.0	1393	26
I a	Earliest Dryas	367.5	108	0.0	97.5	0.0	0.0	2.5	0.0	80.0	7.0	0.0	13.0	296	23

[1] Cf. the explanation of the apparent disagreement between the two methods of calculation, p. 16.

Table IV. pH-spectra set up on the basis of ecological investigations of recent diatoms from Danish waters; worked out from Boye Petersen (1943) and Jørgensen (1948).

	% of number of individuals						% of number of species and varieties					
I. Constantly acid waters.	Alkalibiontic	Alkaliphilous	Indifferent	Acidophilous	Acidobiontic	?	Alkalibiontic	Alkaliphilous	Indifferent	Acidophilous	Acidobiontic	?
a. Strongly acid waters (pH under 5.0)												
Bøllemosen pH: 3.7—4.4	..	..	29.2	70.1	0.2	0.5	0.0	0.0	21.5	64.3	7.1	7.1
Bøndernes mose „ <4	..	..	0.0	43.8	56.2	0.0	0.0	0.0	0.0	50.0	50.0	0.0
Lille Øksø „ 3.6—4.2	..	..	13.0	60.0	27.0	0.0	0.0	11.1	33.3	33.3	11.3	0.0
Mossø (Roldskov) „ 4.0—4.3	..	..	2.2	96.1	0.0	1.7	0.0	0.0	11.1	72.2	11.1	5.6
St. Øksø „ 4.0—4.3	..	..	8.7	67.9	23.4	0.0	0.0	0.0	17.9	71.4	10.7	0.0
Rejkjær Pl.sø „ 4.3	..	..	1.8	87.0	0.3	10.9	0.0	0.0	15.0	65.0	10.0	10.0
Løvenholm Langsø „ 4.0—4.7	..	..	17.8	76.9	5.3	0.0	4.6	9.1	9.1	54.5	9.1	13.6
b. Alternately strongly and weakly acid waters												
Kragesø pH: 6.0—6.3	..	0.2	8.1	88.3	3.4	0.0	2.5	5.2	27.7	50.0	11.1	2.5
Hjortesøle „ 4.8—6.8	..	0.0	0.0	96.7	0.2	3.1	0.0	0.0	7.6	77.0	7.7	7.7
Skørssø „ 5.0—5.9	..	0.0	4.2	80.6	3.0	12.2	0.0	2.6	25.0	62.0	7.8	2.6
Store Gribsø „ 3.9—6.5	..	0.0	33.9	64.5	1.6	0.0	0.0	0.0	18.8	75.0	6.2	0.0
Lyngby Mose „ 3.6—6.0	..	0.0	0.0	0.0	85.9	14.1	0.0	0.0	16.3	16.3	50.0	16.3
Madum Sø „ 4.4—5.2	..	0.0	0.0	97.0	2.1	0.9	0.0	0.0	4.3	73.9	13.2	8.6
Hjortesøle Lagg „ 5.4	..	4.1	6.9	81.6	0.0	7.4	0.0	13.4	40.0	30.0	0.0	16.6
Lille Gribsø „ 4.5—5.3	..	0.0	2.5	81.4	16.1	0.0	0.0	0.0	15.5	69.0	15.5	0.0
Hindsø „ 5.3	..	0.0	0.6	86.2	10.2	3.0	0.0	0.0	8.3	66.7	16.7	8.3
Skånsø „ 5.4	..	4.2	4.2	82.3	1.9	7.4	0.0	7.6	15.4	54.0	7.6	15.4
Øjesø „ 5.3	..	0.3	1.0	94.2	4.5	0.0	0.0	3.4	6.8	79.4	10.4	0.0
Langsø v. Torup „ 5.4	..	0.8	6.3	79,5	9.5	3.9	0.0	10.8	18.9	62,2	5.4	2.7

(To be continued)

Table IV. (Continued)

	% of number of individuals						% of number of species and varieties					
II. Alternately acid and alkaline waters	Alkalibiontic	Alkalifilous	Indifferent	Acidophilous	Acidobiontic	?	Alkalibiontic	Alkalifilous	Indifferent	Acidophilous	Acidobiontic	?
a. Chiefly acid waters												
Snabe—Iglsø pH: 6.0	0.0	11.3	25.2	57.1	0.0	6.4	0.0	20.4	28.8	40.7	0.0	10.1
Kalgaardssø „ 6.6—7.1	0.0	6.5	23.6	58.1	2.5	9.3	0.0	12.1	31.0	37.9	3.5	15.5
Raabjerg mile Sø „ 6.4	0.0	5.8	28.7	61.0	1.3	3.2	0.0	9.0	31.1	46.6	2.2	11.1
Bissehule klitsø „ 6.0	0.0	2.7	33.0	62.2	1.9	0.2	0.0	3.7	44.4	40.7	7.5	3.7
Klaresø „ 4.8—7.5	0.0	15.3	26.1	57.2	0.0	1.4	0.0	25.0	25.0	45.8	0.0	4.2
Agersø „ 6.3—8.8	0.0	6.2	22.8	70.7	0.0	0.3	0.0	23.8	33.3	38.0	0.0	4.9
Hampen Sø „ 5.4—8.5	0.5	35.3	20.7	42.5	0.0	1.0	2.8	43.2	21.6	27.0	0.0	5.4
b. Chiefly neutral—alkaline waters												
Gadevang Nørresø pH: 6.3—8.7	0.0	44.0	27.1	23.0	0.7	5.2	0.0	35.8	28.7	19.4	3.6	12.5
Sunds Sø „ 6.9—7.1	3.0	50.4	14.7	26.3	0.0	5.7	11.8	49.2	13.6	8.5	0.0	16.9
Skovsø n. f. Mørkedam „ 6.7—(6.9)	12.9	58.6	13.2	10.5	0.0	4.8	8.7	47.6	22.3	12.7	0.0	8.7
Jægerbakkedam „ 6.6—9.8	0.6	67.0	25.1	2.0	0.3	5.0	1.8	43.8	27.6	12.5	1.8	12.5
III. Constantly alkaline waters (pH minimum value always ≥ 7.0)												
a. Slightly alkaline waters												
Norssø pH: (6.8) 7.0—8.7	2.9	79.8	4.4	5.9	0.0	8.0	..	..	..	..	..	..
Brabrand Sø „ 7.2—7.8	13.5	80.5	4.8	0.0	0.0	1.2	12.9	65.1	13.9	0.0	0.0	8.1
Karlsø „ 7.4—7.7	1.9	84.1	5.5	8.1	0.0	0.4	2.6	68.4	13.2	10.5	0.0	5.3
Store Funkedam „ 7.0—8.1	6.4	74.1	9.3	3.8	0.4	6.0	6.8	63.6	15.9	9.1	2.3	2.3
Esrom Sø „ 7.4—8.7	25.1	74.4	0.5	0.0	0.0	0.0	18.8	75.0	3.1	0.0	0.0	3.1
Sorø Sø „ 7.7—8.6	4.3	95.4	0.3	0.0	0.0	0.0	14.8	82.3	2.9	0.0	0.0	0.0
Arresø „ 7.8—8.3	8.5	90.5	0.0	0.0	0.0	0.0	12.0	84.0	0.0	0.0	0.0	4.0
Furesø „ 7.5—8.6	2.1	94.3	0.0	0.0	0.0	3.6	17.9	75.0	0.0	0.0	0.0	7.1
b. Strongly alkaline waters (maximum value of pH ≥ 9.0)												
Badstue Ødam pH: 7.4—9.0	35.7	57.3	4.5	2.0	0.0	0.5	17.5	62.5	7.5	10.0	0.0	2.5
Kongskilde Molledam „ 7.8—9.0	10.2	85.8	3.7	0.3	0.0	0.0	6.6	63.2	17.0	7.9	0.0	5.3
Badstuedam „ 7.4—9.0	0.0	96.7	2.4	0.9	0.0	0.0	3.0	72.7	18.1	6.2	0.0	0.0
Tyrstrup Sø „ 7.5—9.0	6.2	92.6	0.9	0.3	0.0	0.0	21.3	63.8	8.5	2.1	0.0	4.3
Skanderborg Sø „ 7.7—9.0	5.7	91.6	1.1	0.0	0.0	1.6	24.4	64.4	4.5	0.0	0.0	6.7
Bagsværd Sø „ 7.5—9.0	2.0	95.4	2.6	0.0	0.0	0.0	10.7	73.2	13.4	0.0	0.0	2.7
Frederiksborg Slots Sø „ 7.2—9.7	54.3	45.7	0.0	0.0	0.0	0.0	50.0	50.0	0.0	0.0	0.0	0.0
Sjælsø „ 7.7—9.0	3.0	92.1	2.9	1.0	0.0	1.0	10.8	67.8	10.8	3.5	0.0	7.1
Lyngby Sø „ 7.7—9.0	0.9	98.2	0.0	0.0	0.0	0.9	..	..	..	..	..	..

Table V. pH spectra on the basis of epiphytic diatoms – recent material from Danish waters, set up on the basis of JØRGENSEN's work (1948).

Localities	Available analyses		% of number of individuals						% of numbers of species and varieties					
	pH	Alkalinity	Alkalibiontic	Alkalifilous	Indifferent	Acidophilous	Acidobiontic	?	Alkalibiontic	Alkalifilous	Indifferent	Acidophilous	Acidobiontic	?
Store Økssø	4.0—4.3	0.06	..	..	..	..	..	..	..	..	..	..	..	..
Sphagnum	..	..	..	..	7.8	79.8	12.6	0.0	..	..	25.0	66.6	8.4	0.0
Bottom sample (1 m)	..	..	..	..	8.7	67.9	23.4	0.0	..	..	17.9	71.4	10.7	0.0
Løvenholm Langsø	4.0—4.7	0.42	..	..	..	..	..	..	..	..	..	..	..	..
Carex rostrata	..	..	..	0.3	2.7	97.0	0.0	0.0	..	33.3	9.5	52.4	4.8	0.0
Bottom sample near the bank	..	..	..	0.0	17.8	76.9	5.3	0.0	4.6	9.1	9.1	54.5	9.1	13.6
Madum Sø	4.4—5.3	0.08	..	..	..	..	..	..	..	..	..	..	..	..
Isoetes—Lobelia	..	..	..	..	0.3	88.5	1.4	8.0	5.2	0.0	5.2	63.1	10.5	15.0
Bottom sample (10 cm)	..	..	..	..	0.0	97.0	2.1	0.9	..	..	4.3	73.9	13.2	8.6
Store Gribsø	3.9—6.5	0.20	..	..	..	..	..	..	..	..	..	..	..	..
Heleocharis	..	..	..	..	..	100,0	0.0	0.0	..	..	..	100.0	0.0	0.0
Nuphar (submerse leaves)	..	..	..	..	0.3	99.7	0.0	0.0	..	..	14.3	85.7	0.0	0.0
Fontinalis	..	..	..	0.2	0.7	99.1	0.0	0.0	..	18.2	18.2	63.6	0.0	0.0
Bottom sample near the bank	..	..	..	..	33.9	64.5	1.6	0.0	..	..	18.8	75.0	6.2	0.0
Agersø	6.3—8.8	0.42	..	..	..	..	..	..	..	..	..	..	..	..
Myriophyllum	..	..	..	6.2	22.8	70.0	0.0	0.3	..	23.8	33.3	38.0	0.0	4.9
Glyceria	..	..	..	8.9	40.6	49.3	0.0	1.2	..	22.2	38.8	33.4	0.0	5.6
Total numbers	..	..	..	..	..	..	..	..	..	20.8	41.7	33.3	0.0	4.2
Hampen Sø	5.4—8.5	0.14	..	..	..	..	..	..	..	..	..	..	..	..
Heleocharis	..	..	2.1	53.0	26.5	18.1	0.3	0.0	11.8	58.8	7.7	20.5	2.2	0.0
Bottom sample	..	..	0.5	35.3	20.7	42.5	0.0	1.0	2.8	43.2	21.6	27.0	0.0	5.4

Table VI. pH spectra for Bølling Sø – the 1939-material.

Pollen zone	Climatic period	cm. depth	Sample no.	% of number of diatom individuals						% of number of diatom-species and varieties						Number of individuals	Number of species and varieties
				Alkalibiontic	Alkaliphilous	Indifferent	Acidophilous	Acidobiontic	?	Alkalibiontic	Alkaliphilous	Indifferent	Acidophilous	Acidobiontic	?		
IX	Sub-Atlantic	12.5	4	7.9	90.5	0.0	0.0	0.4	1.2	13.0	60.0	0.0	0.0	9.0	18.0	1950	23
VII	Atlantic	85	34	0.0	94.7	0.3	0.0	0.0	0.5	7.1	52.5	10.0	10.0	3.4	17.0	1950	43
V	Boreal	120	49	0.0	90.4	0.8	0.5	0.0	8.4	0.0	51.0	12.0	12.0	4.0	21.0	1850	23
IV	Pre-boreal	160	66	0.7	90.8	8.1	0.0	0.0	0.4	9.0	60.0	17.0	5.0	0.0	9.0	1950	35
III	Late Dryas	210	130	0.0	98.0	0.4	0.4	0.0	1.2	3.7	52.3	14.0	5.0	0.0	25.0	1850	61
II b	Allerød b	275	117	diatoms absent													
II a	Allerød a	307.5	86	0.6	97.9	0.6	0.0	0.0	0.9	7.9	64.0	13.0	2.1	0.0	13.0	1850	42
I b	Bølling oscillation	345	97	0.0	97.6	1.1	0.8	0.0	0.5	4.0	64.0	20.0	0.0	0.0	12.0	1393	26
I a	Earliest Dryas	367.5	108	6.1	89.0	2.0	0.0	0.0	2.9	10.0	65.0	15.0	0.0	0.0	10.0	296	23

Table VII. Alkalinity spectra (diatoms).

Subfossil material in Bølling Sø 1939-material			% of number of individuals					% of numbers of species and varieties				
			Calciphobous	Indifferent	Calciphilous	Calcibiontic	?	Calciphobous	Indifferent	Calciphilous	Calcibiontic	?[1]
No.	Depth cm.	Sequence of strata										
4	12.5	Beech time	..	89.9	1.0	..	9.1	..	55.0	35.0	..	10.0
34	85	Early Atlantic time	..	95.8	3.5	..	0.7	..	61.1	19.5	..	19.4
49	120	Pine-hazel time	..	99.3	0.0	..	0.7	..	62.0	12.2	..	20.8
66	160	Birch-pine time	..	88.4	3.4	..	8.2	..	42.8	22.8	..	34.4
130	210	Late Dryas	..	77.8	6.3	..	15.9	2.3	53.5	24.1	2.1	19.0
117	275	Allerød b	..	..	..	..	..	..	..	..	..	..
86	307.5	Allerød a	..	93.9	5.4	..	0.6	..	45.9	16.2	..	37.9
97	345	Bølling oscillation	..	95.0	3.1	..	1.9	..	52.0	12.0	..	36.0
108	367.5	Earliest Dryas	..	74.5	22.6	..	2.9	..	47.6	19.0	..	33.4

(To be continued)

[1] As to the interpretation of the forms whose place in the spectrum is indicated by a ?, see further p. 21.

Table VII. (Continued)

			% of number of individuals					% of numbers of species and varieties				
			Calciphobous	Indifferent	Calciphilous	Calcibiontic	?	Calciphobous	Indifferent	Calciphilous	Calcibiontic	?
Recent material from alkaline Danish waters[1]												
pH	alkalinity											
7.6—>9.0	2.30	Badstuedam	0.9	92.3	7.2	..	0.5	..	77.7	11.1	..	11.2
7.4—8.4	1.99	Lyngby Sø	..	91.1	7.1	..	1.8	..	53.0	14.3	..	32.7
7.5—9.0	1.14	Bagsværd Sø	..	45.9	49.5	..	4.6	..	57.7	13.1	..	29.2
7.7—9.0	1,98	Sjælsø	1.0	78.6	7.7	..	12.7	..	40,0	24.0	..	36.0
7.7—8.6	2.21	Sorø Sø	..	87.6	4.6	..	7.8	..	38.8	19.0	..	42.2
7.7—9.0	2.99	Skanderborg Sø	..	80.9	2.6	..	16.5	..	44.1	18.6	..	37.2
7.8—8.3	2.19	Arresø	..	73.6	18.9	..	7.5	..	50.0	25.0	..	25.0
7.2—7.8	3.81	Brabrand Sø	0.3	75.5	2.7	..	21.5	..	44.1	13.0	..	42.9
7.4—7.7	2.10	Karls Sø	7.3	79.5	4.3	..	8.9	..	42.1	15.8	..	42.1
7.0—8.1	2.04	St. Funkedam	2.2	81.7	9.0	..	7.1	..	46.3	14.6	..	29.1
7.8>9.0—	4.52	Kongskilde Mølledam	0.9	78.8	11.3	..	9.0	..	38.4	13.4	..	48.2

[1] Set up on the basis of JØRGENSEN's work (1948).

Færdig fra trykkeriet den 15. december 1954.

PLATES

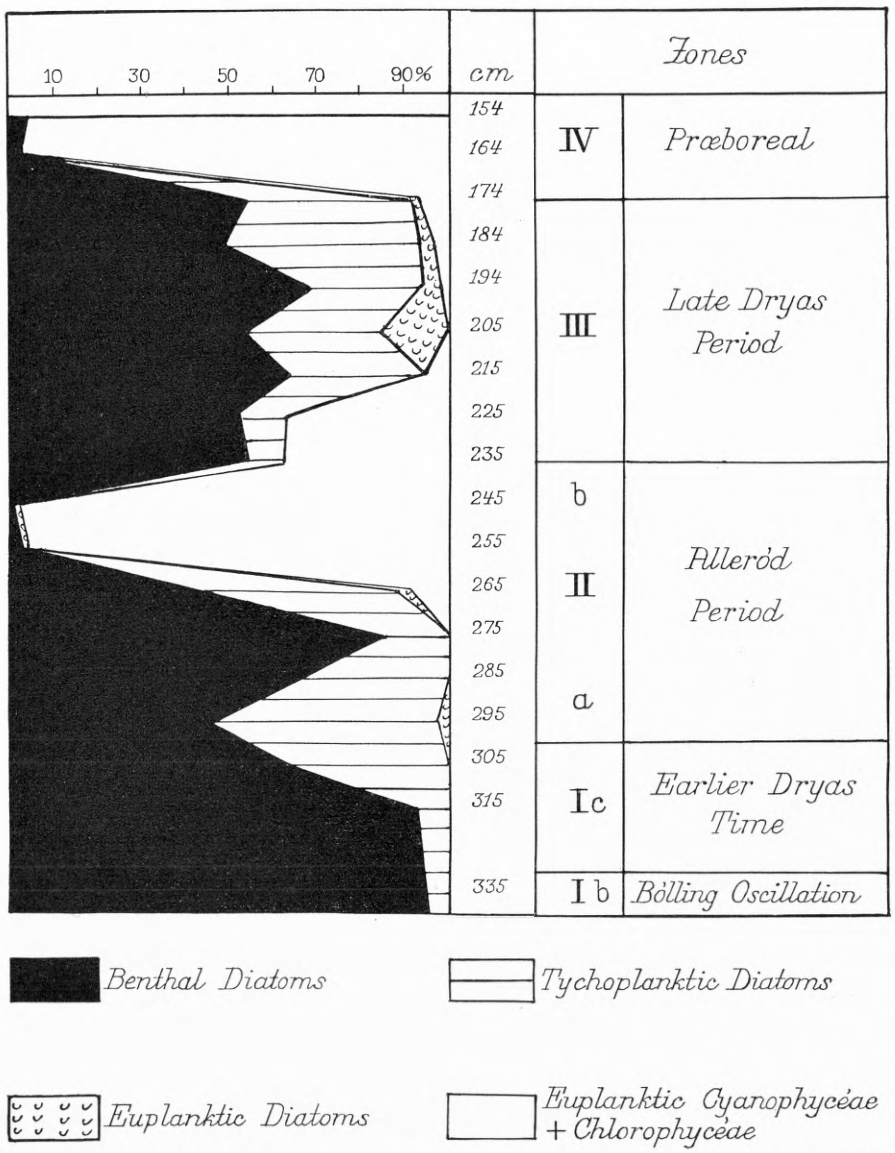

Plate I. Diagram showing the relation between benthic and planktonic organisms in the 1946-material.

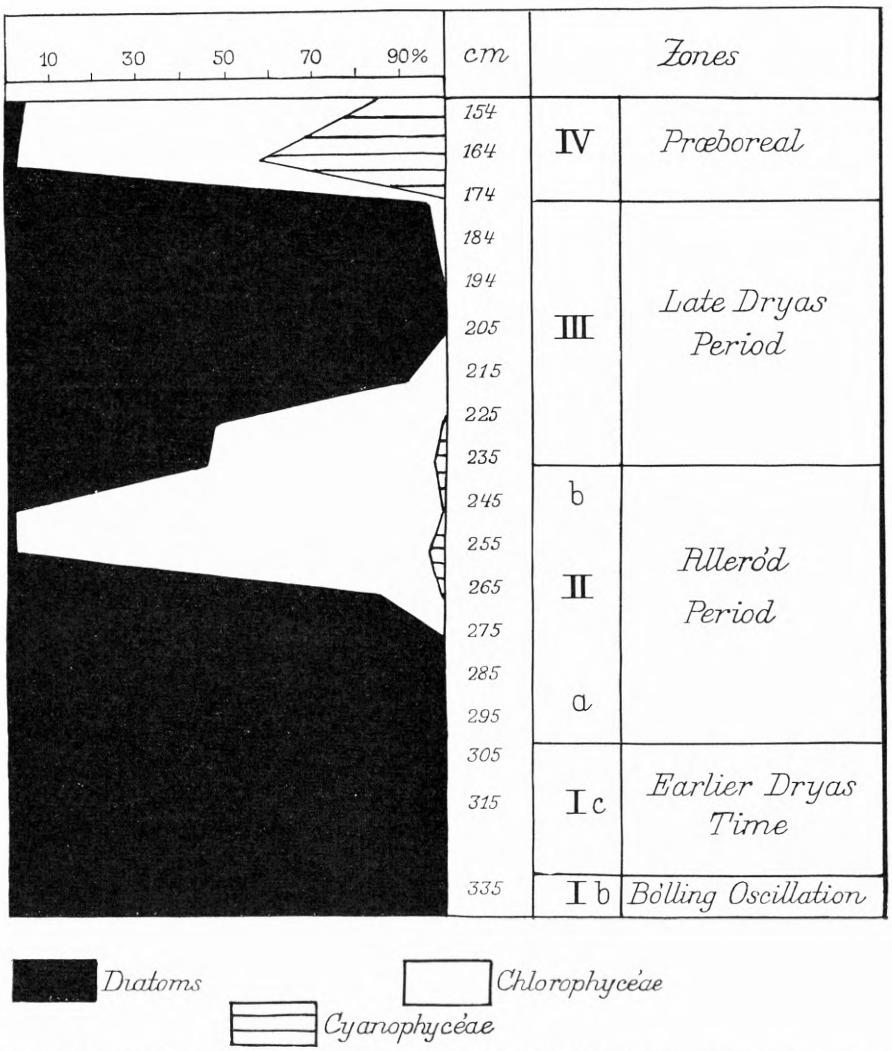

Plate II. Special diagram of groups of organisms in the 1946-material. To obtain a more correct relation between the various groups of organisms in regard to the degree of covering, cf. p. 5, the number of spores of *Aphanizomenon* cfr. *flosaquae*, *Anabaena* cfr. *flos-aquae*, and *Gloeothricia* cfr. *echinulata* were multiplied by 7.9 and 4, respectively, it being thus taken into consideration that the vegetative cells had been destroyed. Measurements of recent material have shown that the numerical values given correspond approximately to the relation between spores and the number of vegetative cells and spores. The numbers of diatoms were multiplied by $^1/_2$.

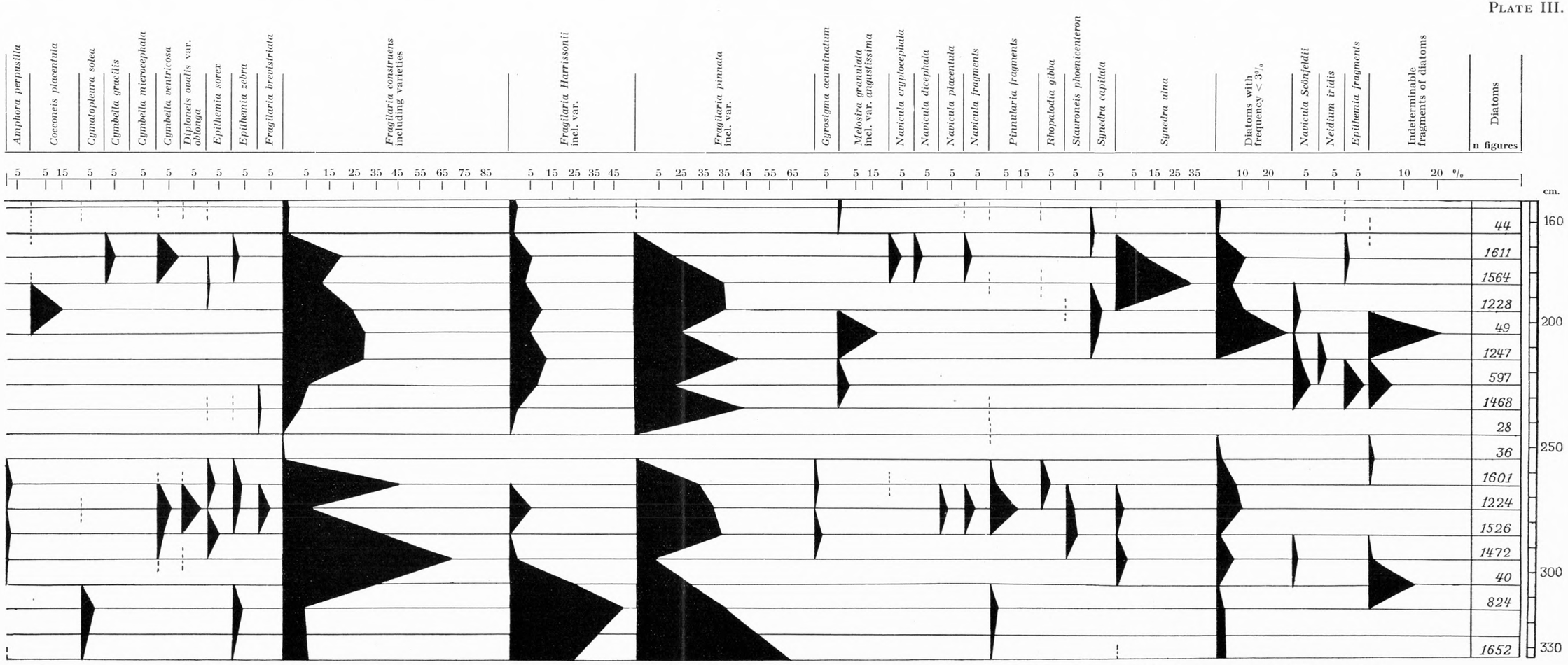

Plate III. Diagram showing the distribution of the diatoms in the sediments (the 1946-material). By the n-figure is here understood the number of organisms on which the percentage calculation was based.

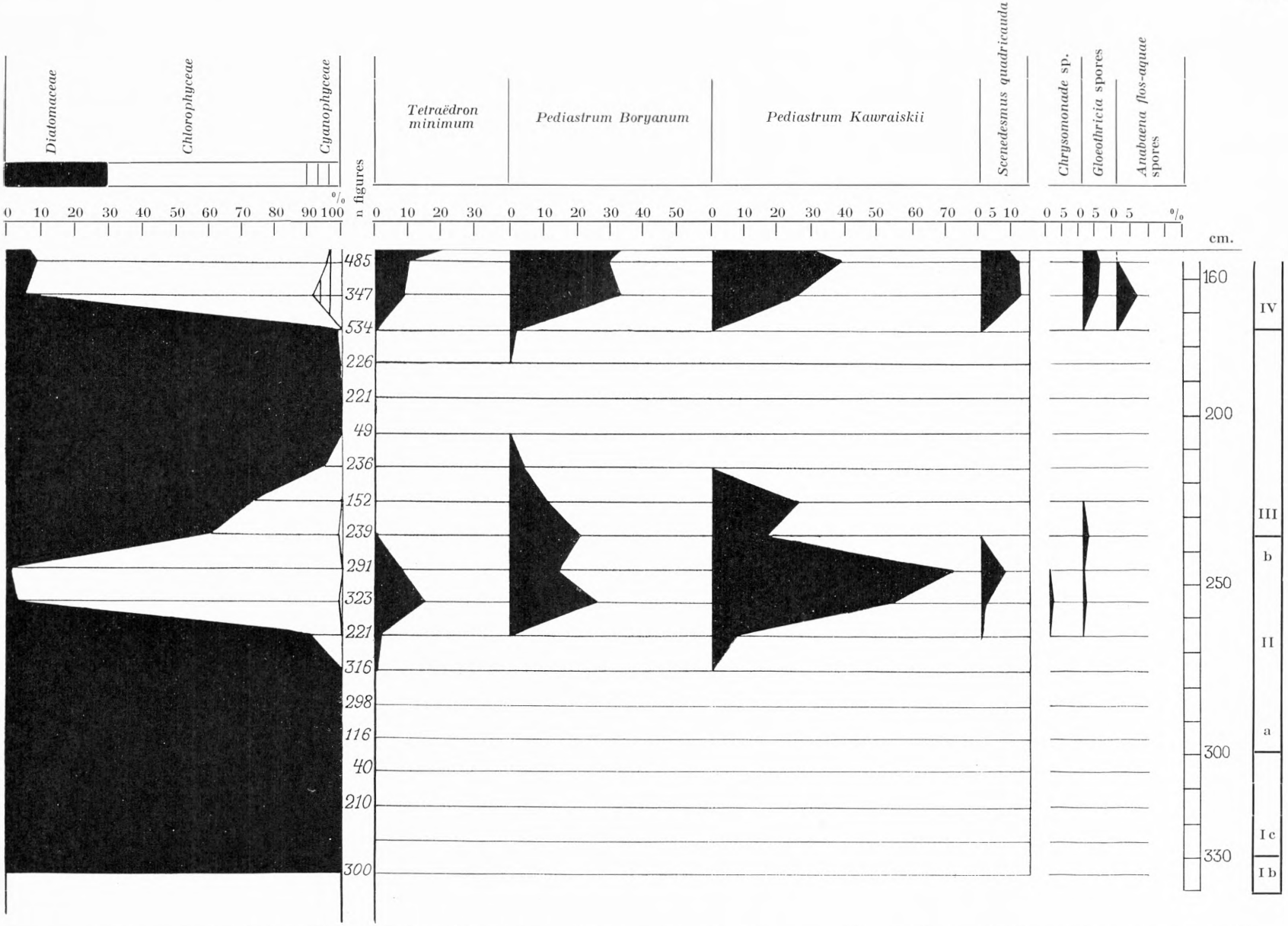

Plate IV. Diagram of the distribution of the Chlorophyceae and the Cyanophyceae in the sediments (the 1946-material). As for the n-figure, see Pl. III.

Fig. 1. *Pediastrum Kawraiskii* SCHMIDLE. × 600.
- 2. — *angulosum* (EHRBG.) MENEGH. × 1000.
- 3. — *Boryanum* (TURPIN) MENEGH. × 1000.
- 4. — *Tetras* (EHRBG.) RALFS. × 1000.
- 5. — *duplex* MEYEN. × 600.
- 6. *Tetraedron minimum* (BRAUN) HANSG. × 1200.
- 7. — *muticum* (BRAUN) HANSG. × 1200.
- 8. — *tumidulum* (REINSCH.) HANSG. × 1200.
- 9. *Cosmarium Botrytis* MENEGH. × 600.
- 10. *Fragilaria construens* (EHRBG.) GRUN. × 1500.
- 11. — — var. *binodis* (EHRBG.) GRUN. × 1600.
- 12. — — var. *venter* (EHRBG.) GRUN. × 1600.
- 13-14. — *pinnata* EHRBG. × 1200.
- 15. *Cyclotella antiqua* W. SM. × 1200.
- 16. *Cymbella Ehrenbergii* KÜTZ. × 1600.
- 17. *Gloeothricia echinulata* (SMITH) RICHTER.
  a. recent material, ca. × 300.
  b. subfossil spores, × 300.
- 18. Various forms of spores of the genus *Anabaena*.
  a. *A. spirioides* KLEBAHN. × 300.
  b. *A. flos-aquae* BREBIS. × 300.
  c. *A. planctonica* BRUNNTH. × 600.
- 19. Spores of *Aphanizomenon flos-aquae* RALFS. × 600.
- 20. Cells of *Chroococcus turgidis* (KÜTZ) NÄG. × 600.
- 21. Cells of *Chroococcus minutus* (KÜTZ.) NÄG. × 1000.
- 22. Cells of *Chroococcus limneticus* LEMM. × 600.
- 23. *Tracelomonas volvocina* EHRBG. × 1600.

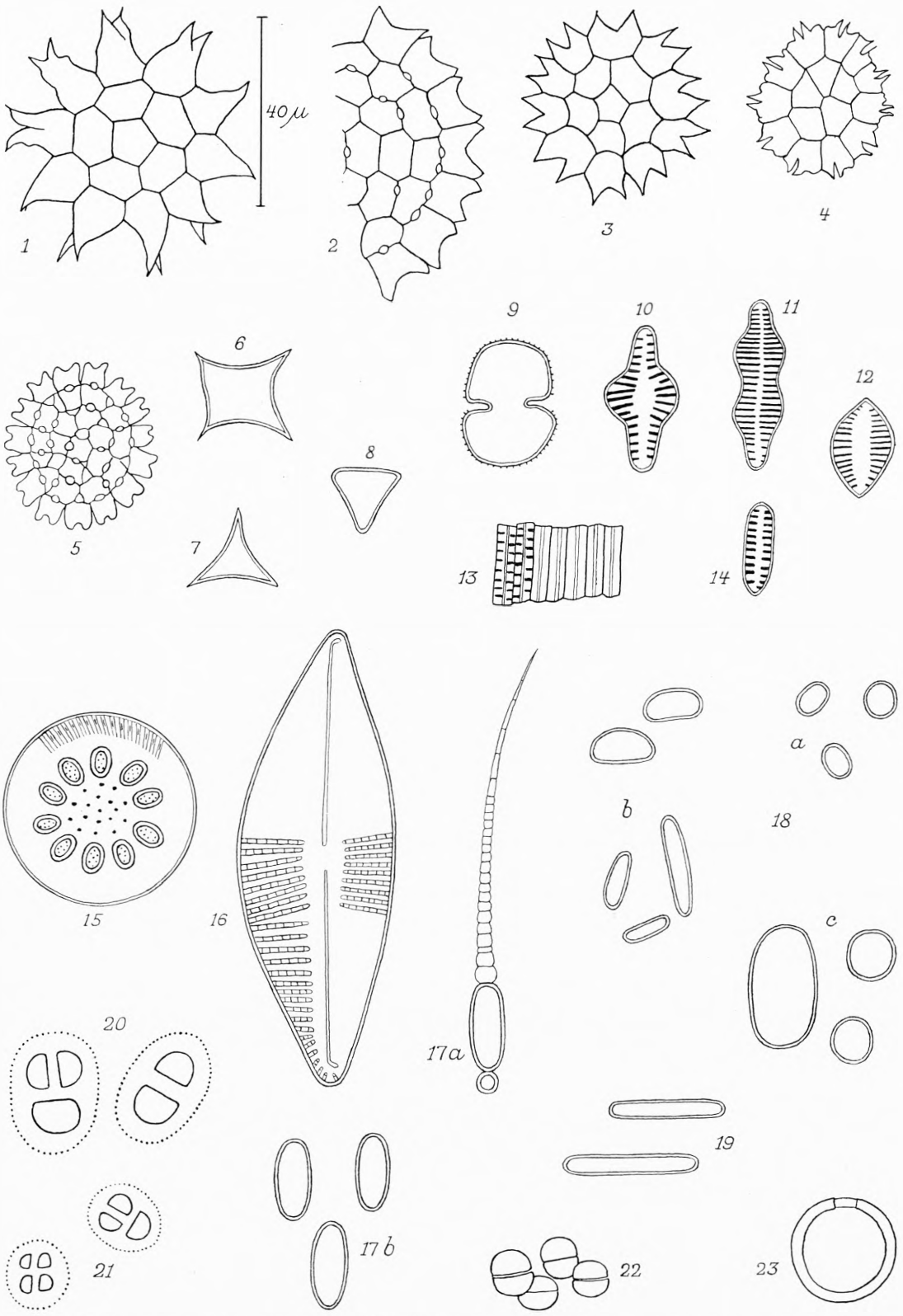

Plate V. Some characteristic components of the micro-communities from late-glacial strata in Bølling Sø.

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