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# Morphogenesis in *Cyclotella ocellata*-Complex from Lake El'gygytgyn (Chukchi Peninsula) during the Pleistocene–Holocene

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**Abstract**—The morphology of valves of *Cyclotella ocellata* from bottom sediments of Lake El'gygytgyn, Chukchi Peninsula, has been studied with help of light and scanning electron microscopes. Considerable variability in the morphology of valves and gradual elimination of forms with big valves were observed upwards the section. The complex evolved by phenotype selection: *kuetzingina-morphotype* was replaced by *ocellata-morphotype* and, in the latest Pleistocene, also by *arctica-morphotype*. Changes in the valve morphology were mainly caused by paleoclimatic fluctuations.

*Key words*: Pleistocene, Holocene, diatoms, *Cyclotella ocellata*, morphology, Lake El'gygytgyn, Chukchi Peninsula.

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## INTRODUCTION

Diatoms are commonly used as ecological indicators for reconstruction of modern and past environments and climatic changes (Douglas and Smoll, 1999). Ecological structure of diatom fossil communities and abundance of valves in the sediments are taken into account as well as morphological peculiarities of phenotypes, which can be considered as reaction of a given taxon to environmental changes. It was repeatedly shown that valve morphology changes in relation to climatic fluctuations: valves become larger in warm climatic epochs and smaller in cold climatic epochs (Jousé, 1962; Pushkar and Cherepanova, 2001); however, no detailed studies of the problem have been so far accomplished. Moreover, problems in taxonomy and, as a consequence, ecology and biogeography of particular taxa lead to inaccurate paleogeographical reconstructions, that is particularly true for remote water pools, inaccessible for investigations. Arctic lakes are the example. As a rule, the commonest members of planktonic communities in Arctic lakes are species of *Cyclotella* (Kütz.) Bréb., with highly variable valves and their morphological elements, which causes many taxonomical problems (Kling and Håkansson, 1988; Kiss et al., 1996, 1999; Hegewald and Hindakova, 1997; Schlegel and Scheffler, 1999; Meyer et al., 2001; Cremer et al., 2005; Genkal and Popovskaya, 2007, 2008). Data on diatoms from water pools in the Russian Arctic are relatively scanty (Duff et al., 1999; Laing et al., 1999; Michelutti et al., 2001; Genkal and Vekhov, 2007). In this context, the diatom flora of Lake El'gygytgyn has received comparatively much attention. Diatoms were studied from the bottom of the lake (Sechkina, 1956; Zhuze and Sechkina, 1960; Cherepanova et al., 2003; Cremer and Wagner, 2003; Cremer et al., 2005; Cherepanova et al., 2007) and in modern communities (Kharitonov, 1980, 1993; Cremer and Wagner, 2003; Cremer et al., 2005). Several papers dealt with new species and morphological variability within particular taxa of planktonic communities of the lake (Genkal and Kharitonov, 1996, 2005; Stachura-Suchoples et al., 2008).

The present study is devoted to some peculiarities of the morphogenesis of *Cyclotella ocellata*-complex from Lake El'gygytgyn during the Pleistocene–Holocene.

## THE REGION UNDER STUDY

Lake El'gygytgyn is situated 100 km to the north of the Polar circle (67°30′N, 172°05′E, 492.4 m a.s.l.), in the northwest of the Chukchi Peninsula (Fig. 1). The crater presumably originated from a meteorite impact 3.6 Ma ago, in the Late Pliocene (Dietz and McHone,

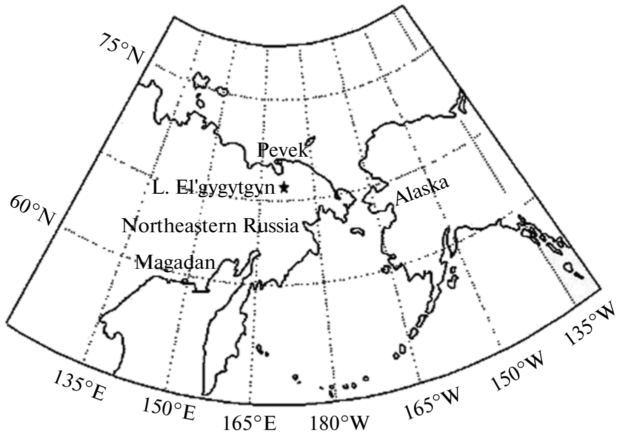



**Fig. 1.** The position of Lake El'gygytgyn.

1976; Gurov et al., 1980). No traces of the Quaternary Glaciation were found in course of geomorphological survey in the surroundings of the lake (Glushkova, 1993), which allows one to consider Lake El'gygytgyn as the oldest lake in the Arctic Region (Nowazcyk et al., 2002). The lake is 11.5 km in diameter; the water-surface area is 117.5 km$^2$; the maximum water depth is 175 m, detected to the northeast of the lake center. The lake is fed by about 50 ephemeral streams (Lagernyi Creek is the largest among them) and has one large outflow, Enmyvaam River. The water catchment area is about 293 km$^2$ (Nolan et al., 2003).

Lake El'gygytgyn is very cold. In August 2000, the temperature was 3.08°C near the center of the lake and 4–5°C in shallow water (Minyuk et al., 2003). Lake El'gygytgyn defrosts not each year. It is ice-covered (up to 2 m thick) nine–ten months per year; the ice cover starts degrading to the mid-June, but new ice formation commences at the end of September (Chereshnev and Skopets, 1993; Nolan et al., 2003). The water salinity in Lake El'gygytgyn is low; the transparency depth is up to nearly 20 m, which is related to low productivity of phytoplankton. The lake is oligotrophic or even ultra-oligotrophic (Cremer and Wagner, 2003).

## MATERIAL AND METHODS

Diatom algae were studied from the Pleistocene–Holocene sediments of core PG-1351, which was took in spring 1998 from the central, deepest, region of the lake. The core is 12.7 m long. The sediments are silts variable in texture and color. The absolute age of the sediments was determined by IRSL (infrared simulated luminescence) and AMS (accelerator mass spectrometry) $^{14}$C methods. The sediments under study were accumulated during nearly 300 kyr (Nowaczyk et al., 2002). Sediments with the highest concentration of diatom valves were sampled. These sediments were accumulated in both warm and cold epochs of the Pleistocene and Holocene. Data on paleoclimatic changes were obtained by Minyuk et al. (2003), in their multifaceted study of the sediments from core PG-1351.

The samples were processed after standard procedure (*Diatom*..., 1974). The diatoms were studied under an Amplival Zeiss light microscope, in immersion oil, under magnification of 2000 times and with help of Philips SEM 525M (Institute of Limnology, Siberian Division, Russian Academy of Sciences) and Carl Zeiss EVO 40 (Institute of Biology and Soil Sciences, Far East Division, Russian Academy of Sciences) scanning electron microscopes.

To reveal trend in change of valve sizes in *Cyclotella ocellata*-complex along the core section, polynomial (average) diameter was determined for each studied sample, which was calculated after the following formula (Gerasimenko, 1998):

$$y = -0.0003x^6 + 0.0114x^5 - 0.1731x^4 + 1.274x^3 - 4.5478x^2 + 7.2011x + 2.7052,\ \text{with correlative coefficient}\ R^2 = 0.5675.$$

Collection PG-1351 is kept at the Institute of Biology and Soil Sciences, Far East Division, Russian Academy of Sciences.

## RESULTS AND DISCUSSION

In spite of the fact that the valve morphology of *Cyclotella ocellata* Pant. has been sufficiently well studied, the taxon is quite disputable primarily due to its considerable morphological variability. Some scientists believe that species of the genus *Cyclotella* have distinct determinative criteria (Håkansson, 2002); whereas other scientists, having studied the huge morphological diversity of valves of *C. ocellata*, conclude that the taxon should be considered as a combination of morphologically diverse related species: *C. ocellata, C. krammeri* Håkansson, and *C. rossii* Håkansson (Kiss et al., 1996; Hegewald and Hindakova, 1997; Knie and Hübener, 2007). Genkal and Popovskaya, who analyzed the morphotypical variability in the population of *C. ocellata* from Lake Khubsugul, Mongolia, additionally included in this complex the morphotypes *C. tripartita* Håkansson and *C. kuetzingiana* Thwaites (Genkal and Popovskaya, 2007, 2008).

Valves of *C. ocellata* were studied from bottom sediments of the lake. The totality of valves of all taxa from a given sample is a fossil community of diatoms. It bears information about the intravital state of the ecosystem and reflects the development of diatom communities in the lake during a particular temporal period. Seasonal differences of species and ecological composition of diatom communities as well as environmental responses of particular taxa are leveled during the formation of the fossil community. Since the principal mode of diatom reproduction is cell division, it should be taken into account that repeated vegetative division leads to gradual diminishing of cells. Cells

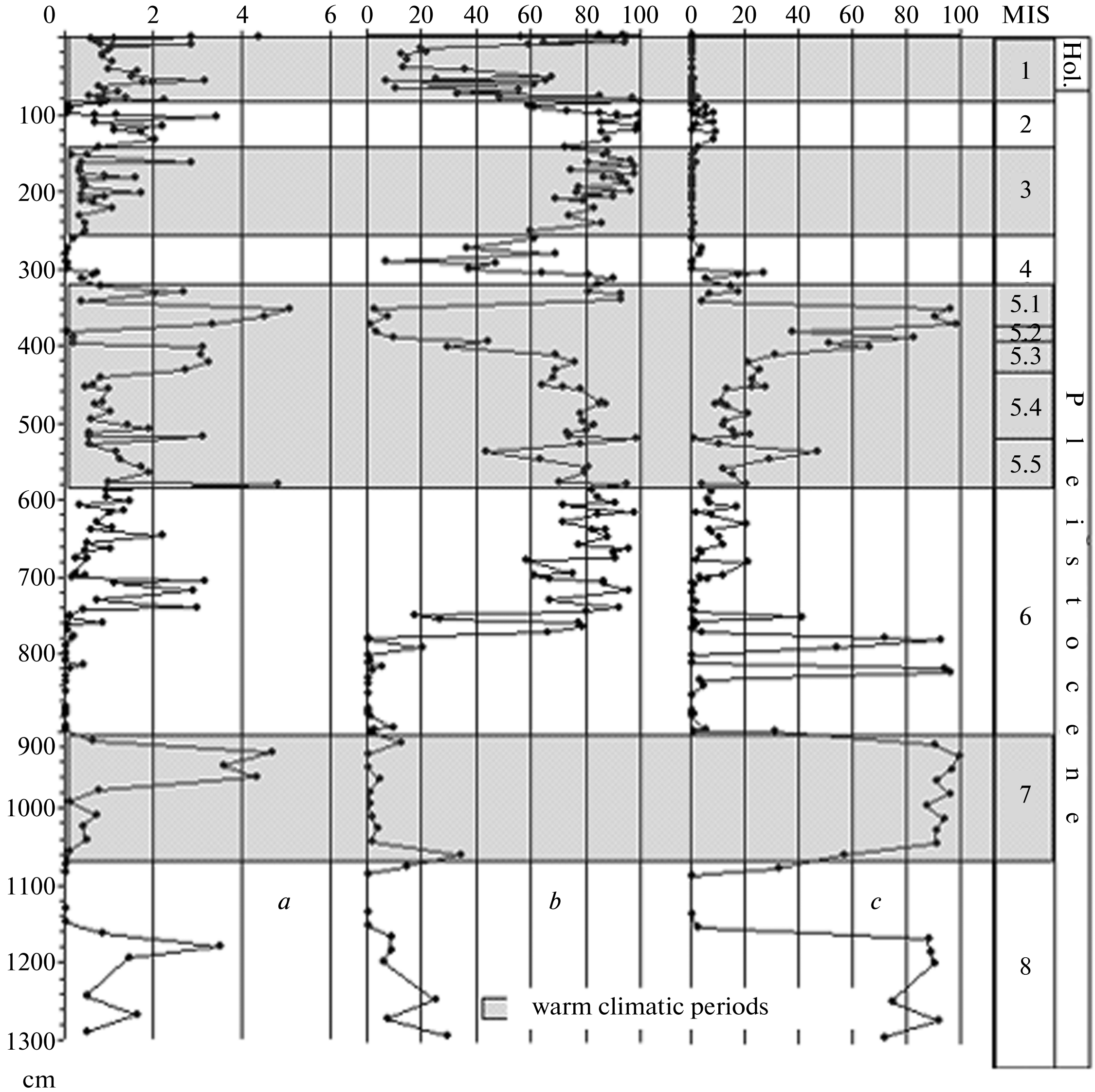



**Fig. 2.** The number of valves in sediments and distribution of members of main morphotypes of *Cyclotella ocellata*-complex along the section: (a) number of diatom valves per 1 g of dry residue ($\times 10^8$); (2) distribution of members of *ocellata-morphotype*; (3) distribution of members of *kuetzingiana-morphotype*.

in some species become three times as small as their initial cells. Original cell sizes restore during germination of resting cells and sexual process with auxospore formation (Vasser et al., 1989). One can suppose that the diversity among dimensional groups of valves will be maximal under favorable conditions. Besides, initial cells, which were formed during auxospore maturation, should occur in sediments. In *C. ocellata*, auxospores are formed when cells less than 10 μm in diameter prevail and the dimensions of initial valves varies from 15 to 35 μm, occasionally reaching 50 μm (Genkal and Popovskaya, 2007).

Members of *Cyclotella ocellata*-complex constitute up to 99.4% in diatom fossil communities from the sediments of Lake El'gygytgyn (Cherepanova et al., 2007). They dominate in diatom fossil communities in virtually all samples of the section, with the exception of sediments formed during the Holocene optimum. The abundance of valves in bottom sediments of the lake, particularly in those formed in that time (up to $4.4 \times 10^8$ valves per gram of dry sediment), allows one to consider these sediments as diatomaceous silts (Fig. 2).

The diameter of frustules in the population of Lake El'gygytgyn varies from 2.6 μm to 24.0 μm (Table 1). The share of large valves, with the diameter greater than 20 μm, is very moderate and was detected only in sample 321–323 cm, where found only 0.8% of such valves (Fig. 3). Maximal sizes of valves are a character of samples from deeper intervals; the shares of valves belonging to dimensional groups from 11 μm and greater than 20 μm are also higher in these samples.

**Table 1.** Indices of diameter and occurrence of valves in different dimensional groups in the samples under study (σ as standard deviation and Cv as variation coefficient)

| Depth, cm | Number of valves | Diameter (μm) | | | | | Occurrence of valves in different dimensional groups | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Min | Max | Average | σ | Cv, % | 3–4 | 5–6 | 7–8 | 9–10 | 11–12 | 13–15 | 16–20 | >20 |
| 0–2 | 310 | 2.6 | 11.6 | 5.7 ± 0.2 | 1.71 | 30.0 | 22.3 | 49.6 | 19.1 | 7.9 | 1.1 | – | – | – |
| 38–40 | 239 | 3 | 12.6 | 6.7 ± 0.2 | 1.88 | 28.0 | 10.5 | 39.7 | 32.6 | 13.0 | 4.2 | – | – | – |
| 58–60 | 308 | 3.3 | 10.9 | 6.4 ± 0.2 | 1.7 | 26.6 | 12.0 | 45.5 | 26.6 | 15.3 | 0.6 | – | – | – |
| 81–83 | 310 | 2.9 | 12.2 | 5.9 ± 0.2 | 1.43 | 24.1 | 12.9 | 58.1 | 23.9 | 4.2 | 0.9 | – | – | – |
| 121–123 | 121 | 2.9 | 13.4 | 7.6 ± 0.4 | 2.52 | 33.0 | 8.3 | 28.1 | 29.7 | 18.2 | 13.2 | 2.5 | – | – |
| 201–203 | 107 | 3.2 | 12 | 7.0 ± 0.4 | 2.17 | 21.0 | 5.6 | 43.9 | 24.3 | 15.0 | 11.2 | – | – | – |
| 321–323 | 124 | 2.9 | 24 | 9.1 ± 0.7 | 4.23 | 38.0 | 8.8 | 26.6 | 21.8 | 8.1 | 11.3 | 12.9 | 9.7 | 0.8 |
| 563–565 | 252 | 2.8 | 18 | 7.0 ± 0.4 | 2.75 | 39.0 | 24.6 | 23.8 | 22.2 | 18.3 | 7.5 | 2.8 | 0.8 | – |
| 575–577 | 133 | 4.4 | 19.2 | 8.9 ± 0.5 | 2.84 | 31.7 | 1.5 | 16.5 | 33.8 | 24.1 | 12.8 | 8.3 | 3.0 | – |
| 670–672 | 136 | 3.0 | 13 | 6.9 ± 0.4 | 2.47 | 36.0 | 17.6 | 31.6 | 27.2 | 11.8 | 9.6 | 2.2 | – | – |
| 718–720 | 71 | 3.0 | 16.7 | 6.3 ± 0.6 | 2.83 | 34.0 | 32.4 | 32.4 | 16.9 | 9.9 | 2.8 | 4.2 | 1.4 | – |

The distribution of valves among particular dimensional groups shows that valves of all groups occur in the lower part of the core, and their amount is very representative; whereas valves of five groups with a sharp domination of the group of 5–6 μm are detected in the upper part of the core.

Valves of the complex were studied along the entire section, but samples from 720–0 cm were studied in maximal detail. We have attempted to trace a correlation between changes in the morphology of diatom frustules and climatic fluctuations during the Pleistocene–Holocene.

Sample 972 cm is dominated by *Cyclotella kuetzingiana*-morphotype, which constitutes up to 99.4% (Fig. 2; Pl. 4, figs. 1, 2). The sediments were formed during warm Marine Isotope Stage (MIS) 7. Valves with 15 fultoportulae with satellite pores were found in these sediments.

Valves were studied from samples 718–720 cm and 670–672 cm, which accumulated during cold MIS 6. Diatom fossil communities of the lake, which developed during that time (Fig. 2), are dominated by *ocellata*-morphotype constituting 57.4–97.2% (Pl. 4, figs. 3, 5); *kuetzingiana*-morphotype becomes a subdominant (up to 20.7%) in some intervals; valves of *triparita*-morphotype were also observed (Pl. 4, figs. 3, 4). The valves are poorly preserved. The diameter of valves in sample 718–720 cm varies from 3.0 μm to 16.7 μm; dimensional groups of 3–4 μm and 5–6 μm prevail. The valve diameter varies within 3–13 μm in sample 670–672 cm; dimensional groups of 5–6 μm and 7–8 μm dominate (Table 1). The number of striae per 10 μm is 16–23; the number of depressions on the external surface of valves, from three to five. The central fultoportula with two satellite pores, situated on the internal surface of the valve, is solitary (Pl. 4, fig. 6). A rimoportula is situated at a distance of 1 μm from costae.

Samples 575–577 cm and 563–565 cm were collected from sediments formed during the warmest phase MIS 5.5 (Valkatlen time, Kazantsev Interglacial, Sangamon). Some data show that the temperature during that phase could have been much higher than nowadays (Pushkar and Cherepanova, 2001). The fossil communities are still dominated by *ocellata*-morphotype constituting from 42.8 to 98.0% (Pl. 4, figs. 7, 8) and subdominated by *kuetzingiana*-morphotype constituted up 28.0%; no valves of *triparita* were found. The diameter of valves of *Cyclotella ocellata*-complex varies in these samples from 2.8 μm to 19.2 μm. It is exactly the interval where valves of groups of 7–8 μm and 9–10 μm become more numerous (Table 1). Valves of group of 16–20 μm also occur in the sediments. Analysis of diameter distribution has revealed that valves of 8 μm in diameter prevail, valves of 10 μm in diameter become slightly more numerous in sample 575–577 cm, and valves of 4 and 6 μm in diameter are common in sample 563–565 cm (Fig. 3). The number of striae per 10 μm is 16–30; the number of depressions, satellite pores, and central fultoportula does not change.

Sample 321–323 cm was collected from sediments accumulated during MIS 5.1. The fossil community is dominated by *ocellata*-morphotype (up 97.7%; Fig. 2; Pl. 4, fig. 9); valves of *kuetzingiana*-morphotype and *arctica*-morphotype occur more rarely (Pl. 4, fig. 10). The sample under study is characterized by relatively equal distribution of valves in groups of 5–6 μm and 7–8 μm; valves of group of 16–20 μm were observed; and insignificant number (0.8%) of valves with the diameter exceeding 20 μm were found (Table 1). The distribution of valves by their diameter shows two pikes: a sharp increase of valves of 6 μm in diameter

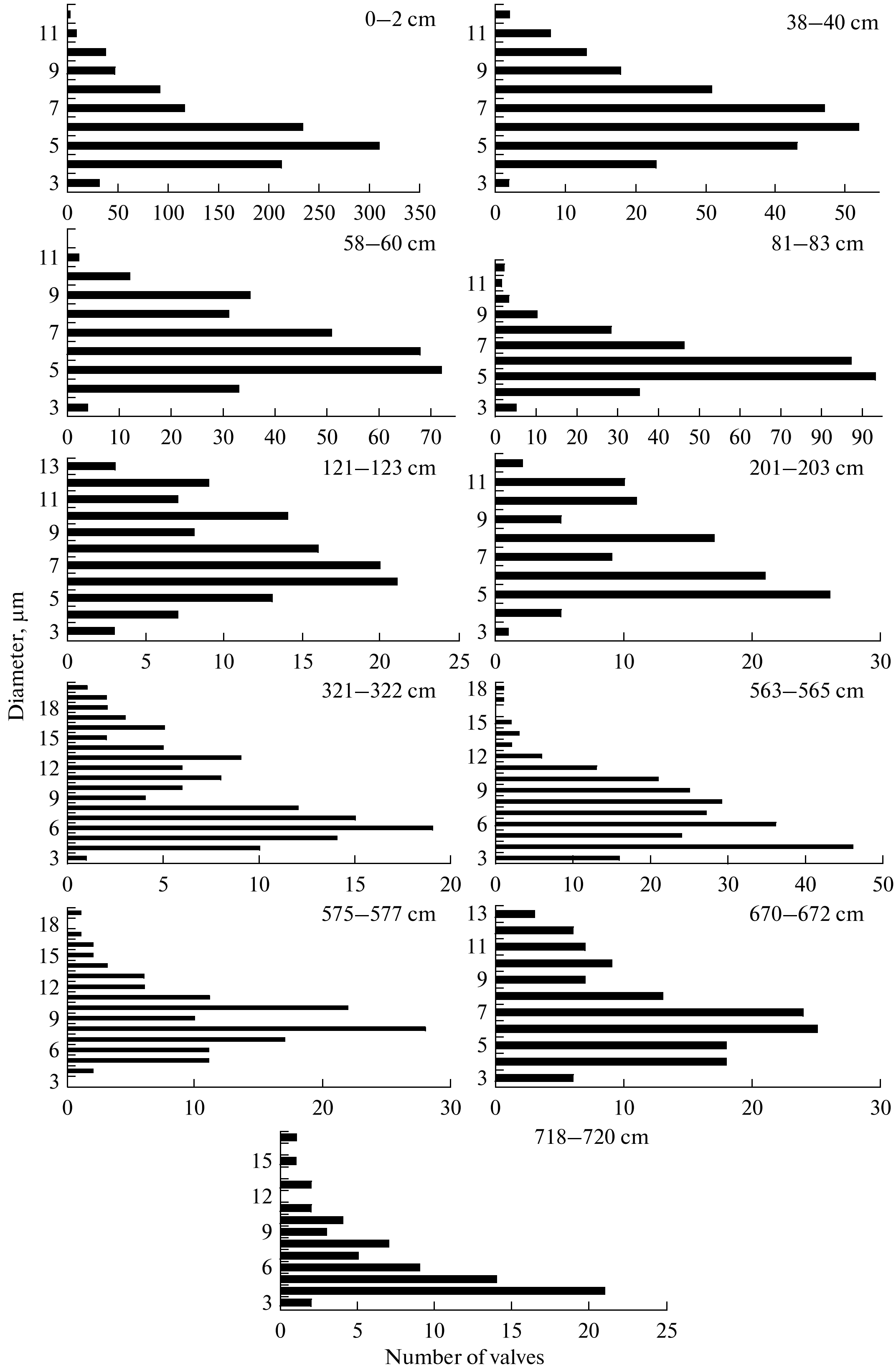
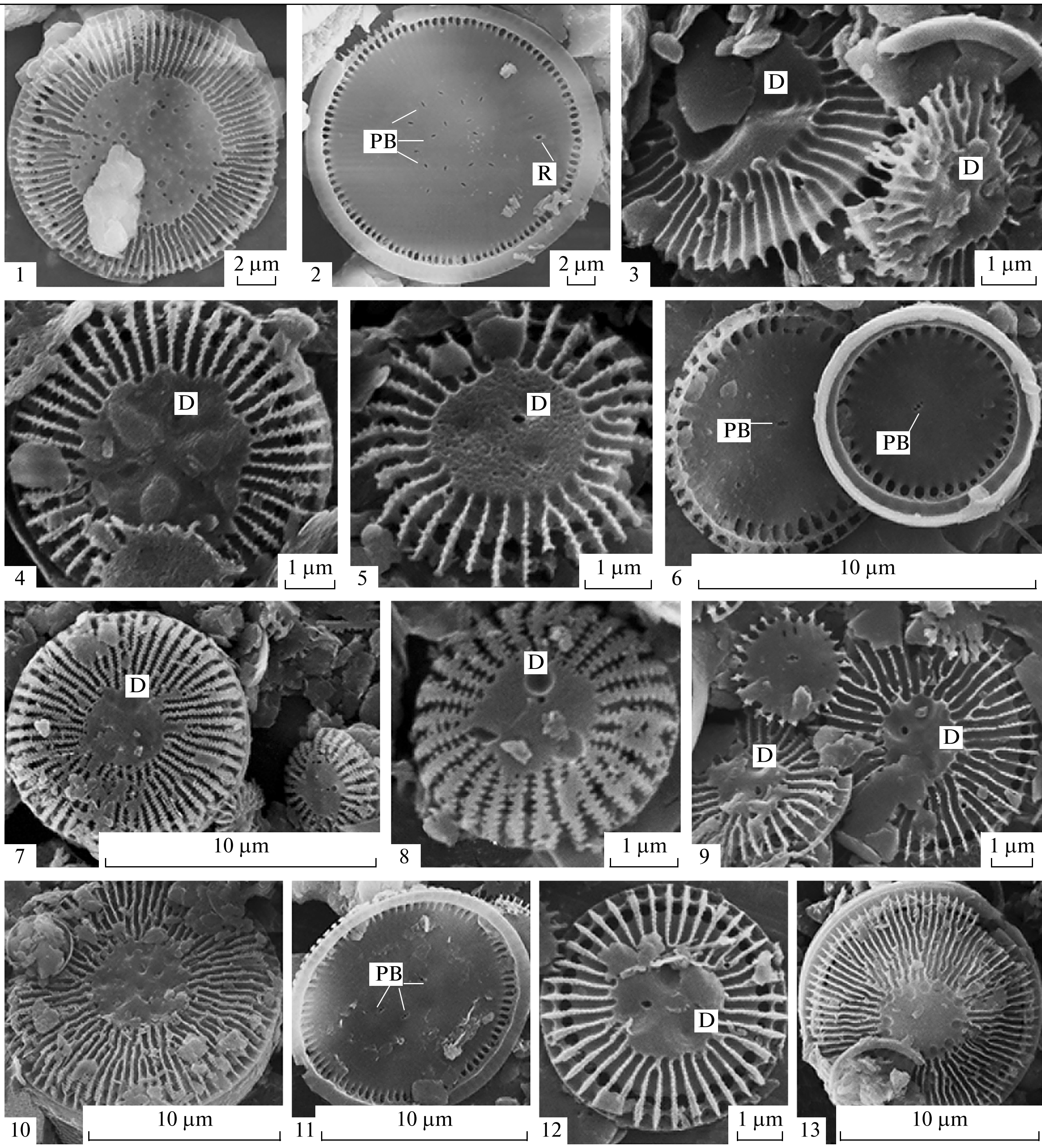



**Fig. 3.** Frequency distribution of valves by their diameter in sediments of Lake El'gygytgyn.

Plate 4




Explanation of Plate 4

**Figs. 1–13.** *Cyclotella ocellata*-complex, morphological diversity in samples of core PG-1351, Lake El'gygyngyn, Chukchi Peninsula, Pleistocene, SEM: (1) *Cyclotella ocellata kuetzingiana*-morphotype, external surface of the valve, 972 cm; (2) *Cyclotella ocellata kuetzingiana*-morphotype, inner surface of the valve (below to the left) with 15 central fultoportulae with satellite pores (F) and rimoportula (R), 972 cm; (3) *Cyclotella ocellata tripartita*-morphotype (left) and *ocellata*-morphotype (right), external surface of valves with depressions (D), 718–720 cm; (4) *Cyclotella ocellata tripartita*-morphotype, external surface of the valve, 670–672 cm; (5) *Cyclotella ocellata ocellata*-morphotype, valve surface, 670–672 cm; (6) *Cyclotella ocellata ocellata*-morphotype, internal surface with one central fultoportula with satellite pores, 670–672 cm; (7) *Cyclotella ocellata ocellata*-morphotype, 563–565 cm; (8) *Cyclotella ocellata ocellata*-morphotype, external surface of the valve, 563–565 cm; (9) *Cyclotella ocellata ocellata*-morphotype, external surface of the valve, 321–323 cm; (10) *Cyclotella ocellata ocellata*-morphotype, external surface of the valve, 321–323 cm; (11) *Cyclotella ocellata ocellata*-morphotype, internal surface of the valve with three central fultoportulae with satellite pores, 201–203 cm; (12) *Cyclotella ocellata ocellata*-morphotype, external surface of the valve, 201–203 cm; (13) *Cyclotella ocellata kuetzingiana?*-morphotype, external surface of the valve, 121–123 cm.
Legend: (D) depression; (R) rimoportula; (F) fultoportulae with satellite pores.

and a certain increase of valves of 13 μm in diameter (Fig. 3). Striae per 10 μm vary from 14 to 27. The number of other ultrastructural elements does not change. Most probably, the environmental conditions were most favorable for the development of *Cyclotella ocellata*. The climatic parameters corresponded to modern ones (Cherepanova et al., 2003).

Sample 201–203 cm was collected from sediments formed during MIS 3, which corresponds to Kargin Interglacial. The sediments are dominated by *ocellata*-morphotype, varying from 8.5% to 97.0% (Pl. 4, fig. 12); solitary valves of *kuetzingiana*-morphotype were found. The valve diameter varies from 3.2 μm to 12.0 μm. Valves of groups of 5–6 μm and 7–8 μm prevail in the sample (Table 1). Valves of 5 μm in diameter are common; the amount of valves of 8 μm and 10 μm in diameter slightly increases (Fig. 3). The number of striae per 10 μm is 19–25; three central fultoportulae with satellite pores were found on the internal surface of some valves (Pl. 4, fig. 11).

Sample 121–123 cm comes from sediments accumulated during cold MIS 2 (Sartan, Late Vüurm). The fossil community is distinctly dominated by the only one morphotype, *ocellata*-morphotype, constituting 60.5–99.5%; the participation of other forms decreases (Fig. 2). Only solitary valves of *kuetzingiana*-morphotype were found (Pl. 4, fig. 13). As far as *Cyclotella ocellata* is able to actively develop on the ice surface (Cremer and Wagner, 2003; Cremer et al., 2005), one can suppose that ice easily transmitted solar rays under conditions of low humidity and insignificant atmospheric precipitation. As a result, vegetation under ice became possible. The valve diameter varies from 2.9 μm to 13.4 μm. Valves of groups of 5–6 μm and 7–8 μm predominate (Table 1). Valves of 3 μm, 7 μm, and 10 μm in diameter become more numerous (Fig. 3). An initial valve of *C. ocellata arctica*-morphotype was found in this sample (Pl. 5, fig. 1). The diameter is 10 μm. This finds allows to supplement the dimensional characteristics of initial valves of *C. ocellata*, which were earlier revealed by Genkal and Popovskaya (2007). There are 17–26 striae per 10 μm.

Samples 81–83 cm, 58–60 cm, 38–40 cm, and 0–2 cm were collected from sediments accumulated during warm MIS 1. The fossil communities are prevailed by *Cyclotella ocellata*-morphotype constituting from 32.4% to 89.1% (Pl. 5, figs. 2, 4–6, 8–13); valves of *tripartita*-morphotype (Pl. 5, fig. 3) and *arctica-morphotype* (Pl. 5, figs. 3, 6, 7) are occasionally present. The diameter varies from 2.6 to 12.6 μm. The samples under study are dominated by valves of groups of 5–6 μm and 7–8 μm (Table 1). Valves of 5 μm and 6 μm in diameter are common (Fig. 3). Valves of 6 μm in diameter become more numerous in sample 38–40 cm, which was collected from sediments formed during the Atlantic Period of the Holocene Optimum, when temperatures were 1–2°C higher than nowadays (*Atlas...*, 1992). Valves from group of 11–12 μm also become slightly more abundant in this sample. Striae vary from 20 to 26 per 10 μm.

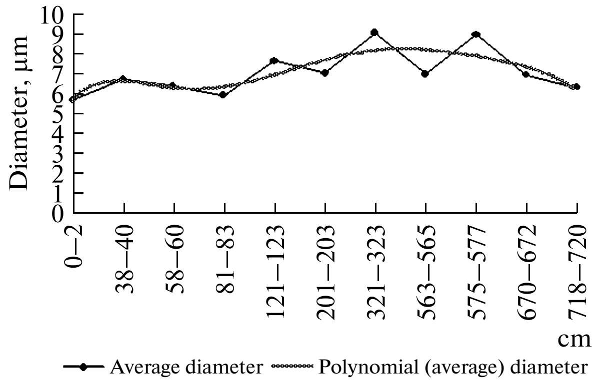



**Fig. 4.** Distribution of indices of polynomial (average) diameter along the section of core PG 1351.

The best preservation of valves was observed in sample 0–2 cm, where unsolved fine morphological elements of frustules were observed. Valves of *Cyclotella ocellata*-complex from this sample have central (one or, more rarely, two) and marginal fultoportulae supplied with two satellite pores (Pl. 5, figs. 11–13); the position of rimoportula relative to the marginal zone can vary from 0.2 μm to 1 μm.

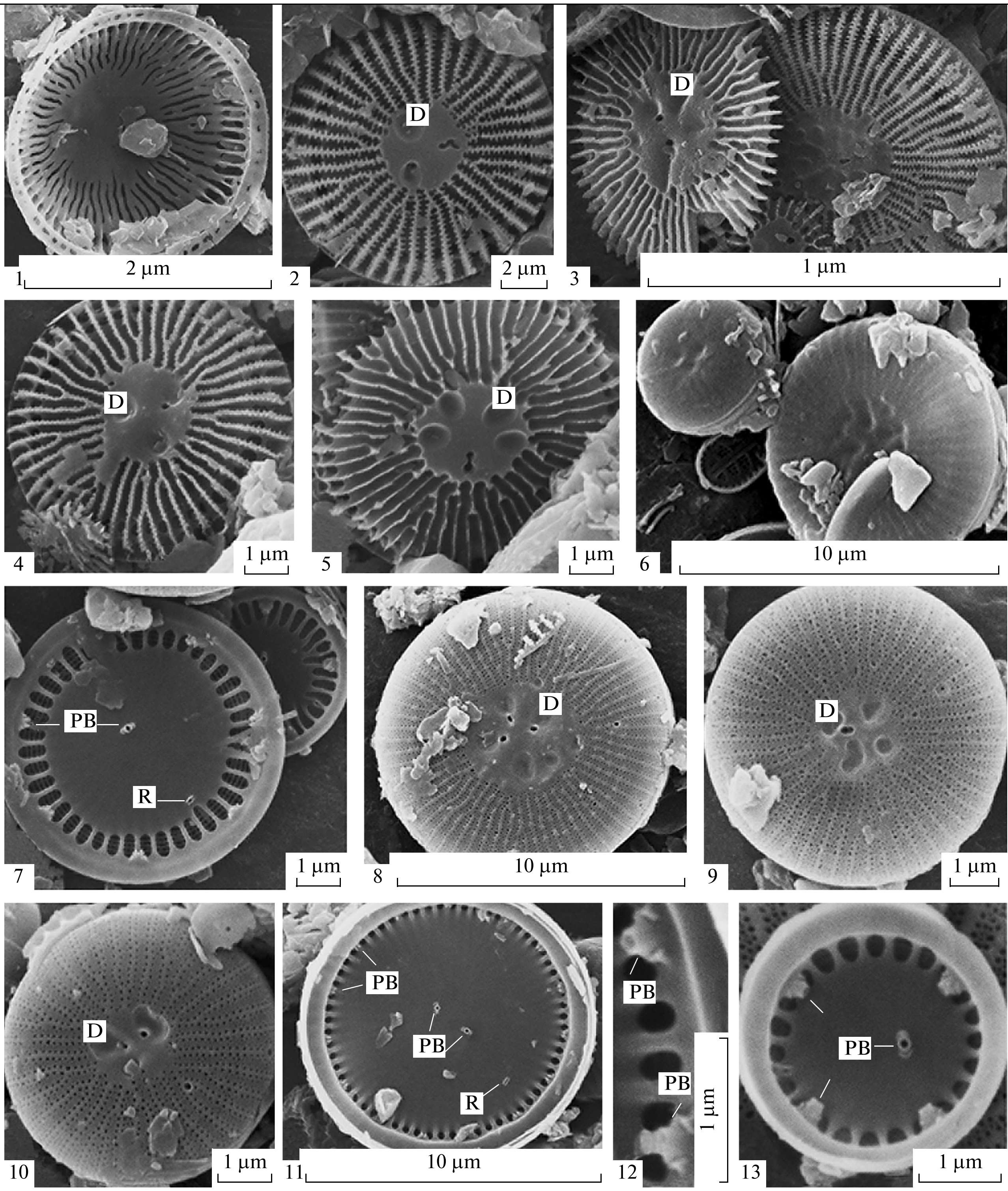
## CONCLUSIONS

Valves of *Cyclotella ocellata*-complex show considerable morphological diversity in sediments of Lake El'gygytgyn. Valves of *kuetzingiana-, ocellata-, tripartita*-,- and *arctica*-morphotypes were recorded in fossil state. The following variations have been revealed: valve diameter (2.6–24.0 μm), number of striae per 10 μm (14–30), number of orbicular depressions (3–5), number of central fultoportulae with satellite pores (1–15), the position of central fultoportulae on the valve, and the distance between the rimoportula and valve margin (0.2–1 μm).

Our analysis of changes in valve diameter in *Cyclotella ocellata* shows that forms with large valves become less numerous and the diameter decreases upwards the section. The directed diminishing of valve diameter in the complex is additionally confirmed by changes in polynomial (average) diameter (Fig. 4).

This trend is most probably related to ecological changes in the water pool, caused by paleoclimatic fluctuations. Lower temperatures that took place after Valkatlen (Kazantsev) Interglacial prevented that plentiful nutrients could have entered the lake. Forms with large valves also could have been eliminated due to relative isolation of the water pool. The complex developed by phenotype selection: *C. ocellata kuetzingina*-morphotype was gradually replaced by *ocellata*-morphotype, and in the late Late Pleistocene by *arctica*-morphotype.

Plate 5




The correlation between data on changing valve morphology in *Cyclotella ocellata*-complex and climatic events in the Pleistocene and Holocene shows that population response to temperature oscillations is synchronic and primarily expressed in changes in morphotype diversity, dimensional groups, and occurrence of valves of a particular diameter.

Explanation of Plate 5

**Figs. 1–13.** Morphological diversity of *Cyclotella ocellata*-complex in samples from core PG-1351, Lake El'gygytgyn, Chukchi Peninsula, Pleistocene, Holocene, SEM: (1) *Cyclotella ocellata arctica*-morphotype, internal surface of the initial valve, 121–123 cm; (2) *Cyclotella ocellata ocellata*-morphotype, external surface of a valve with depressions (D), 58–60 cm; (3) *Cyclotella ocellata tripartita*-morphotype (left) and *arctica*-morphotype (right), external surface of valves, 58–60 cm; (4) *Cyclotella ocellata ocellata*-morphotype, external surface of the valve, 38–40 cm; (5) *Cyclotella ocellata ocellata*-morphotype, external surface of the valve, 38–40 cm; (6) *Cyclotella ocellata ocellata*-morphotype (left) and *arctica*-morphotype (right), external surface of valves, 0–2 cm; (7) *Cyclotella ocellata arctica*-morphotype, internal surface of a valve supplied with a fultoportula with satellite pores (F) and rimoportula (R), 0–2 cm; (8) *Cyclotella ocellata ocellata*-morphotype, external surface of the valve, 0–2 cm; (9) *Cyclotella ocellata ocellata*-morphotype, external surface of the valve, 0–2 cm; (10) *Cyclotella ocellata ocellata*-morphotype, 0–2 cm; (11) *Cyclotella ocellata ocellata*-morphotype, internal surface of the valve, 0–2 cm; (12) *Cyclotella ocellata ocellata*-morphotype, internal surface of the valve, –2 cm; (13) *Cyclotella ocellata ocellata*-morphotype, internal surface of the valve, 0–2 cm.

Our study shows that changes in valve morphology can be used as an additional criterion in course of paleogeographic interpretation and to date sediments of a particular water pool.

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