

THE DIATOM STRATIGRAPHY AND PALEOECOLOGY OF LAKE OHRID, YUGOSLAVIA

ADRIENNE KEHDE ROELOFS¹ and PETER KILHAM

School of Natural Resources, The University of Michigan, Ann Arbor, MI 48109 (U.S.A.)
Division of Biological Sciences, The University of Michigan, Ann Arbor, MI 48109 (U.S.A.)

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ABSTRACT

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An 8.85 m core (No. 9) was taken from Lake Ohrid, Yugoslavia, in August 1973 at a depth of 210 m, approximately 6 km offshore of Gorica, Yugoslavia. The core was sampled at 10-cm intervals and analyzed for moisture, organic and CaCO₃ content, and diatoms.

There is a slight but steady decrease of moisture with depth, probably due to sediment compaction. The organic content showed little variation throughout the core ($\bar{x} = 2.73 \pm 0.39\%$ of total weight). The CaCO₃ content from 885–110 cm depth also showed little change ($\bar{x} = 2.32 \pm 0.55\%$ of total weight) but increased in the top meter of the core (100–0 cm, $\bar{x} = 11.03 \pm 8.86\%$ of total weight). Throughout the core there is an inverse relationship between organic and CaCO₃ content, particularly in the top meter.

Extrapolation to the bottom of the core using linear regression based on ¹⁴C-dating yields a date of ca. 30,000 years B.P.

Results indicate that Lake Ohrid has remained an oligotrophic lake throughout the period represented by Core 9. Diatom analysis shows one persistent group of diatoms throughout the core. This group consists of *Cyclotella fottii*, *C. hustedtii*, and *C. hustedtii* var.1 and is referred to as the *Cyclotella* complex.

Between 885–650 cm (ca. 30,000–20,000 yr B.P.) there is a sharp increase in numbers and a slight increase in diversity of species. This may correspond with the beginning of the warmer, more humid middle Pleniglacial.

Between 650–100 cm (ca. 20,000–10,000 yr B.P.) the *Cyclotella* complex appears usually alone in small numbers. There are a few other scattered species in this section, mainly *Opephora martyi* and *Fragilaria pinnata*. This section of the core probably corresponds with the cold upper Pleniglacial of the Würm (Weichselian).

Between 100–0 cm (ca. 10,000–0 yr B.P.) there is the largest increase in number and diversity of species, particularly above 60 cm. The *Cyclotella* complex, *C. ocellata*, *Cyclotella* sp.1, *Stephanodiscus astraea* var. *intermedia* fo.1 and *Stephanodiscus* sp.1 are dominant. This is the only section of the core in which *Stephanodiscus* species occur, and probably corresponds with the Holocene.

¹ Present address: Department of Botany, The University of British Columbia, Vancouver, B.C. V6T 1W5 (Canada).

INTRODUCTION

Lake Ohrid is one of the large (surface area = 348 km²), deep (maximum depth = 298 m, mean depth = 145 m) and ancient lakes of the world. Some geologists believe that the southern basin of the lake is of Miocene age (Ivanovski and Stračkov, 1974) and it is generally agreed that the lake has existed in its present form since the Pliocene (Stanković, 1960; Ivanovski and Stračkov, 1974). The marked endemism of Lake Ohrid's fauna and flora attests to the great antiquity of the lake (Stanković, 1960). This initial paper on the paleolimnology of Lake Ohrid is focused on the diatom stratigraphy of an 8.85 m sediment core.

The four lakes of the Dassaretes (Lakes Ohrid, Prespa, Korča, and Bilište) located in Yugoslavia and Albania (41°N 20°E) are believed to have been connected until the late Pliocene or early Pleistocene (Stanković, 1960; Ivanovski and Stračkov, 1974) when tectonic events occurred which closed the connections. Korča and Bilište eventually became dry lacustrine basins. Prespa is now a shallow (mean depth = 19–20 m) oligotrophic, calcareous, graben lake (Stanković and Šapkarev, 1959; Kozarov, 1960).

Lake Ohrid is also an oligotrophic, calcareous, graben lake. The chemical and physical limnology, general history, and endemism of the lake have been extensively investigated (Stanković and Hadžišče, 1953; Stanković, 1960). Zooplankton (Serafimova-Hadžišče, 1959), bacteria (Oceviski, 1953, 1958a, b), phytoplankton population dynamics (Kozarov, 1954, 1958), and primary production by phytoplankton (Kozarov, 1959; Allen and Oceviski, 1976) have also been studied.

These investigations indicate that the present highly oligotrophic state of the lake is possibly maintained through the suppression of photosynthetic activity as a consequence of Lake Ohrid's physical and chemical characteristics. It is a marl-producing lake that is generally oligomictic. With the exception of occasional winter overturn, the lake is thermally stratified with an upper heterothermic layer (0–70 m) and a lower homothermic layer (70–298 m). The temperature of the lake is always above 4°C. The highly stable thermal characteristics of Lake Ohrid can be attributed to a very stable summer stratification caused by intense insolation, shelter from the winds by the high mountains, and to an upper heterothermic zone isolated from a massive hypolimnion with almost no variation in temperature (Stanković, 1960).

Lake Ohrid has a very high transparency (1% of the light penetrating the surface reaches depths of 30–35 m; Stanković, 1960) owing to the low abundance of phytoplankton and low allochthonous detritus. The lake is fed almost exclusively by underground karstic springs. Detrital material apparently settles out of the influent water underground before it enters the lake.

Lake Ohrid is a typical calcium-bicarbonate marl lake, in which Ca(HCO₃)₂ predominates. There is frequent precipitation of CaCO₃ in the littoral zone, particularly during periods of peak phytoplankton photosynthesis (Stanković, 1960).

Wetzel (1975) describes marl lakes as a "type of maintained oligotrophy" where reduced productivity is maintained by decreased nutrient availability rather than "true" oligotrophy, in which nutrient inputs to the system are deficient. Decreased nutrient availability is due to adsorption of phosphate, iron, manganese, and organic compounds to colloidal and sedimenting particulate CaCO_3 . These particles are insoluble and thus are effectively lost to the system owing to sedimentation. Bioassay experiments (Allen and Ocevski, 1976) appear to indicate that the phytoplankton in Lake Ohrid are often limited by silica, phosphorus, iron, etc.

The purpose of this study was to determine the extent to which the present oligotrophy and unique endemism represented by the diatom community was typical of the past. The core which was examined allows interpretation of the diatom stratigraphy in relation to the degree of oligotrophy, and chemical—physical, climatic, and cultural changes over the past 30,000 years of lacustrine history.

METHODS

Collection of the core

The 8.85 m core (No. 9) was taken in August 1973 by André Lambert and Peter Kilham at a depth of 210 m approximately 6 km offshore of Gorica, Yugoslavia (Fig.1). A modified Kullenberg corer was used. This corer was designed and constructed by Uli Briegel of the Eidg. Technische Hochschule in Zürich, Switzerland. Cores were collected in plastic liners (drain pipe) that had a 6 cm inside diameter. After collection the core was split longitudinally and sampled for diatom, chemical, and radiocarbon analyses.

Radiocarbon dating

Samples were taken between 76–80 cm (No. GX-5848), 160–170 cm (No. GX-6372), and 300–310 cm (No. GX-6373). The samples were radiocarbon dated after treatment to remove carbonates by Krueger Enterprises, Cambridge, MA., U.S.A. The dates are based on a Libby half life of 5570 years for ^{14}C .

Chemical profiles

Samples ($\bar{x} = 1.96 \pm 0.41$ gram wet weight) were taken at 10 cm intervals for analysis of moisture, organic, and CaCO_3 content. Moisture content was determined by weight loss of fresh sediment after 24 h at 110°C . A modified ignition loss method (Dean, 1974) was used to determine organic and carbonate content. Organic content was estimated by weight loss from dried sediment, after 4 h at 550°C . Carbonate content was determined by weight loss of dried sediment after 4 h at 1000°C . The CO_2 content was converted to CaCO_3 by multiplying by 2.27.

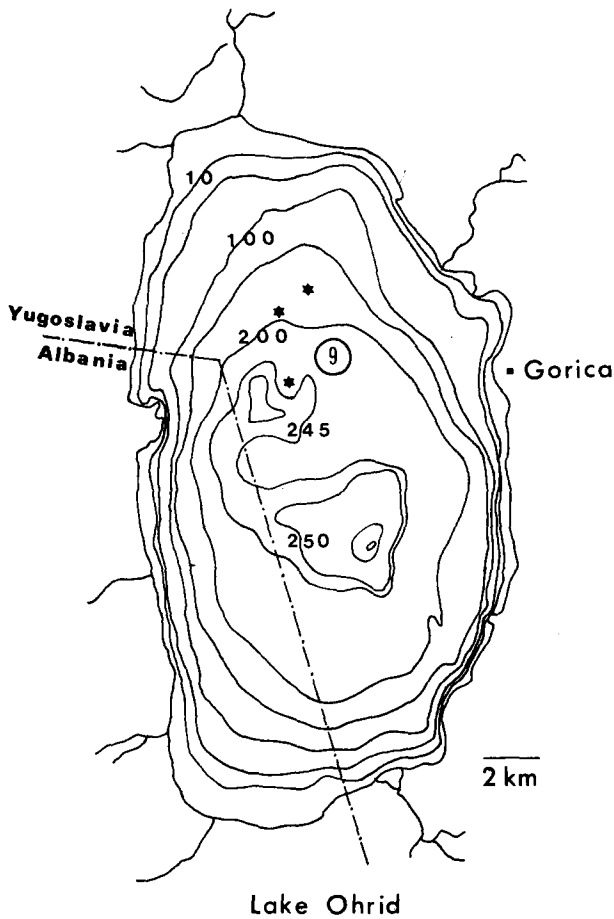


Fig.1. Location of sediment Core 9 and surface sediment samples (*), August 1973 (redrawn after Allen and Ocevski, 1976). Contours are in meters.

Diatom profile

Sediment samples were removed at the same 10 cm intervals by pressing a size 00 gelatine capsule into the non-smearred inner surface of the core (Stevenson, 1968). Carbonate was removed with a 10% HCl solution, and dichromic acid solution was used to oxidize organic matter. Counts were made for each sample and expressed as numbers of valves/gram dry weight. Counting and identification of diatoms were done under oil immersion using a Zeiss Standard Research microscope with Nomarski optics.

RESULTS

Core lithology

The core displayed a distinct change in lithology over the top meter. From 0–20 cm the sediment was olive gray to olive (Munsell Soil Color Chart, 1975; 5Y 5/2–5/3) and from 21–96 cm, black (5Y 2.5/1). The remainder of the core varied around dark gray (5Y 4/1).

Radiocarbon dating

The ^{14}C -dating of the core is shown in Fig.2. Extrapolation to the bottom of the core using linear regression ($D = 0.046T - 496.9$; D = depth of sediment in cm and T = time in years) yields a date of ca. 30,000 yr B.P. Below approximately 70 cm the ^{14}C -dating gives a sedimentation rate of 0.045 cm yr^{-1} . Lead-210 dating (Robbins, 1978) of a 20 cm core taken near the Core 9 site gave a sedimentation rate of 0.08 cm yr^{-1} between 1920–1960 and a rate of ca. 0.2 cm yr^{-1} after 1960.

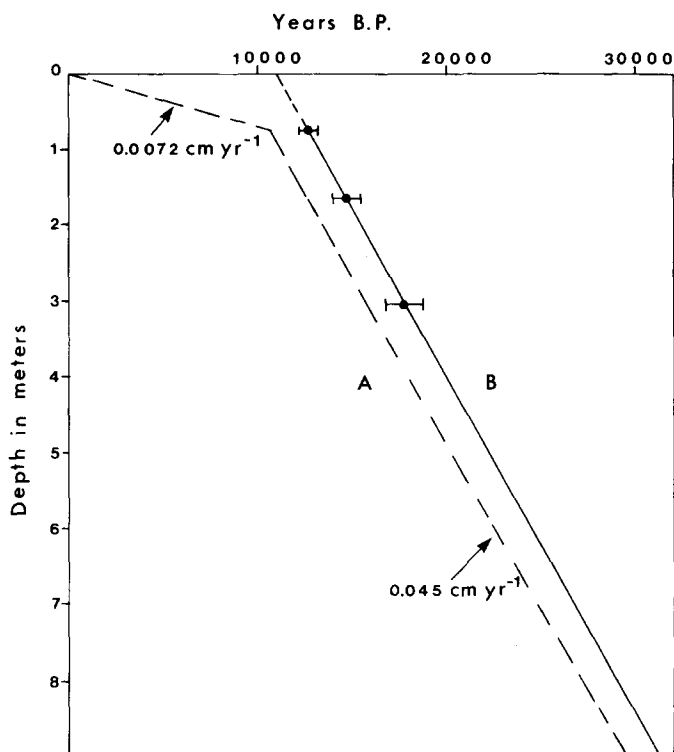


Fig.2. Regression line for ^{14}C -dates ($\pm^{14}\text{C}$ counting error) for Core 9. A = corrected regression line; B = uncorrected regression line.

The mean of three surface sediment samples (E. E. Kopczyńska, personal communication, 1974; Fig.1) taken within 3 km of Core 9 shows a different percent relative abundance of valves from samples from the top of the core. In the surface sediment samples (mean total number of valves = 432 ± 4) the percent relative abundance was *Cyclotella ocellata* 65%, *C. fottii* 22%, and *C. kutzingiana* 12%, in Core 9 (0 cm, total valves = 441) *C. complex* 30%, *Stephanodiscus* sp.1 (cf. *S. hantzschii*) 24%, *C. sp.1* 15%, and *C. ocellata* 9%. Lead-210 dating of the top of Core 9 would aid in the explanation of these discrepancies.

Chemical profile

Sediment moisture (Fig.3) varies between 50 and 60% of wet weight. The low value at 340–350 cm is the result of the sediment drying out. A 4-cm band of sand between 697–701 cm resulted in the low value at 700 cm. The sand grains at 700 cm are long (ca. 200–400 μm) with shear lines and are probably loess. The organic content (Fig.3) varies between 2 and 3% of total weight ($\bar{x} = 2.73 \pm 0.39$). The CaCO_3 content (Fig.3) from 885–110 cm also varies between 2 and 3% ($\bar{x} = 2.32 \pm 0.55\%$ of total weight) but increased in the top meter of the core ($\bar{x} = 11.03 \pm 8.86\%$ of total weight).

Diatom profile

The diatom profile of Core 9 is shown in Fig.4. Like many deep oligotrophic lakes (e.g., Lake Superior, Schelske et al., 1972; Lake Biwa, Mori and Horie, 1975; Lake Baikal, Chernyaeva, 1970), Lake Ohrid is dominated by a group of centric diatoms. Hustedt (1945), who sampled this lake mainly in the littoral zone and Jurilj (1954), who sampled the benthic zone, recorded 355 species and varieties, representing 40 genera. Among these species 75 were new records and many are considered endemics.

The 62 species found in the core can be divided into five groups (Table I) according to the regions in which they were found (Fig.5). Group I consists of seven species distributed throughout the entire core (885–0 cm). *Cyclotella fottii*, a prominent member of Group I, may also be a relict species as it closely resembles the fossil *C. iris* Brun found in the Neogene layers of Aurillac, France (Stanković, 1960).

Three *Cyclotella* forms of Group I (*C. fottii* 40–90 μm , *C. hustedtii* 20–30 μm , *C. hustedtii* var.1 10–20 μm) were designated as the “*Cyclotella* complex” because they were all found throughout the core, appeared to respond to changes as a unit (Fig.6), and were morphologically similar. This *Cyclotella* complex strongly dominated the core.

Although the species diversity index (Shannon and Weaver, 1949) is not particularly useful throughout most of the core, it clearly shows how often the *Cyclotella* complex, marked by dots, was the only diatom assemblage found in the sampled intervals (Fig.7).

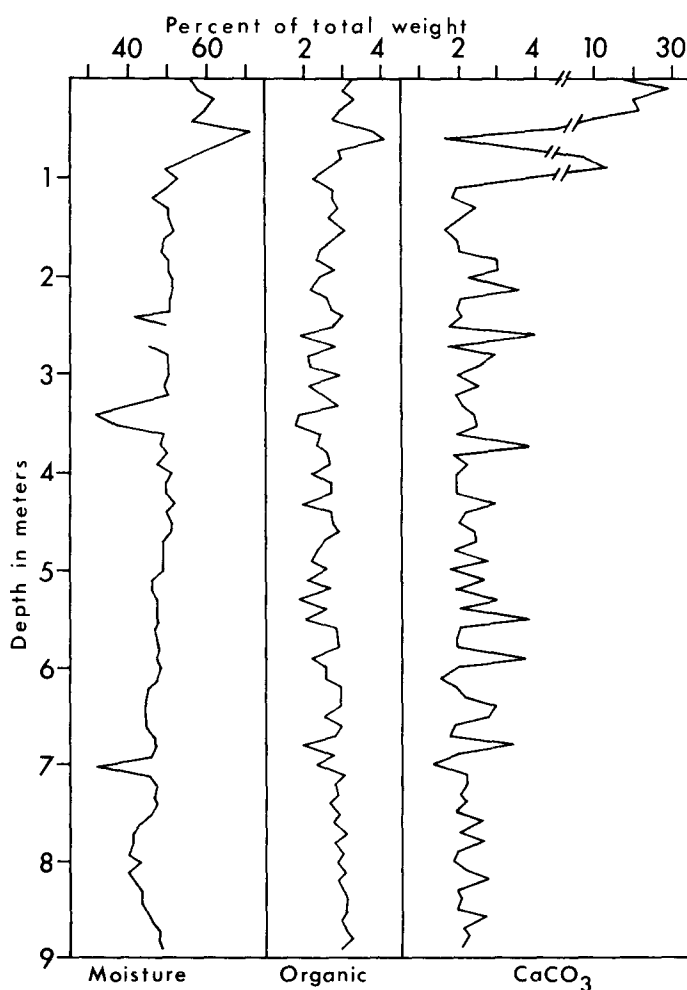


Fig. 3. Moisture, organic, and CaCO₃ content as a percent of total weight. Datum point is missing for moisture content at 260 cm.

Group II is the largest group in terms of number of species (26) and was found only between 100–0 cm. *Cyclotella stelligera* is the only exception, in that it was also found at 260 cm. A fossil *C. kutziana* (Schmidt, 1874–1927) was found at 0 cm and has not been previously reported for the Balkan region.

A more detailed study was made of the core samples at 190, 450, 600, and 800 cm to determine if any of the species from Group II (which appeared to be restricted to the zone from 100–0 cm) would be found if a larger sample (ca. 18 times the usual area) was counted. More species were indeed found, but the results were not significantly different from the original counts, and only one species (*Cymbella microcephala*) from Group II was found as a result of this more intensive survey.

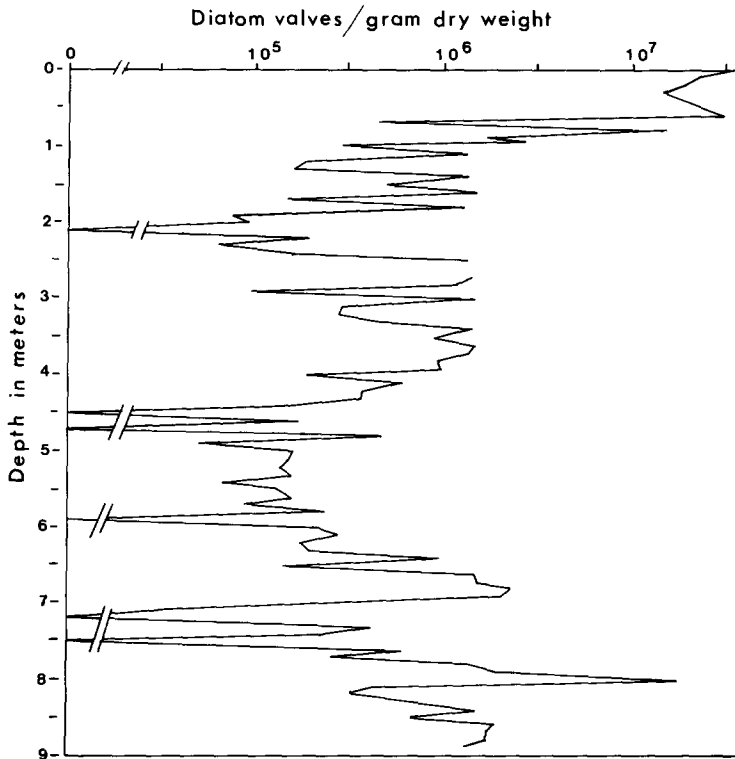


Fig. 4. Diatom profile for Core 9. Datum point is missing at 260 cm.

Group III consists of five littoral species found only between 630–110 cm. All but *Achnanthes fonticolla* have been recorded for the modern flora (Hustedt, 1945; Jurilj, 1954). *Achnanthes fonticolla* is recorded as a new species for the headwaters of the Krka near Laibach in the Balkan region (Hustedt, 1945). The abundance of this group is very low with the majority of occurrences between 360–300 cm.

Group IV consists of twelve species found only between 885–640 cm. *Diploneis (Navicula) budayana* is considered to be a relict species of the Tertiary (Jurilj, 1954).

Group V consists of twelve species found in two regions: from 885–630 cm and from 270–0 cm. *Cyclotella* sp.1 and 2 are very small forms, 2–6 μm and 5–10 μm respectively. *Navicula balcanica* is considered a Balkan endemic (Hustedt, 1945).

TABLE I

List of species in groups (see Fig.5)

Group I (0—885 cm)	Group III (110—630 cm)
<i>Cocconeis disculus</i> (Schum.) Cl. LO ¹	<i>Achnanthes fonticola</i> Hust. LB
<i>Cyclotella fottii</i> Hust. PO	<i>Amphipleura</i> sp. 1
<i>Cyclotella hustedtii</i> Jur. PO	<i>Diploneis domblittensis</i> (Grun.) Cl. LO
<i>Cyclotella hustedtii</i> var. 1	<i>Fragilaria construens</i> v. <i>venter</i> (Ehr.) Grun. LO
<i>Fragilaria construens</i> (Ehr.) Grun. LO	<i>Pinnularia borealis</i> Ehr. LO
<i>Fragilaria pinnata</i> Ehr. LO	
<i>Opephora martyi</i> Herib. LO	Group IV (640—885 cm)
Group II (0—100 cm)	<i>Achnanthes biasoletiana</i> (Kütz.) Grun.
<i>Asterionella formosa</i> Hass. PO	<i>Achnanthes oestrupi</i> (A.Cl.) Hust. LB
<i>Cyclotella kützingiana</i> Chauvin (fossil)	<i>Achnanthes ploenensis</i> Hust.
<i>Cyclotella</i> sp. 3	<i>Amphora perpusilla</i> (Grun.) Grun.
<i>Cyclotella stelligera</i> (Cl. and Grun.) V.H. PO	<i>Cocconeis diminuta</i> Pant. LO
<i>Cymbella microcephala</i> Grun. LO	<i>Diatoma vulgare</i> v. <i>brevis</i> Grun. LO
<i>Cymbella prostata</i> (Berk.) Cl. LO	<i>Diatoma vulgare</i> v. <i>ovalis</i> Grun. LO
<i>Denticula elegans</i> Kütz.	<i>Diploneis (Navicula) budayana</i> (Pant.) Jur. O
<i>Diatoma vulgare</i> v. <i>grandis</i> (W.Sm.) Grun. LO	<i>Diploneis mauleri</i> (Brun.) Cl. LO
<i>Epithemia lunata</i> v. <i>obesa</i> Jur. LO	<i>Gomphonema olivaceum</i> (Lyngb.) Kütz. LO
<i>Epithemia turgida</i> (Ehr.) Kütz. LO	<i>Navicula (Achnanthes)</i> sp. 1
<i>Epithemia zebra</i> (Ehr.) Kütz. LO	<i>Synedra vaucheriae</i> Kütz. LO
<i>Fragilaria crotonensis</i> Kitton PO	
<i>Fragilaria leptostauron</i> (Ehr.) Hust. LO	Group V (0—270 and 630—885 cm)
<i>Fragilaria leptostauron</i> v. <i>dubia</i> (Grun.) Hust. L	<i>Achnanthes clevei</i> Grun. LO
<i>Gomphonema intricatum</i> v. <i>pumila</i> Grun. LO	<i>Achnanthes conspicua</i> A. Mayer LO
<i>Navicula bacillum</i> Ehr. LO	<i>Amphora ovalis</i> v. <i>pediculus</i> (Kütz.) V.H. LO
<i>Navicula modica</i> Hust. LO	<i>Cyclotella ocellata</i> Pant. PLO
<i>Navicula placentula</i> (Ehr.) Kütz. LO	<i>Cyclotella</i> sp. (aff. <i>kützingiana</i>)
<i>Navicula stankovici</i> Hust. LO	<i>Cyclotella</i> sp. 1
<i>Nitzschia filiformis</i> (W.Sm.) Schutt	<i>Cyclotella</i> sp. 2
<i>Nitzschia gracilis</i> Hantz. LB	<i>Diploneis elliptica</i> (Kütz.) Cl. LO
<i>Nitzschia kützingiana</i> Hilse LO	<i>Frustulia rhomboides</i> v. <i>saxonica</i> (Rabh.) DeT. LB
<i>Stephanodiscus astraea</i> v. <i>intermedia</i> Fricke PO	<i>Navicula anglica</i> Ralfs LO
<i>Stephanodiscus astraea</i> v. <i>intermedia</i> f. 1	<i>Navicula balcanica</i> Hust. PLO
<i>Stephanodiscus</i> sp. 1	<i>Stauroneis smithii</i> v. <i>incisa</i> Patr. LO
<i>Synedra acus</i> Kütz. LO	

¹P = planktonic species; L = littoral species; O = species previously reported for Lake Ohrid; B = species previously reported for the Balkan region.

DISCUSSION

Dating the core

Providing an entirely satisfactory interpretation of the radiocarbon dates obtained for Core 9 is not yet possible. However, we currently believe that the core represents ca. 30,000 yr of lacustrine history. This estimate is based on the results of pollen analyses done on sediments from the core by W. A. Watts (personal communication, 1981), ¹⁴C-dates, and the stratigraphic patterns found for Cladocerans (L. Frey, personal communication, 1979) and diatoms.

Extrapolation of the regression line for the uncorrected ¹⁴C-dates for Core 9 (Fig.2 and Results) to the surface of the sediment gives an unusually large

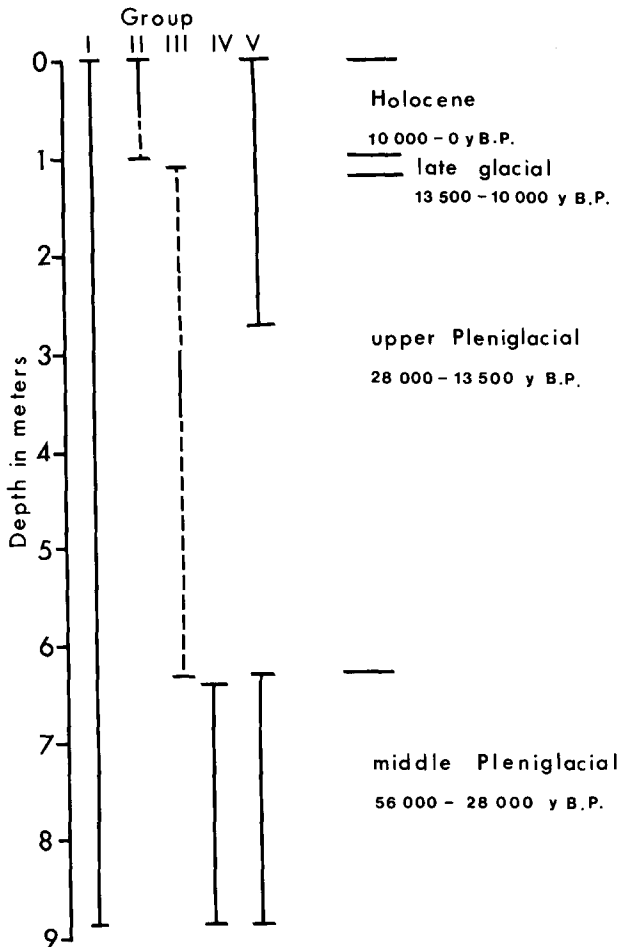


Fig.5. Distribution of diatom groups (see Table I) with stratigraphic units and corresponding dates.

surface age of 11,042 yr B.P. We have identified three potential explanations for this large age discrepancy:

(1) The surface sediments are in reality ca. 11,000 yr old. In this case, all the sediments of more recent age have been eroded away by some unknown process.

(2) The large finite surface is an artifact resulting from ^{14}C -deficiency in the dissolved inorganic carbon pool of the lake. ^{14}C -deficiency is generally observed in waters that have leached ancient calcareous rocks (Deevey et al., 1954; Broecker and Walton, 1959) containing little if any ^{14}C . The most prevalent rocks in the drainage basin of Lake Ohrid are Triassic limestones (Ivanovski and Stračkov, 1974).

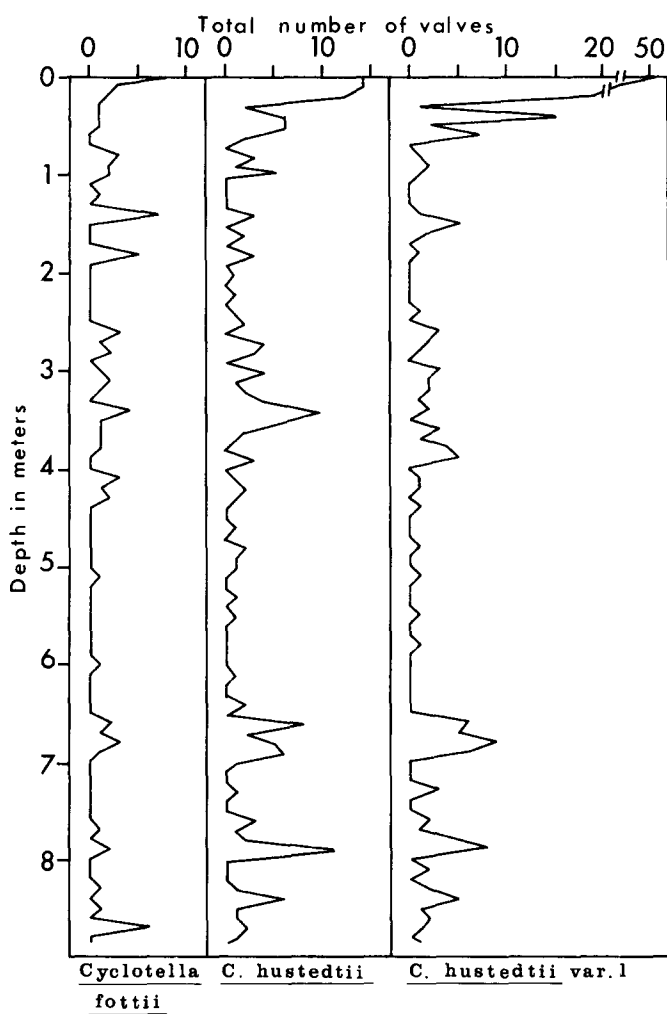


Fig.6. Stratigraphic distribution of the *Cyclotella* complex.

(3) A major change (decrease) in sedimentation rate occurred above 80–76 cm in the core. Therefore, the regression line for the uncorrected dates cannot be legitimately extrapolated to the surface of the sediments.

If one were to attempt to date the core using only the stratigraphic information obtained for the microfossils, one would conclude that the top meter of the core contains an unbroken sedimentary record for the entire Holocene. Comparisons of the pollen stratigraphy of the core with pollen diagrams available for other localities in Macedonia (Ioannina, Bottema, 1967; Philippi, Wijnstra, 1969) indicate that the Holocene/late glacial boundary (ca. 10,000 yr B.P.) occurs within the first meter of the core. This boundary is characterized by a sharp rise in the percentages of *Artemisia* and *Chenopodiaceae*

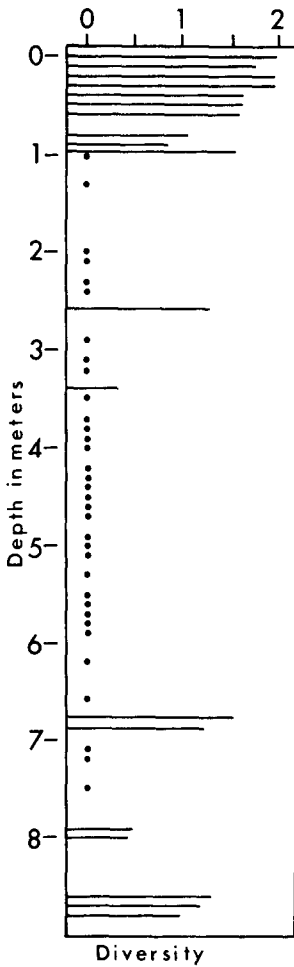


Fig.7. Diversity for intervals with a total count of greater than twenty valves. Dots indicate intervals where the *Cyclotella* complex was the only species found.

pollen. These observations concerning the location of the Holocene/late glacial boundary in the core provide little support for the first two potential explanations. If the first explanation were correct, the Holocene/late glacial boundary would not be present in the core at all and if the second explanation were correct this boundary should be found at ca. 5 m (assuming that one could correct for ^{14}C -deficiency by simply sliding the regression line for the ^{14}C -dates over to the left in Fig.2 until it went through the origin). Explanation two has an additional problem in that a ^{14}C -deficiency of 11,000 yr is 5-times larger than any ^{14}C -deficiency ever reported. For theoretical reasons, ^{14}C -deficiencies are generally less than 2000 yr (Broecker and Walton, 1959). However, theoretical calculations of maximum ^{14}C -deficiency

assume that all the CO_2 involved in the leaching of ancient calcareous rocks is of recent atmospheric origin. If this were not the case, owing to the recycling of ancient carbon by biota in the system, ^{14}C -deficiencies even higher than those currently considered possibly might occur.

Our interpretation of the age B.P.—sediment depth relationship for Core 9 is shown (see dashed line) in Fig.2. To obtain this line we first corrected for ^{14}C -deficiency by subtracting 2000 yr (the maximum age discrepancy commonly observed as a result of ^{14}C -deficiency; Broecker and Walton, 1959) from each of the uncorrected ^{14}C -dates. Therefore, our corrected age—depth relationship (Fig.2, line A) for Core 9 gives minimum values for each date (\pm the counting error). The actual dates lie somewhere between the corrected (line A) and uncorrected (line B) regression lines. All of the dates presented in this paper were obtained from the corrected regression line. We then drew a line from the corrected ^{14}C -date for 80–76 cm (10,765 yr B.P.) through the origin (0 cm, 0 yr B.P. or 1950 A.D.). This interpretation of the age—depth relationship gives a sedimentation rate of 0.045 cm yr^{-1} prior to ca. 10,000 yr B.P. and a rate of $0.0072 \text{ cm yr}^{-1}$ since that time.

How plausible is our proposed 6-fold decrease in sedimentation rate for the Holocene? During the late glacial when the climate in this part of Europe was cooler and drier than it is at present (Van der Hammen et al., 1971), Lake Ohrid was probably a typical dimictic lake; but at the beginning of the Holocene, when the climate became warmer and wetter, it is quite likely that the lake became oligomictic, as it remains to this day. Such a change in mixing regime can have a pronounced effect on sedimentation rates.

Sediment focusing is the process by which sediments are directed toward the deepest part of a lake basin (Lehman, 1975). This occurs as a consequence of mixing. Sediments may be initially deposited fairly evenly over the lake basin, but when mixing occurs shallow-water sediments are resuspended more extensively than sediments from deep water. Thus a net movement of sediments occurs from shallow to deep water (Davis and Brubaker, 1973). It is therefore reasonable to suspect that the process of sediment focusing produced considerably higher rates of sedimentation at the Core 9 site when the lake was dimictic than it has since the lake became oligomictic. It is also conceivable that the loading of sedimentary material to the lake basin has decreased since the late glacial when rates of mechanical weathering in the mountains may have been higher than they are at present. Such a decrease in sediment loading would also decrease the rate of sediment accumulation throughout the lake basin.

The higher rates of sedimentation computed from ^{210}Pb -dates (i.e., 0.08 and 0.2 cm yr^{-1}) for a surface core taken near the Core 9 site probably reflect higher sedimentation rates brought about by man's recent activities in the drainage basin (Robbins, 1978). Since the beginning of the century, the population of this region has increased markedly and the Sateska River that formerly flowed to the north of the lake now flows into it.

The sedimentary record of Core 9 appears to be complete and unbroken. The ^{210}Pb -dates indicate that the surface sediments are intact. The pollen

stratigraphy determined for cores from other localities in Macedonia, and the Holocene/late glacial boundary (ca. 10,000 yr B.P.) occurs within the first meter of the core. Because our ^{14}C -dates fall on a straight line (Fig.2), breaks in the sedimentary record between the first and third meters of the core are unlikely. Except for the band of sand between 697–701 cm, Core 9 is very homogeneous from 110 cm to the bottom (885 cm). There is little variation in the content of moisture, organic matter, and CaCO_3 . If breaks in the sedimentary record have occurred, they are not reflected in the pollen stratigraphy, ^{14}C -dating, or the chemistry of the core.

Diatom stratigraphy

The 8.85 m Core 9 represents a period of ca. 30,000 yr, covering half of the Pleniglacial, the late glacial, and the Holocene. A very distinct floristic difference exists between the diatom assemblages above and below 60 cm. Below 60 cm (i.e., below the Holocene/late glacial boundary), the *Cyclotella* complex was almost always dominant and the total number of valves at each sampling interval was low. The peaks in number of valves and species diversity in the assemblages at 885–630 cm, 360–300 cm, and 110–80 cm were probably the result of the amelioration of the climate over these periods.

The Pleniglacial (ca. 60,000–13,500 yr B.P.) can be split into three intervals: the upper, middle, and lower. There were glacial advances during the upper and lower Pleniglacial and the climate seems to have been generally colder and less humid than during the middle Pleniglacial (Van der Hammen et al., 1971). The ice sheet did not reach the Ohrid area but local glaciers formed (Stanković, 1960). There were no interstadials in the lower Pleniglacial, six in the middle, and two in the upper Pleniglacial (Wijmstra, 1969).

The five littoral species of Group III (630–110 cm) occur at seven intervals in the core with the majority between 360–300 cm which corresponds with the slight warming of the Philippi interstadial during the cold upper Pleniglacial. A more pronounced increase in numbers and species occurs between 885–630 cm which corresponds with the beginning of the warmer, more humid middle Pleniglacial. Of the twelve species of Group IV (885–630 cm) five are not recorded in the modern flora; these may not have survived the Glacial Age in Lake Ohrid.

Amelioration of the upper Pleniglacial climate seems to have begun between 14,000–13,000 B.P., which marks the boundary with the late glacial during which the ice sheet retreated to central Sweden (West, 1968). In pollen diagrams from Philippi, northeastern Greece (Wijmstra, 1969) and Ioannina, northwestern Greece (Bottema, 1967), ca. 300 km east and 100 km south of Lake Ohrid respectively, the late glacial exhibits a sharp floral peak. Between 110–70 cm, which corresponds to the late glacial, an analogous diatom peak occurs. Climate diagrams for northwest Europe indicate fluctuations from sub-arctic through boreal to cool temperature climate, back to sub-arctic during the Allerød (Xanthi) interstadial. This was followed by the

warm temperate climate of the Holocene (West, 1968). In the Philippi pollen diagram this climatic fluctuation is evidenced by a change from the open *Artemisia*/Chenopodiaceae vegetation of the cold upper Pleniglacial, through an open oak forest, back to an *Artemisia*/Chenopodiaceae vegetation at the late glacial/Holocene boundary. The effect of this short (ca. 600 yr) cold period before the Holocene is represented in the diatom diagram by a marked decrease in valve numbers from 141 at 80 cm, to 5 at 70 cm, followed by a marked increase at 60 cm (298 valves).

An analysis of the top 230 cm of Core 9 (10 cm intervals) for zooplankton (L. Frey, personal communication, 1979) shows a similar pattern but one which lags behind the changes in numbers of diatoms. *Bosmina*, the most abundant Cladoceran in the sediment, first occurs at 100 cm. There are also low numbers of microfossils (less than 1000 per cm³ of sediment at 80 and 70 cm). At 60 cm, where the diatom numbers increase, there are no zooplankton remains; but at 50 cm there are greater than 10,000 microfossils/cc of sediment.

The *Cyclotella* complex is dominant throughout the core except at six intervals (40, 50, 80, 800, 860, and 880 cm), all of which are dominated by *Cyclotella* sp.1 which is the major member of Group V (885–630 cm and 270–0 cm). *Cyclotella* sp.1 and *C. ocellata*, like the *Cyclotella* complex, seem to respond as a unit (Fig.8). The *Cyclotella* complex and *Cyclotella* sp.1/*C. ocellata* tend to alternate, so that when one is dominant, the other declines (Fig.9). The occurrences of Group V species during warmer periods (below 630 and 110–80 cm) and their disappearance between 620–280 cm is possibly related to climate.

Cyclotella fottii (Group I) is found throughout the year in the Lake Ohrid phytoplankton with significant populations between 50–200 m; it is also a dominant of the spring bloom between 0–200 m (Kozarov, 1954). The annual cycle of *C. fottii* shows an inverse relationship between temperature and cells/liter (Kozarov, 1954).

Throughout the core there is an inverse relationship between organic and CaCO₃ content (Fig.3). The basis for the relationship is the scavenging effect of CaCO₃ discussed above. The similarity of the diatom assemblages between 100–80 cm and below 630 cm indicates that the marked inverse chemical relationship between 110–70 cm is likely the result of a natural influx of nutrients and/or carbonates owing to increased precipitation. However, the inverse chemical relationship at 60 cm, the influx of Group II species, and the large increase in valves/gram dry weight indicate eutrophication, in the classical sense of increased supplies of nutrients beyond what would have occurred naturally. A similar inverse relationship between CaCO₃ and organic content was found for core samples from Lawrence Lake Michigan (Wetzel and Manny, 1978). This was interpreted as evidence of a settlement horizon.

Archaeological evidence establishes human occupation of Yugoslavia in the Lower Paleolithic Period (the Riss glaciation, ca. 200,000–100,000 yr B.P.) (Alexander, 1972). The Paleolithic inhabitants were a cave-dwelling,

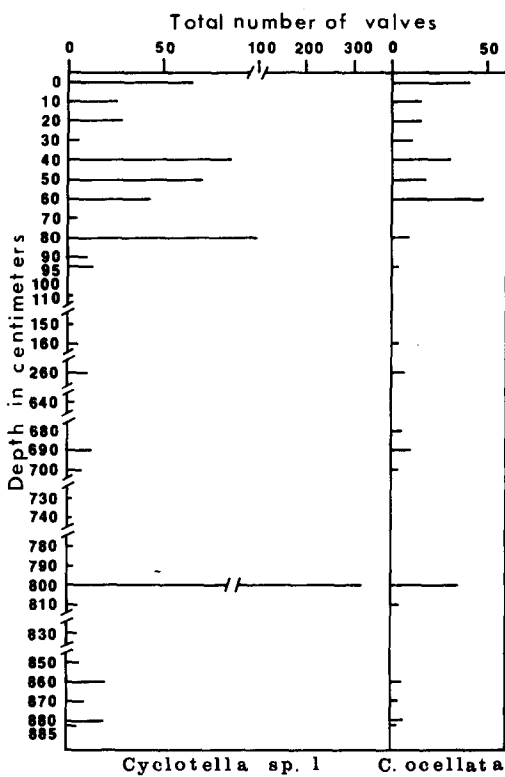


Fig.8. Stratigraphic distribution of *Cyclotella sp.1* and *C. ocellata*.

Old Stone Age, hunter/gatherer/fisher people who would have had little or no effect on the lake's ecology.

Early experiments in cultivation and domestication began in the Middle Stone Age or Mesolithic (early Holocene, ca. 10,000–8000 yr B.P.). The Bitolj Culture flourished in the Lake Ohrid area during the Copper Age or Middle Neolithic (ca. 8000–5000 yr B.P.). A dynastic cemetery, of the iron-using Trebeniste Culture (Late Bronze Age, ca. 2600 yr B.P.), has been found at Trebeniste on the north shore of Lake Ohrid (Alexander, 1972). By the Early Iron Age (350–11 B.C.) the tribes along the southern frontier between Macedonia and Greece established fortified settlements. In 360 B.C., Bardylis, ruler of the Lynxus region beside Lake Ohrid, overran much of Greek Macedonia but was driven back a few years later by Philip II, Alexander the Great's father. Bardylis' successor was defeated in either Philip and Alexander's 346–343 B.C. or Alexander's 335 B.C. northern expeditions (Philip was assassinated in 336 B.C.). Alexander established the first known town in the region, Aerachia Lynxi (Ohrid town) (Alexander, 1972).

Because the sedimentation rates are probably not constant above 70 cm, there can be no accurate interval correlation with the Bitolj and Trebeniste

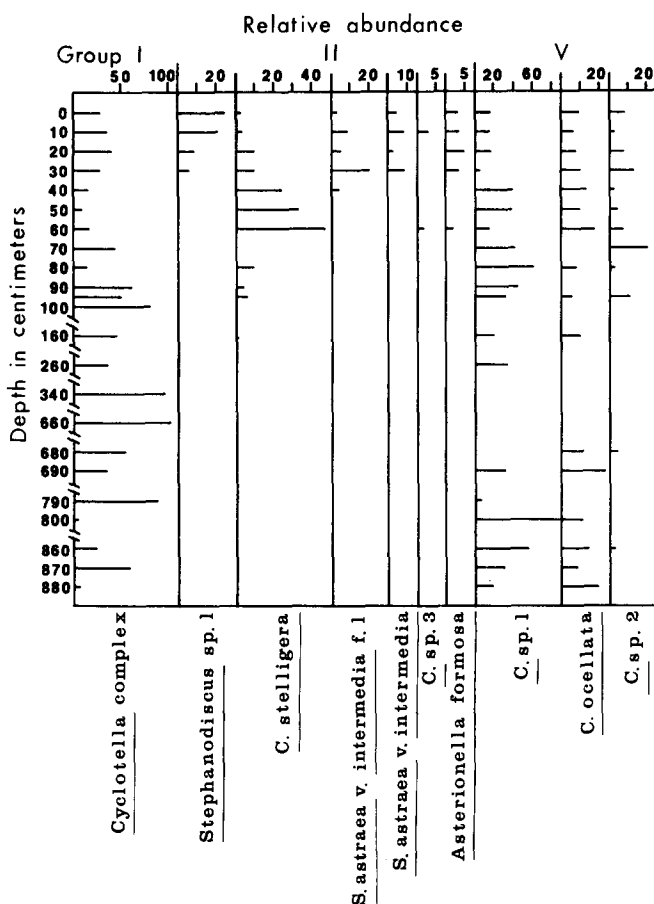


Fig. 9. Relative abundance of dominant and subdominant species in Core 9.

Cultures or Alexander's *Aerachia Lynxi*. However, there is evidence that these influences have led to eutrophication. Deforestation and farming, which would have caused an increased influx of carbonates and nutrients, is the probable cause of the changes above 70 cm.

Stockner and Benson (1967) used an Araphidineae/Centrales index for Lake Washington (Washington, U.S.A.) as a measure of cultural eutrophication. Their reasoning was that Centrales as a group achieved their greatest diversity in oligotrophic waters and that mesotrophic—eutrophic waters had a greater proportion of Araphidineae. As *Cyclotella* species are predominate in Lake Ohrid and the frequency of Araphidineae is very low, the A/C index is always less than 1.0, an indication of an oligotrophic lake (Stockner, 1971). There are eleven Araphidineae in the core. Three are in Group I, six in Group II, one each in Groups III and IV, and none in Group V. Of the six in Group II, *Asterionella formosa*, *Synedra acus*, and *Fragilaria crotonensis* are regarded

as araphidinate species in Stockner's (1971) A/C index. Although their absolute abundance is still very low in the Lake Ohrid core, there is a small but steady increase between 100–30 cm and a more pronounced increase above 30 cm, perhaps indicating a degree of eutrophication.

Brugam (1979) working in Minnesota (U.S.A.) found that *Stephanodiscus hantzschii* can be used as an indicator of increasing nutrient input in lakes with high alkalinity, whereas the A/C index is more efficient in low alkalinity lakes. Lake Ohrid is a karstic lake and *S. sp.1* (cf. *S. hantzschii*) is a co-dominant in surface sediments with the *Cyclotella* complex. *S. hantzschii* has also been identified as one of the dominants of the spring bloom in Ohrid (Stanković, 1960).

Various factors may explain the origin of the immigrant species of Group II and the reappearance of Group V; two possible explanations are: (1) cultural and natural introduction and/or (2) introduction via the subterranean connection with Lake Prespa. Cultural effects are more likely to act through an increase in nutrient input rather than through actual introduction of species. Another possibility is that eels which migrate up the Drim River from the Adriatic Sea (Jurilj, 1954) and other immigrant animals in Lake Ohrid may have been responsible for introducing diatoms (Stanković, 1960).

Stanković (1960) believes there may be a subterranean connection between Lake Ohrid and Lake Prespa (158 m higher and 16 km to the east) through the calcareous strata of the Galicica Range. If this is true, Lake Prespa may have been a refuge for many of the new or re-introduced species in Lake Ohrid. A comparison of the species lists (Hustedt, 1945) shows that 85% of Lake Prespa's diatoms are also found in Lake Ohrid.

Although Lake Ohrid is more productive now than it was below 60 cm, the increased influx of nutrients which may have allowed the increase in diatom diversity and numbers is also a factor in the suppression of total phytoplankton production. Increased stimulation of photosynthesis in the littoral zone may reduce the overall availability to the phytoplankton of inorganic and organic nutrients owing to their co-precipitation with CaCO_3 .

At present the factors controlling the diatom populations in Lake Ohrid are poorly known, but stratification, temperature, transparency, light intensity, CaCO_3 dynamics, low bacterial activity, and the rate of influx of nutrients are among them (Allen and Ocevski, 1976). Assuming that the present-day suppressive mechanisms were functioning similarly below 60 cm, it is unlikely that a change in climate alone could explain the differences above 60 cm. Some of the species in Group II (100–0 cm) can tolerate low temperatures and oligotrophic conditions. It appears that below 60 cm nutrients were not plentiful enough or in the right proportions to support the species of Group II because their occurrence coincides with the increased nutrient supply resulting from cultural eutrophication.

None of the species in Group I (885–0 cm) have decreased in number and although the *Cyclotella* complex has a lower relative abundance above 60 cm, it has a higher absolute abundance. Allen and Ocevski's (1976) study showed

that many nutrients are probably limiting in the hypolimnion, yet *C. fottii* maintains significant populations there. However, in Lake Ohrid, the *Cyclorella* complex and many of the endemic species evolved in an environment of limitations. Their continued existence and increase above 60 cm and the increased species diversity in the upper layers of the core indicate that resources in the present environment are not yet inhibiting.

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