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THE SUBFOSSIL ALGAL FLORA OF THE LAKE BØLLING SØ AND ITS LIMNOLOGICAL INTERPRETATION

BY

E. FJERDINGSTAD

København 1954
i kommission hos Ejnar Munksgaard

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BIANCO LUNOS BOGTRYKKERI A-S

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 $^0/_0$ 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 $^0/_0$ 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 $\times$) 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 $^0/_0$ 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 micro-community 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 $^0/_0$, respectively, while *F. Harrissonii* and its varieties exhibit 2.0, 3.6, 8.0, and 0.5 $^0/_0$, and *F. pinnata* and its varieties 7.8, 42.1, 36.4, and 24.9 $^0/_0$, respectively. Together these three species and their varieties constitute 75.4, 84.7, 54.6, and 71.5 $^0/_0$, 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 $^0/_0$), *E. sorex* (only in sample 275 with 2.6 $^0/_0$), *Fragilaria brevistriata* (only in sample 275 with 4.6 $^0/_0$), *Gomphonema constrictum, Melosira granulata* (sample 275 with 1.6 $^0/_0$), *Navicula anglica, N. placentula* (only in sample 275 with 1.1 $^0/_0$), *N. Schönfeldii* (only in sample 295 with 1.3 $^0/_0$), *N. tuscula* forma *minor* (only in sample 265 with 1.1 $^0/_0$), *Rhopalodia gibba* (only in sample 265 with 3.8 $^0/_0$), *R. gibberula* (only in sample 265 with 1.4 $^0/_0$), *Stauroneis phoenicenteron, Stephanodiscus astraea* var. *minutula* (only in sample 265 with 0.6 $^0/_0$), 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 $^0/_0$), 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 $^0/_0$) and *Scenedesmus quadricauda* (0.9 $^0/_0$). 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 $^0/_0$, 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 $^0/_0$, respectively, *Pediastrum Boryanum* with 25.4 and 14 $^0/_0$, respectively, and *Tetraedron minimum* with 14.6 and 7.5 $^0/_0$.

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 $^0/_0$, of which *Fragilaria pinnata* constitutes the 43.4 $^0/_0$, while the remaining *Fragilaria* species together amount to 16.6 $^0/_0$.

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 $^0/_0$ and *P. Kawraiskii* 25.6 $^0/_0$. Of the diatoms, *Fragilaria pinnata* is dominant with 12.3 $^0/_0$, while the other diatoms attain frequencies below 10 $^0/_0$.

In sample 658/46 the share in the spectrum taken by the Chlorophyceae has fallen to 4.9 $^0/_0$, 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 $^0/_0$, 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 $^0/_0$. 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 $^0/_0$, 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 $^0/_0$), but a considerable decline in frequency for *F. pinnata* (from 33.5 to 14.1 $^0/_0$) and for *F. Harrissonii* including its varieties a small rise in frequency (from 6.3 to 9.6 $^0/_0$). Together these *Fragilaria* components constitute 46.5 $^0/_0$.

The following diatoms jointly attain to a total frequency of 44.0 $^0/_0$: *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 $^0/_0$.

In the following sample, no. 580, the Chlorophyceae entirely dominate the spectrum, constituting together 85.3 $^0/_0$, distributed as follows: *Pediastrum Boryanum* 31.7 $^0/_0$, *P. Kawraiskii* 35.4 $^0/_0$, *Scenedesmus arcuatus* 10.3 $^0/_0$, and *Tetraedron minimum* 7.9 $^0/_0$. The Cyanophyceae together constitute 9.5 $^0/_0$, and are represented by spores of *Anabaena* cfr. *flos-aquae* (5.5 $^0/_0$) and spores of *Gloeothricia* (4.0 $^0/_0$). Thus the diatoms form only 5.2 $^0/_0$ and are represented by the species *Cocconeis placentula* (0.6 $^0/_0$), *Fragilaria construens* (2.5 $^0/_0$), and *F. Harrissonii* (1.8 $^0/_0$).

Similarly, the Chlorophyceae with 84.9 $^0/_0$ dominate the spectrum for sample 575, but *Scenedesmus arcuata* has now been replaced by typical *S. quadricauda* (10.2 $^0/_0$). The frequency for the Cyanophyceae proves to have been halved (4.8 $^0/_0$), still spores of *Gloeothricia* constitute 4.5 $^0/_0$, *Anabaena* cfr. *flos-aquae* is absent, but cells of *Microcystis* sp. occur (0.3 $^0/_0$). A Chrysomonade sp., probably *Tracelomonas volvocina,* attains 1.0 $^0/_0$.

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 $^0/_0$, 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 $^0/_0$, 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 $^0/_0$, while *Fragilaria construens* with var. *venter* has re-captured its great frequency of former periods, totalling 80.6 $^0/_0$ or 55.3 and 25.3 $^0/_0$, respectively.

Of the other types, *Melosira islandica* subsp. *helvetica* constitutes 7.9 $^0/_0$, 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 $^0/_0$).

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 $^0/_0$.

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 $^0/_0$, while in the bottom sample the acidophilous individuals dominate with 42.5 $^0/_0$. 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 $^0/_0$ 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 $^0/_0$. 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 $^0/_0$ (minimum 42.5 $^0/_0$, maximum 70.7 $^0/_0$) and the indifferent individuals 20—33 $^0/_0$; 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 $^0/_0$ for the indifferent ones 20.7 $^0/_0$, and for the acidophilous individuals 42.5 $^0/_0$. 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 $^0/_0$.
(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 $^0/_0$, while the alkaliphilous individuals constitute 44—67 $^0/_0$.

III. Constantly alkaline waters, in which the alkalibiontic and the alkaliphilous individuals together constitute ca. 90 $^0/_0$. 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 $^0/_0$ (minimum) in sample 108 from the earliest Dryas, and 98.0 $^0/_0$ (maximum) in sample 130 from the late Dryas. The alkalibiontic species attain the greatest frequency, 7.9 $^0/_0$, in sample 4 from the beech period, while the indifferent species have their greatest frequency, 8.1 $^0/_0$, in sample 66 from the birch-pine period. The acidophilous and acidobiontic species are represented in very small numbers only (< 1 $^0/_0$) 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 $^0/_0$ in sample 49 from the pine-hazel period, and the maximum 65 $^0/_0$ in sample 108 from the earliest Dryas. The alkalibiontic species in these spectra constitute from 0—13 $^0/_0$, with the maximum in sample 4 from the beech period, while the indifferent species constitute 0—20 $^0/_0$, 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 $^0/_0$; no. 97, 92.0 $^0/_0$; no. 86, 89.6 $^0/_0$; no. 130, 68.4 $^0/_0$; no. 66, 74.1 $^0/_0$; no. 49, 4.3 $^0/_0$; no. 34, 4.1 $^0/_0$; no. 4, 80.6 $^0/_0$, are precisely dominant in bottom samples from eutrophic ponds and lakes, thus in Arresø (15.1 $^0/_0$), Skanderborg Sø (var. *venter*: 22.6 $^0/_0$), Sorø Sø (29.0 $^0/_0$), Sjælsø (30.3 $^0/_0$), Bagsværd Sø (29.3 $^0/_0$), Lyngby Sø (62.5 $^0/_0$, var. *venter*: 21.2 $^0/_0$), forest lake north of Mørkedam (var. *venter*: 16.4 $^0/_0$), Karlssø (12.0 $^0/_0$), Funkedam (11.6 $^0/_0$,

[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 $^0/_0$ from the early Dryas and the maximum 99.3 $^0/_0$ from the pine-hazel period.

In the early Dryas the calciphilous species constitute 22.6 $^0/_0$ 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 $^0/_0$ calciphobous species, Sjælsø with 1.98 mvl. has 1.0 $^0/_0$ calciphobous species, Brabrand Sø with 3.81 mvl. has 0.3 $^0/_0$ calciphobous species, Karlssø with 2.1 mvl. has 7.3 $^0/_0$ calciphobous species, Funkedam with 2.04 mvl. has 2.2 $^0/_0$ calciphobous species, and even Kongekilde Mølledam with 4.52 mvl. has 0.9 $^0/_0$ 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 $^0/_0$ of indifferent and 22.6 $^0/_0$ of calciphilous species, totalling 97.1 $^0/_0$. Comparing this with recent material from a lake with a fairly similar spectrum, viz. Arresø, which has 73.6 $^0/_0$ of indifferent and 18.9 $^0/_0$ of calciphilous species, totalling 92.5 $^0/_0$, 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 $^0/_0$ of indifferent and 6.3 $^0/_0$ of calciphilous species, and comparing this with the recent lake Sjælsø, which has 78.6 $^0/_0$ of indifferent and 7.7 $^0/_0$ of calciphilous species, totalling 86.3 $^0/_0$, 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 $^0/_0$ hydrogen peroxide, cf. BRANDER (1936, p. 135), while the special preparations of Chlorophyceae and Cyanophyceae were treated with 10 $^0/_0$ 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 $^0/_0$ and *Tetraedron minimum* with 0.9 $^0/_0$ 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 $^0/_0$, but decrease to 4.9 $^0/_0$ 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 $^0/_0$ (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 $^0/_0$, while the Cyanophyceae constitute 9.5 $^0/_0$, and the diatoms 5.2 $^0/_0$. 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 $^0/_0$ 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 fresh-water 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 $^0/_0$ 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 $^0/_0$ (minimum 42.5 $^0/_0$, maximum 70.7 $^0/$), the indifferent species 20—33 $^0/_0$, 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 $^0/_0$, while the alkaliphilous species constitute 44—67 $^0/_0$. III. constantly alkaline waters, in which the alkalibiontic and the alkaliphilous species combined constitute ca. 90 $^0/_0$; 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.	Bolling oscillation	Tundra time Earliest Dryas	Cl-affinity	pH	Alkalinity
Late-glacial							
III	II b	II a	I b	I a			
$^0/_0$	$^0/_0$	$^0/_0$	$^0/_0$	$^0/_0$			
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: Halophobous	Indifferent	Halophilous	Mesohalobous	?	% of numb. of spec. and variet.: Halophobous	Indifferent	Halophilous	Mesohalobous	?	Number of individuals	Number of species and varieties
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: Alkalibiontic	Alkaliphilous	Indifferent	Acidophilous	Acidobiontic	?	% of number of species and varieties: Alkalibiontic	Alkaliphilous	Indifferent	Acidophilous	Acidobiontic	?
I. Constantly acid waters.													
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					
	Al-kali-bion-tic	Al-kali-phil-ous	In-diffe-rent	Aci-do-phil-ous	Aci-do-bion-tic	?	Al-kali-bion-tic	Al-kali-phil-ous	In-diffe-rent	Aci-do-phil-ous	Aci-do-bion-tic	?
II. Alternately acid and alkaline waters												
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
Karlssø „ 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 Mølledam „ 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
Sjælssø „ 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	Alkaliphilous	Indifferent	Acidophilous	Acidobiontic	?	Alkalibiontic	Alkaliphilous	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)

pH	alkalinity	Recent material from alkaline Danish waters[1]	% of number of individuals: Calciphobous	Indifferent	Calciphilous	Calcibiontic	?	% of numbers of species and varieties: Calciphobous	Indifferent	Calciphilous	Calciobiontic	?
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

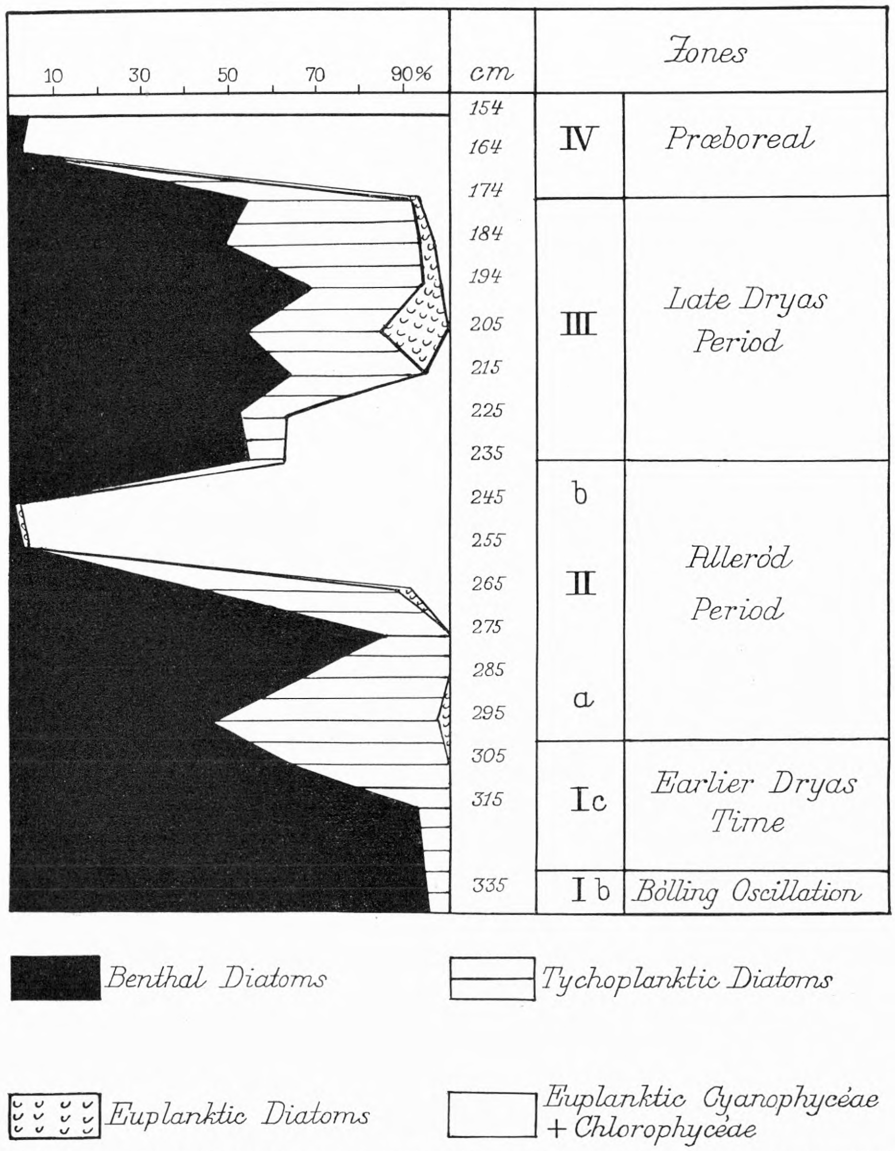

Plate I. Diagram showing the relation between benthic and planktonic organisms in the 1946-material.

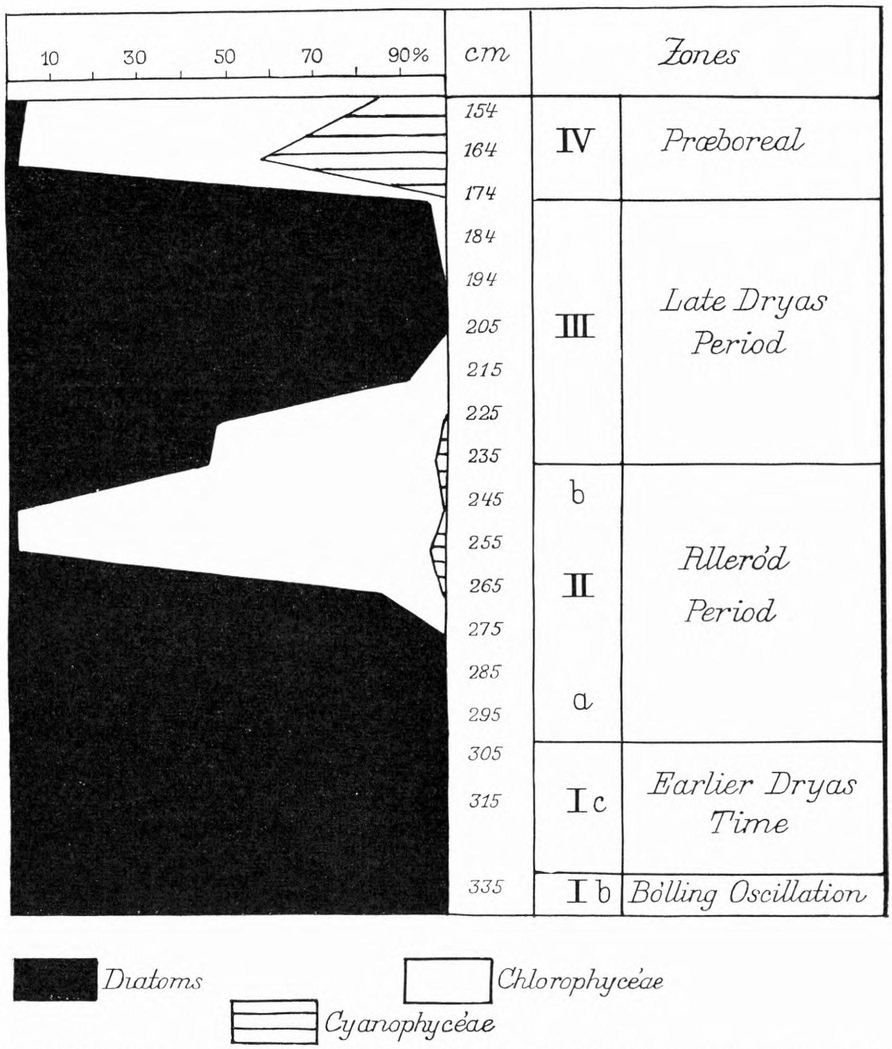

Plate II. Special diagram of groups of organisms in the 1946-material. To obtain a more correct relation between the various groups of organisms in regard to the degree of covering, cf. p. 5, the number of spores of *Aphanizomenon* cfr. *flosaquae*, *Anabaena* cfr. *flos-aquae*, and *Gloeothricia* cfr. *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 $^1/_2$.

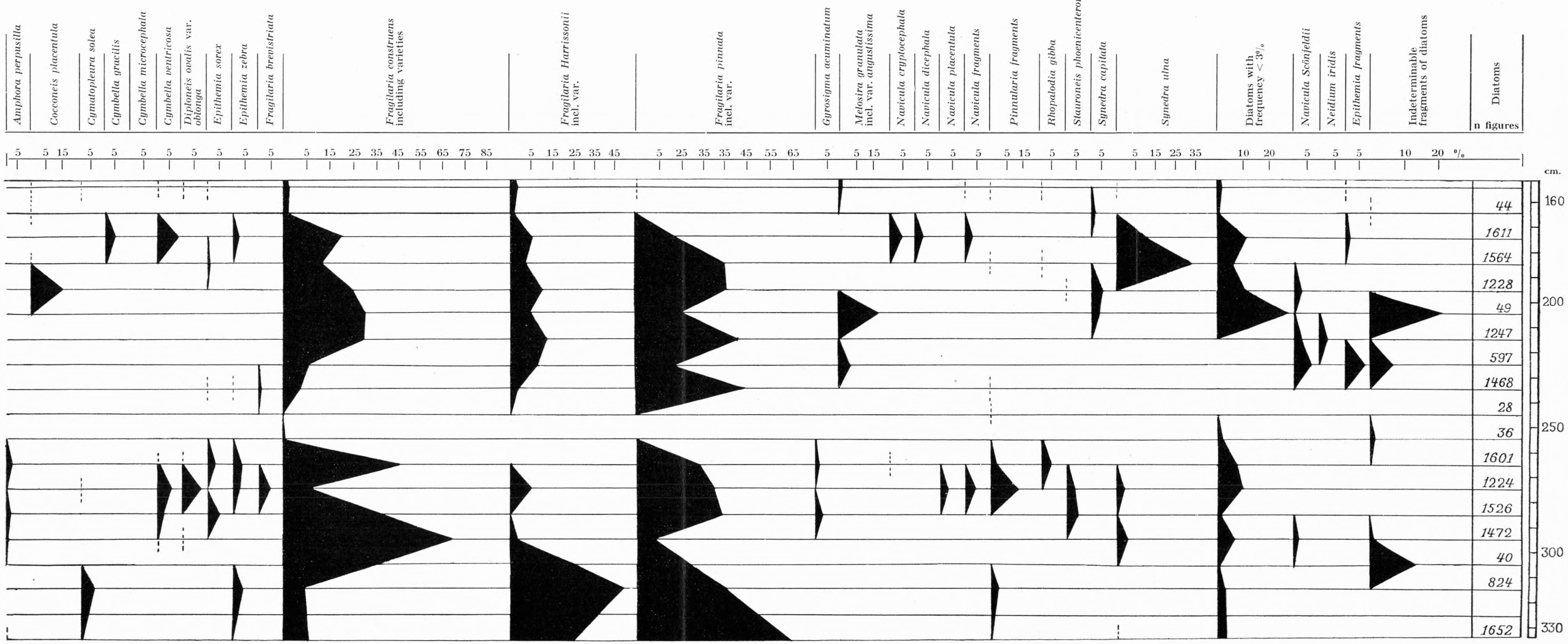

Plate III. Diagram showing the distribution of the diatoms in the sediments (the 1946-material). By the n-figure is here understood the number of organisms on which the percentage calculation was based.

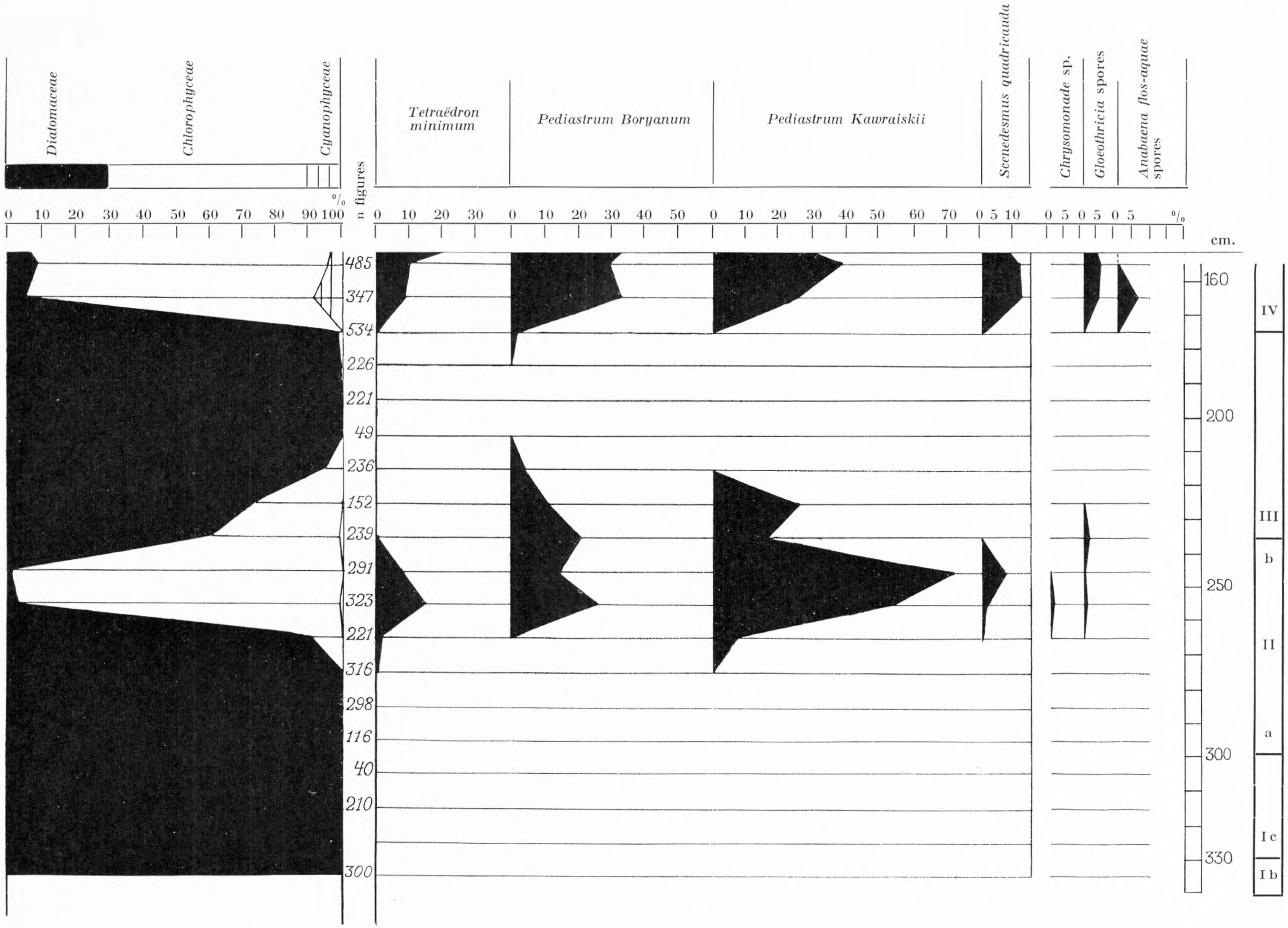

Plate IV. Diagram of the distribution of the Chlorophyceae and the Cyanophyceae in the sediments (the 1946-material). As for the n-figure, see Pl. III.

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.

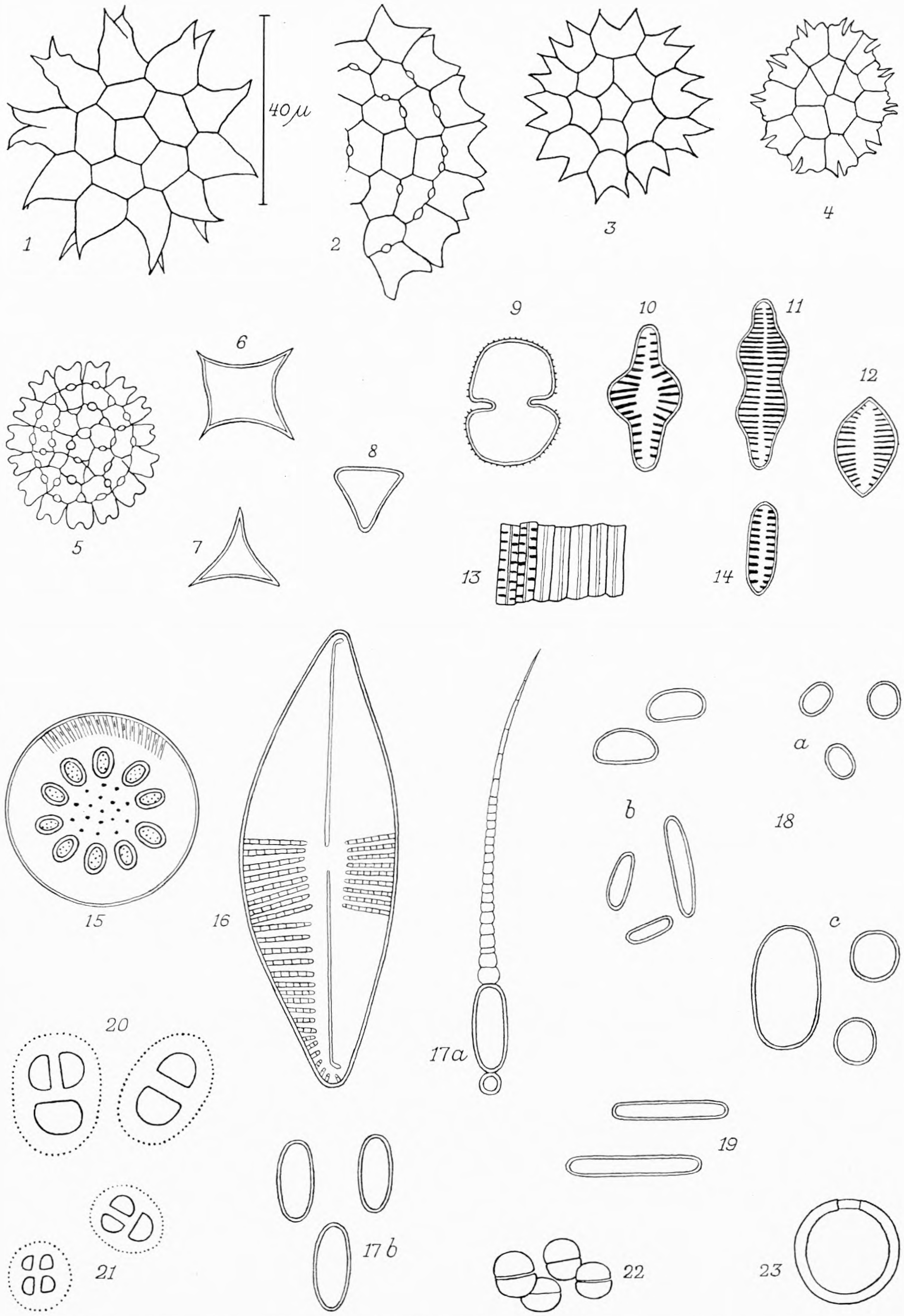

Plate V. Some characteristic components of the micro-communities from late-glacial strata in Bølling Sø.

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