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Climate-related morphological changes in *Pantocsekiella* (Mediophyceae) spanning 0-1.2 Ma in the Lake El'gygytgyn, northeastern Russia including *Pantocsekiella elgygytgynensis sp. nov.*

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Abstract

The distribution of diatom species and their evolutionary histories are largely a result of the complex feedback mechanisms in their environment. Arctic lakes are particularly sensitive to climate changes, and the species within these environments reflect these histories. The diatom genus *Pantocsekiella* is widespread and notably morphologically diverse. Valves from *Pantocsekiella* in the Arctic Lake El'gygytgyn spanning the last 1.2 Ma were analyzed using light and scanning electron microscopy to investigate how morphological transitions are related to known regional climate events. Quantitative and qualitative observations yielded a high degree of morphological diversity with multiple morphological shifts often associated with inferred extreme cold events. Principal components analysis (PCA) on quantitative morphological variables demonstrates a gradient in morphological variability through time, with a distinct morphology persisting uninterrupted from ~550-~230 ka warranting the establishment of a new species. Valve size within this interval responds to interglacial-glacial cycles, with the largest initial valves occurring during interglacials suggesting sensitivity to lake conditions related to climate.

Keywords: *Lindavia, Cyclotella*, Thalassiosirales, Stephanodiscaceae, diatoms, Lake El'gygytgyn, Arctic, ancient lakes

Introduction

The Arctic is characterized by complex feedback mechanisms among the ocean, atmosphere, cryosphere, and lithosphere (Vogel *et al.*, 2013), which vary in time and space influencing the distribution and evolutionary history of species. Diatoms, photosynthetic siliceous algae, are important components of Arctic freshwater ecosystems and respond rapidly to changes in their environment. One of the most common members of the freshwater Arctic and subarctic diatom flora is the planktic genus *Pantocsekiella* K.T. Kiss & E. Ács in Ács *et al.* (2016: 61), previously reported as *Cyclotella* (Kützing) Brébisson (1838: 19) (Kiss *et al.*, 1999; Schlegel & Scheffler, 1999; Cremer & Wagner, 2003; 2004; Cremer *et al.*, 2005; Cherepanova *et al.*, 2007; Genkal *et al.*, 2008; Cherepanova *et al.*, 2010; Genkal & Bondarenko, 2010; Genkal *et al.*, 2013; Snyder *et al.*, 2013). *Pantocsekiella*, and associated cyclotelloid genera, represent one of the most taxonomically, ecologically, and morphologically diverse groups of freshwater planktic diatoms (Fourtanier & Kociolek 2011), and these taxa are widely used in reconstructions from paleolimnological records.

Lake El'gygytgyn is an ancient lake with a record spanning the last ~3.6 Ma, preserving the longest continuous continental record of climatic and environmental change in the Arctic. The modern diatom community of Lake El'gygytgyn is dominated numerically by what has been described as the *Pantocsekiella ocellata* (Pantocsek 1901: 134) K.T. Kiss & E. Ács in Ács *et al.* (2016: 62) (or previously *Cyclotella ocellata*) complex (Cremer & Wagner, 2003; Cremer *et al.*, 2005; Kharitonov & Genkal, 2010). According to Cremer and others (2005) modern valves in the *P. ocellata*-complex range from 3–12 µm in diameter with variable central area characteristics (e.g. number of orbicular depressions) and heterovalvy. Another important component of the modern plankton is larger (16–46.5 µm length, 14–34 µm width) *Pliocaenicus* Round et Håkansson (1992: 116) (syn. *Lindavia* (Schütt) De Toni et Forti 1900: 553) (Cremer & Van de Vijver, 2006; Stachura-Suchoples *et al.*, 2008). Genkal & Kharitonov (1996) described a new species *Pantocsekiella arctica* (Genkal et Kharitonov 1996: 69) K.T. Kiss & E. Ács in Ács (2016: 62), although some

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previous studies include diatoms with this description as part of the *P. ocellata*-complex. Several other taxa have been observed in modern lake samples including *Pantocsekiella tripartita* (Håkansson 2002: 98) K.T. Kiss & E. Ács in Ács *et al.* (2016: 69)*, Cyclostephanos dubius* (Hustedt 1928: 367) Round in Theriot *et al.* (1988: 346)*, Pliocaenicus seczkinae* Stachura-Suchoples, Genkal & Khursevich (2008: 173), and *Pliocaenicus costatus* (L.P Loginova, E.P. Lupikina, & G.K. Khursevich 1984: 170–173) R.J. Flower, Ozornina & Kuzmina in R.J. Flower *et al.* (1992: 123) (Cremer & Wagner, 2003; Cremer *et al.*, 2005; Kharitonov & Genkal, 2010).

Previous studies of the Lake El'gygytgyn diatom flora from sediment cores show multiple shifts in the dominant planktic species through time. Prior to ~1.2 Ma in the composite core, the genus *Pantocsekiella* occurs either as a minor component, or it is not observed (Snyder *et al.*, 2013). Between ~1.2 Ma and ~550 ka, *Pantocsekiella* dominates some intervals but is not observed in others. From ~550 ka to present, *Pantocsekiella* is consistently the most dominant planktic diatom, occasionally co-existing with other planktic genera, such as *Stephanodiscus*, *Aulacoseira* and *Pliocaenicus* during intervals of peak warmth. From their analysis of the ~250 ka record collected in 1998, Cherepanova *et al.* (2010) describe successive shifts in the abundance of informal morphotypes up-section from *P. kuetzingiana* (Thwaites 1848: 169) K.T. Kiss et E. Ács in Ács *et al.* (2016: 67) to *P. ocellata* and *P. arctica*.

Here, we present a longer record (1.2 Ma to present) of morphological variability in *Pantocsekiella* with a focus on the long-lived unique morphology from 550-230 ka from the Lake El'gygytgyn sedimentary record. We construct a more detailed characterization of morphological change than prior studies. *Pantocsekiella* valves were observed using scanning electron microscopy (SEM) and light microscopy (LM) to document quantitatively and qualitatively the morphological variability in the context of the paleoclimatic and paleoenvironmental record. On the basis of these observations we describe and interpret the occurrence of a new species of *Pantocsekiella* endemic to Lake El'gygytgyn.

Taxonomic review

Within the last few decades the monophyly of the genus *Cyclotella* has been scrutinized (Theriot *et al.*, 1987; Alverson *et al.*, 2007). Ongoing morphological and genetic analyses recently justify dividing this genus into five new genera: *Cyclotella* sensu stricto*, Discostella* (Houk et Klee 2004: 208)*, Tertarius* (Håkansson et Khursevich 1997: 22)*, Lindavia,* and *Pantocsekiella* (Ács *et al.*, 2016). Divisions among these taxa are based on the placement of the rimoportula on the valve face. Only diatoms that have been identified as part of the *P. ocellata* species complex are discussed below.

Pantocsek first described the species *P. ocellata* (as *Cyclotella ocellata*) from Lake Balaton in western Hungary. The description stated that valves were circular, ranged from 12.5–13 µm diameter, had a marginal ring of striae 1.8–2 µm wide, and a flat valve face with "3 large pearls" (=orbicular depressions) arranged in a triangular orientation (Pantocsek 1902, p. 104, fig. 15: 318). A similar taxon, *Cyclotella crucigera* (Pantocsek 1902: 134), was described as containing "4 large pearls" in the central area. Subsequent studies regarding this taxon considered *P. ocellata* and *C. crucigera* as conspecific (Kiss *et al.*, 1996; 1999).

Recent observations of *P. ocellata* have demonstrated a much higher range of morphological variability than originally reported (see **Table 1**). Current debate centers on whether this variability represents multiple distinct species or a single highly variable species-complex. Håkansson (1990; 1993; 2002) suggested that species including *Pantocsekiella polymorpha* (B. Meyer & H. Håkansson 1996: 64) K.T. Kiss & E. Ács in Ács *et al.* (2016: 68) , *Pantocsekiella comensis* (Grunow in Van Heurk 1882: 93) K.T. Kiss & E. Ács in Ács *et al.* (2016: 65), *Pantocsekiella rossii* (H. Håkansson 1990: 267) K.T. Kiss & E. Ács in Ács *et al.* (2016: 68), and *Pantocsekiella kuetzingiana* (syn. *Cyclotella krammeri* Håkansson 1990: 263) were closely related to *P. ocellata* with fine morphological differentiation (**Table 2**).

Contrasting opinion places *P. ocellata-polymorpha-comensis-rossii-kuetzingiana* as a species-complex. Kiss and others (1996) reported a much larger range of morphological variability in *P. ocellata* from Lake Madras, Spain including larger valve diameters (5.6–25 µm), 3–4 orbicular depressions, 14–20 striae/10 µm, 0–5 central fultoportulae, marginal fultoportulae situated on every 6th costa, and 1–3 rimoportulae. The medium-sized valves in Lake Madras were identical to those described by Pantocsek. They also observed heterovalvy, or frustules with morphologically different valves, and ultimately concluded that the valves belonged to one highly morphologically diverse species. Similarly, in a study by Hegewald & Hindáková (1997), the species *P. kuetzingiana* and *P. rossii* were considered as synonyms of *P. ocellata,* representing a morphological continuum or species-complex. This debate has led to a growing number of analyses on the causes and patterns of morphological variability of *P. ocellata* (Kiss *et al.*, 1996;

1999; Edlund *et al.*, 2003; Cremer *et al.*, 2005; Genkal & Popovskaya, 2008; Cherepanova *et al.*, 2010; Cvetkoska *et al.*, 2012; Edlund *et al.*, 2003; Duleba *et al.*, 2015).

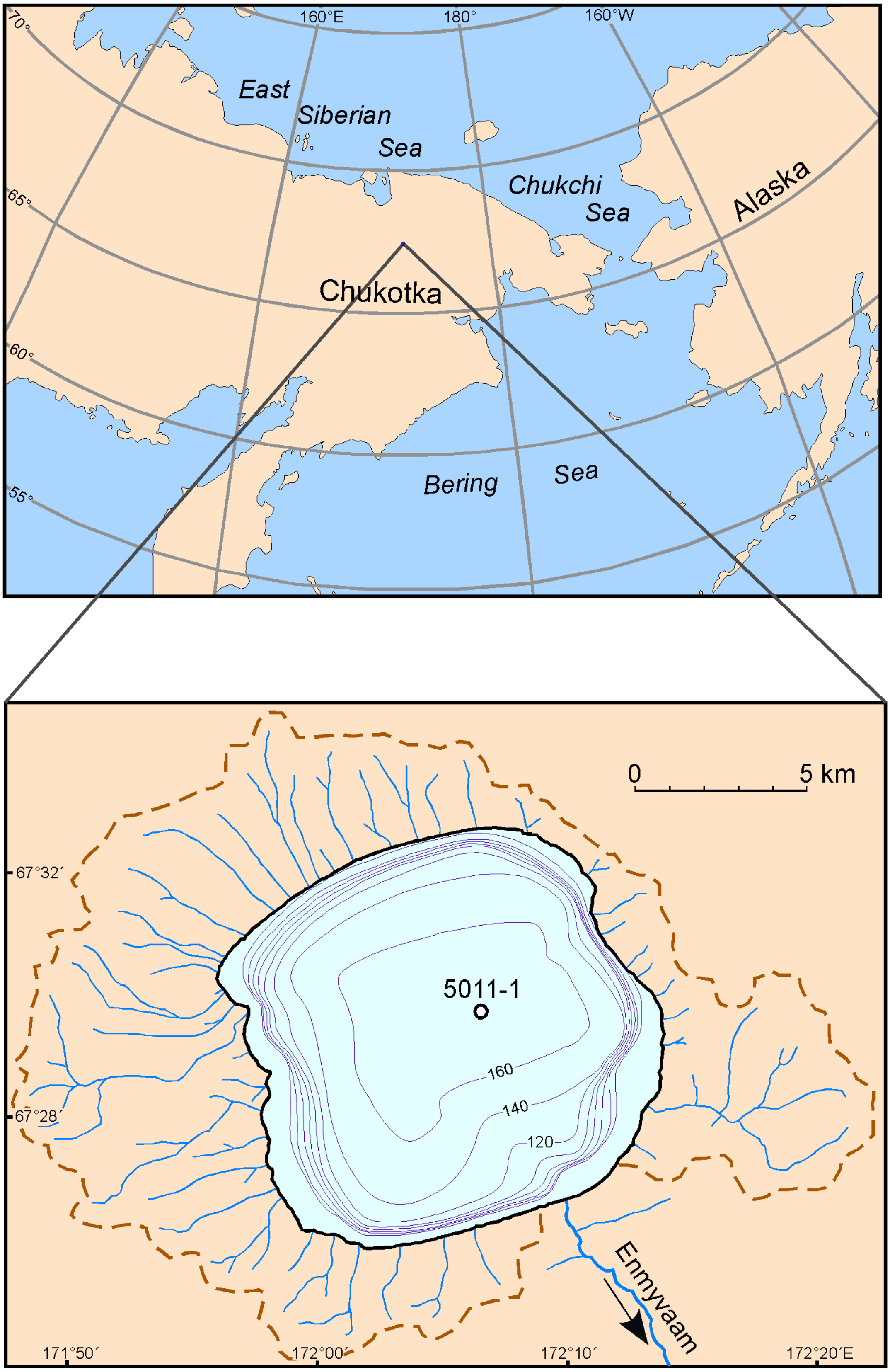


FIGURE 1. Location of Lake El'gygytgyn (top) and map of the lake hydrology (bottom) with core location 5011-1. (Modified from Nolan & Brigham-Grette, 2007)

TABLE 1. Morphological variability of *P. ocellata* described in the literature including valve diameter (VD), central area diameter (CD), striae in 10 µm, central fultoportulae (CF), marginal fultoportulae (MF), number of rimoportulae (R), orbicular depressions, and other notes. See Figure 2 for reference.

	VD (µm)	CD(µm)	Striae/10 µm	CF	MF	**R**	**Depressions**	**Notes**
Pantocsek (1902)	12.5–17		18–20				3–4	
Håkansson (1990)				1–2	Every 5–6 costae	1	3–4	
Kiss *et al.* (1996)	4–27	Small-large	14–25	1–6	Every 1–6 costae	1–3	3–5	
Schlegel & Scheffler (1999)	4.3–21	Small-large	14–25	1–3	Every 1–6 costae	1–2	(0)3–5	Central area with variable colliculate protuberances
Edlund *et al.* (2003)	2.5–43		10–14	1–7	Every 1–5 costae	1–4	2–5	
Knie & Hübner (2007)	4.8–33.2	Small-large						Suggest a smooth transition of the *P. ocellata-krammeri-rossii* complex
Genkal & Popovskaya (2008)	3.4–44.2		11–25	1–13	Every 1–8 costae	1–4	0–7	
Houk *et al.* (2010)	5–22	Small-large	14–20	1–4(5)	Every 2–5 costae	1	3–6	
Cherepanova *et al.* (2010)	2.6–24		14–30	1–15		1–2	3–5	Division of different “morphotypes” through time
Duleba *et al.* (2015)	4–15.5	1.4–10.3	14–26	1–4		1–3	0–6	Divided the species into “morphs”

TABLE 2. A summary of the characteristics of the different members of the *P. ocellata* species complex as recorded in Houk *et al.* (2010) and Genkal & Kharitonov (2005). See Figure 2 for reference.

	VD	**Striae/10 µm**	**CF**	**MF**	**Central Area Pattern**	**Notes**
P. ocellata	5–22	14–20	1–4(5)	Every 2–5 costae	Flat to colliculate	3-6 orbicular depressions
P. kuetzingiana	8–45	12–18	1–5(7)	Every 2–4(5) costae	Transversally undulate to nearly flat	Short radial and irregular fovi
P. polymorpha	4.5–45	16–24	1–5(7)	Every 2–5 costae	Flat to colliculate	Central fultoportulae radially scattered, variable radial, (1-5) orbicular depressions
P. rossii	5–18	16–18	2–3(5)	Every 2–3(5) costae	Flat to colliculate	2-8 radial rows of fovi
P. tripartita	2–18	19–22	(1)2–3	Every 5–7 costae	Radially undulate and colliculate	Divided into 3 elevations and 3 depressions; central fultoportulae situated within undulations
P. arctica	3–15	24–32	1-3	Every 4–8 costae	Flat	Delineated with several orbicular depressions, rarely with radially divergent ribs dichotomously branching, sometimes pitted or tubercular
P. comensis	4-15	16-22	1-2	Every 2-4(5) costae	Transversally undulate	Flat to bumpy valve face with occasional fovi

Methods

Site Description

Lake El'gygytgyn is located in northeastern Russia (67.5 N, 171.083 E) about 100 km north of the Arctic Circle (**Fig. 1**) at surface elevation of ~492 m.a.s.l (Nolan & Brigham-Grette, 2007). The lake is situated inside a meteorite impact crater that is 3.58±0.4 Ma (Layer, 2000). The lake accounts for 12 km of the 18 km impact crater, with a total watershed area of 293 km^2 (Nolan & Brigham-Grette, 2007). Lake El'gygytgyn is cold, monomictic, and oligotrophic, with the water temperature never exceeding 4°C (Nolan & Brigham-Grette, 2007). Ice covers the lake for 9 months of the year, during which the lake is thermally stratified. It is only ice free between July to October, with complete mixing of the water column during these summer months (Nolan & Brigham-Grette, 2007). The low productivity of the lake, combined with complete mixing of the water column in the summer, leads to well oxygenated bottom waters (Melles *et al.*, 2012).

The bathymetry of the lake is asymmetrical, with shallow eastern and southern slopes, and steep western and northern slopes (Nolan & Brigham-Grette, 2007). The central portion of the lake is the deepest portion at ~175 m (Nolan & Brigham-Grette, 2007). Several shallow shelves or benches are present in the lake; these may be representative of paleo-shorelines because of difference in lake levels (Nolan & Brigham-Grette, 2007; Juschus *et al.*, 2011). Deep-water sediments on the shelf and raised shoreline features indicate higher than present lake levels during a period of warmth in the mid-Pleistocene (Juschus *et al.*, 2011). Fifty ephemeral streams drain into the lake, with only one major outflow to the Enmyvaam River (Melles *et al.*, 2011).

The Lake El'gygytgyn Drilling Project

The sediment of site 5011-1 (**Fig. 1)** was drilled during Spring 2009 in the central area of the lake as part of the Lake El'gygytgyn Drilling Project. Three holes were drilled 1A, 1B, and 1C (Melles *et al.*, 2011). 1A and 1B were abandoned after twist offs at 143.7 m and 108.4 m respectively; 1C penetrated the rest of the lake sediments to 315 m, and into the impact rocks up to 517 m (Koeberl *et al.*, 2013). A composite core was created from splices of parallel sediment cores recovered from 5011-1, coupled with samples from an earlier sediment core from the deepest part of the lake taken in 2003 (LZ1024).

An age model was created using multiple methods including magnetic reversals, orbital tuning, and tephras (Nowaczyk *et al.*, 2013). Reversals of the magnetic field were used to establish initial tie points (Nowaczyk *et al.*, 2013). Stratigraphic parameters, including biogenic silica and magnetic susceptibility were tuned to Northern Hemisphere spring-summer insolation and the marine oxygen isotope stages (MIS) (Nowaczyk *et al.*, 2013). Eight tephra layers deposited in the sediment have not yet provided age information (Nowaczyk *et al.*, 2013). According to the age model the upper ~160 m of sediment records the last ~3.3 Myr, with sedimentation rates of 4–5 cm ka-1; while the lower ~160 m contains the first ~0.3 Myr of the lake with sedimentation rates of ~45 cm ka-1 (Nowaczyk *et al.*, 2013).

Laboratory and Analytical Methods

A systematic analysis of *Pantocsekiella* valves spanning the last ~1.2 Ma (composite core depths 0.005–51.017 m) was performed using LM and SEM. Sample pretreatments for microscope analyses followed standard procedures (Battarbee, 1973; Scherer, 1994). SEM cover slips were sputter coated with gold palladium. LM analyses were performed using a Leica DMLB with differential interference contrast, and a DFC 425 digital camera was used to take images and measurements. SEM analyses were performed at the University of Toledo using the Hitachi S-4800; SEM measurements were taken using the tpsDig2 version 2.30 software (Rohlf, 2004).

Forty-five samples were selected for detailed analysis in the SEM based on preliminary LM observations of high abundance and morphological variation within *Pantocsekiella*. SEM images (20 for each sample) were taken of both the internal (10) and external (10) valves. Quantitative features observed in SEM included measurements of valve diameter (VD), central area diameter (CD), the ratio of valve CD to VD (CD/VD), striae/10 μm, costae/10 μm, number of central fultoportulae (CF), number of marginal fultoportulae (MF), number of orbicular depressions, the number of fovi (small depressions), and the ratio of the distance of the rimoportulae (RD) from the valve perimeter (RD/VD) (**Fig. 2**). Qualitative features observed included the pattern of the orbicular depressions, the pattern of the central fultoportulae, and the central area undulation (flat, transverse, tri-undulate, etc.).

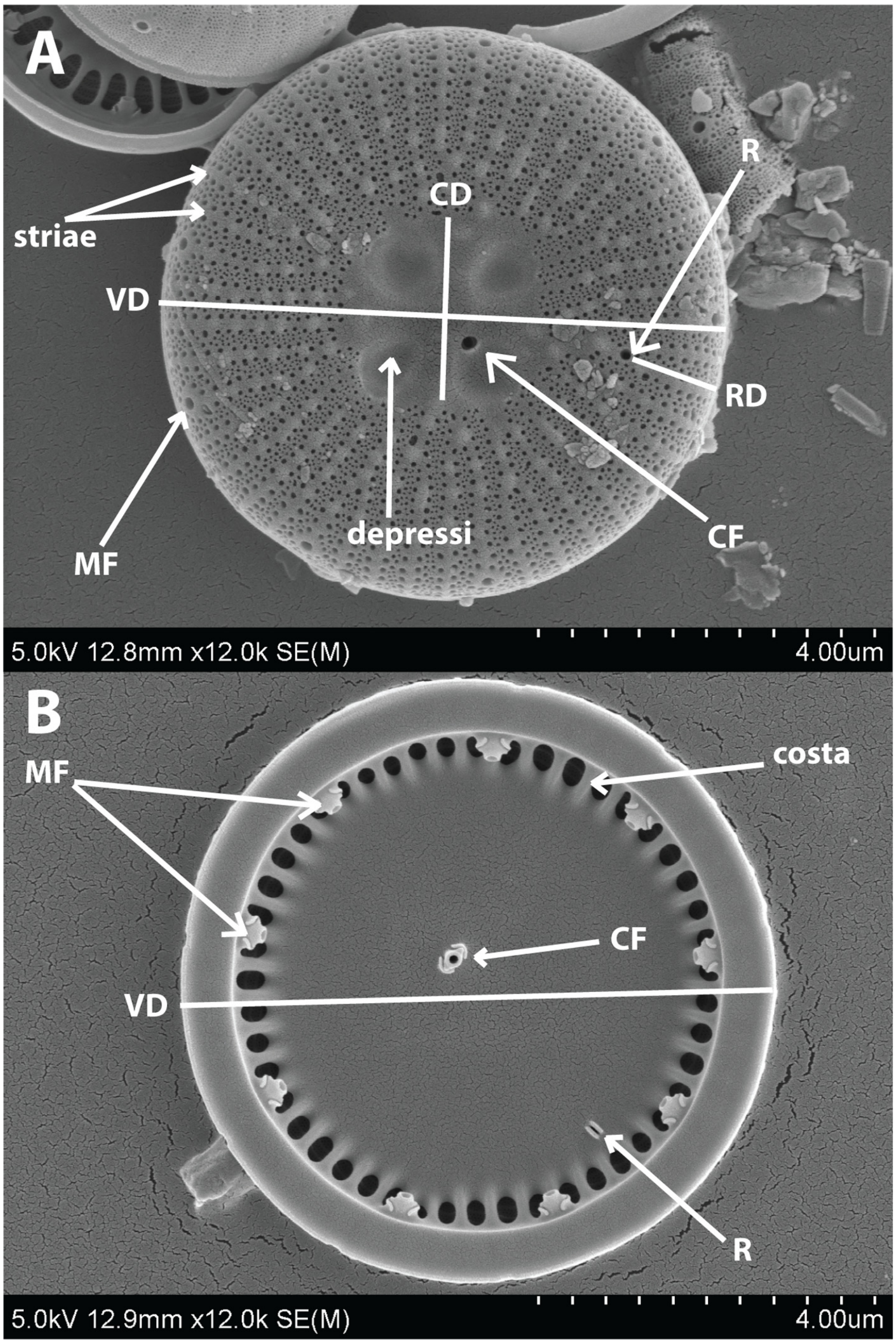
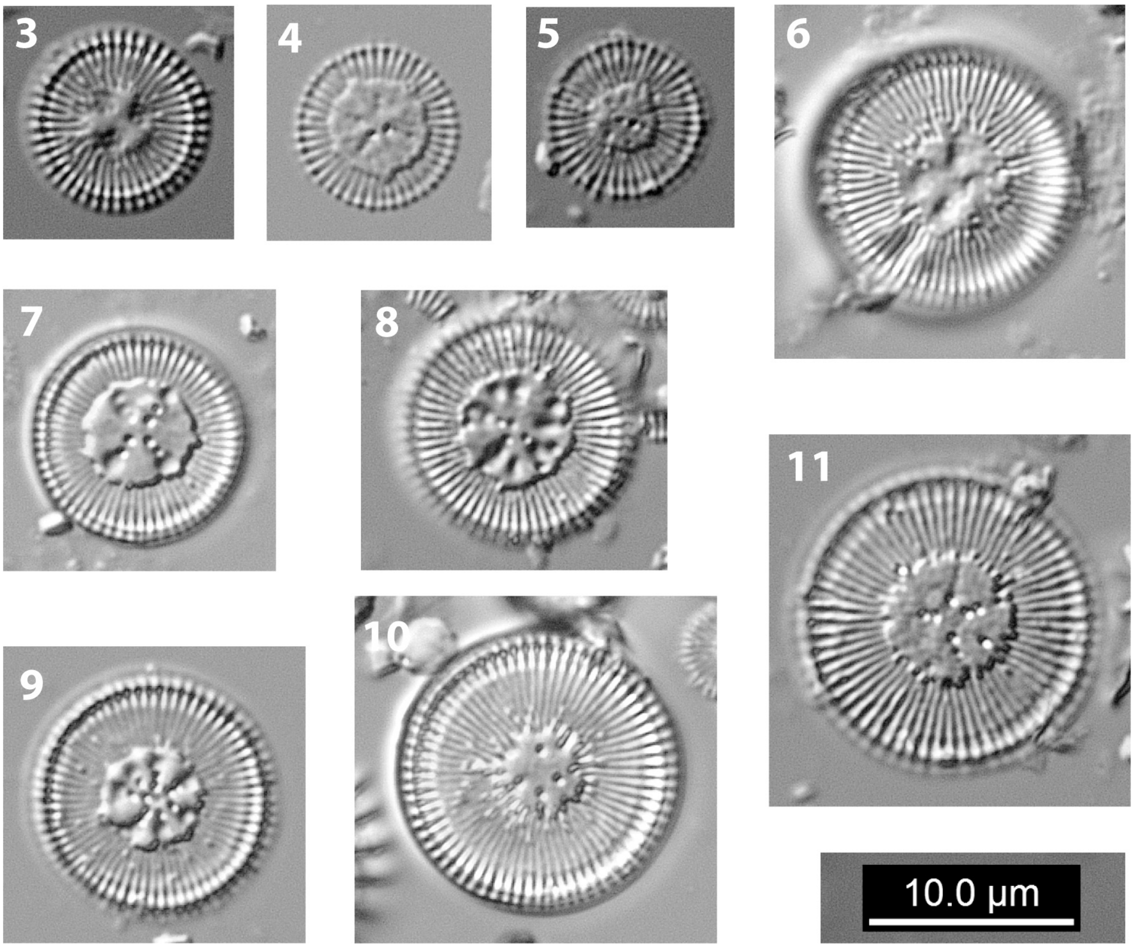


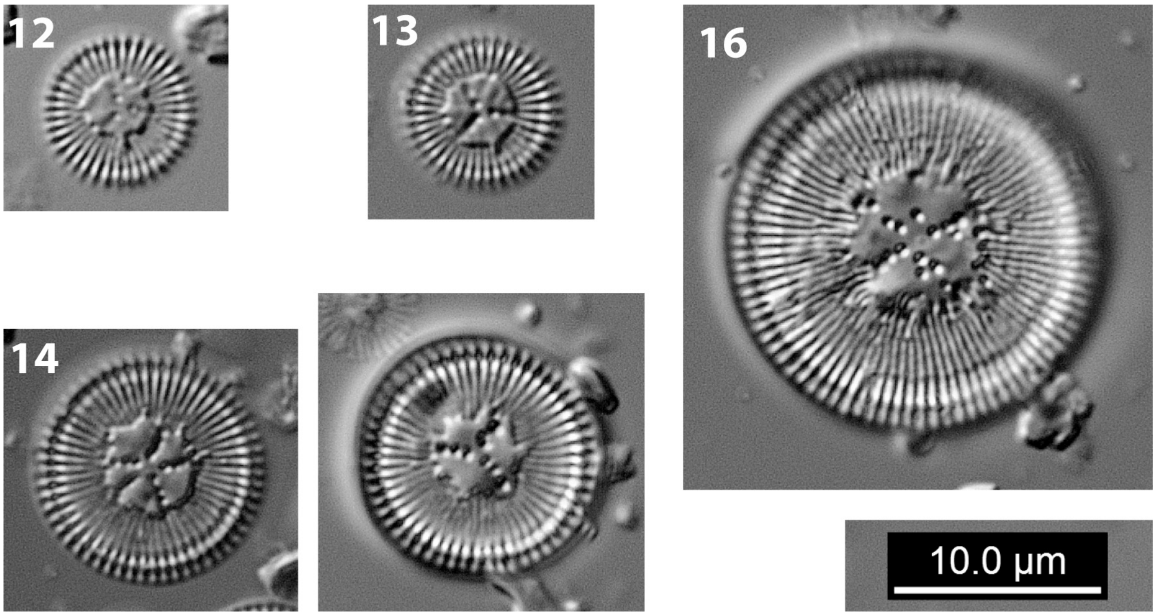
FIGURE 2. Measurements taken on SEM images of valves. A) external. B) internal. (VD: valve diameter, CD: central area diameter, R: rimoportula, RD: distance of the rimoportula from the margin, Striae: number of striae in 10 µm, Costae: number of costae in 10 µm, CF: number of central fultoportulae, Depressi: number of orbicular depressions, MF: number of marginal fultoportulae).

Each of the 45 SEM samples were also examined under LM. To evaluate trends in *Pantocsekiella* valves through time, 50 valve diameter measurements were taken per sample in LM. In an additional 25 samples from 550-220 ka, valve diameter was systematically measured for 100 valves with scans extended to observe at least five initial valves per sample.

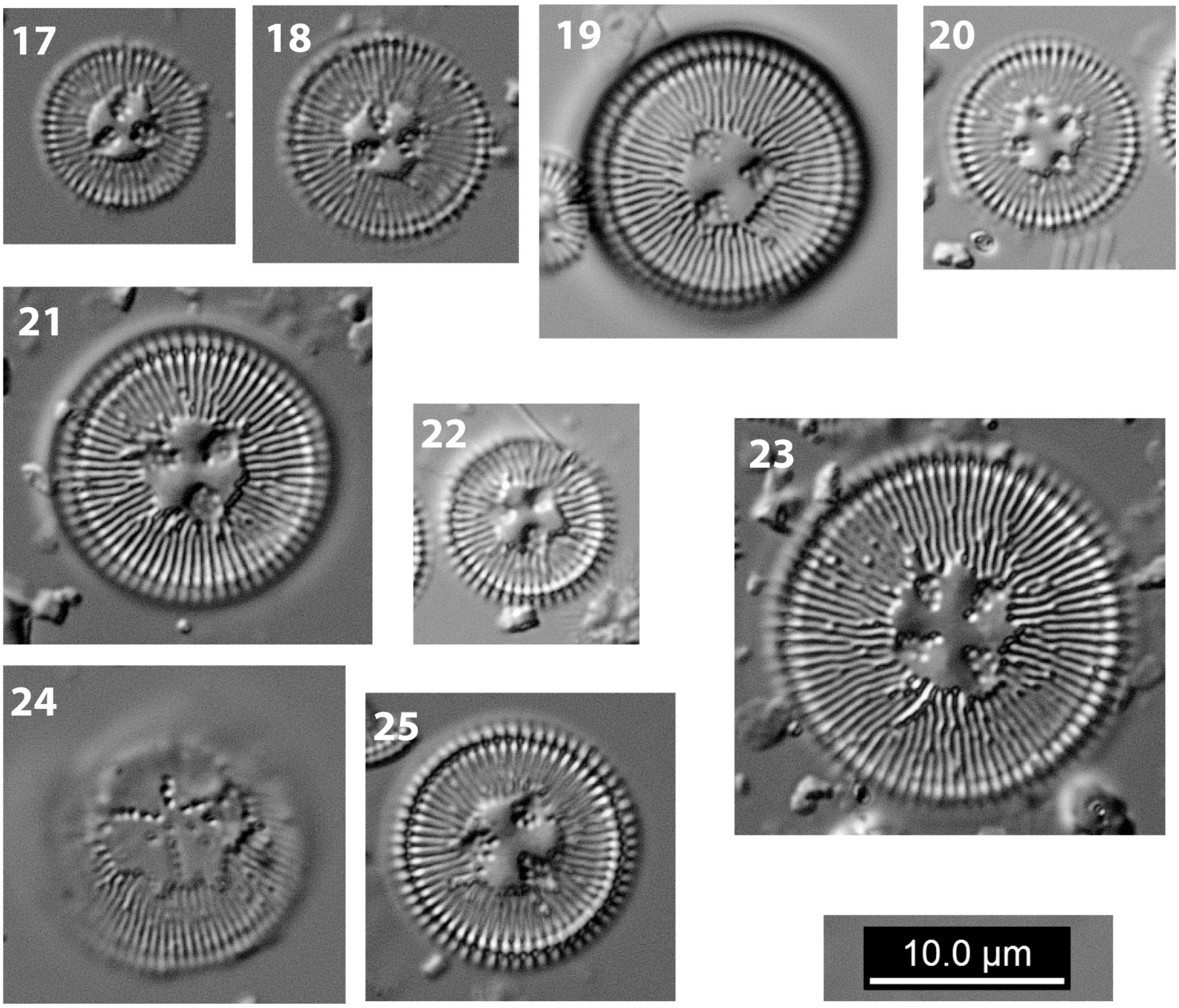
All statistical analyses were run using RStudio (Version 1.1.383). First, the summary statistics (mean, median, minimum, maximum, standard deviation) were calculated for each of the quantitative variables to evaluate morphological variability in the core. Next, to observe the main gradients of variance in *Pantocsekiella* valve morphology and elucidate patterns in the data, principal components analysis (PCA) was performed using the *prcomp* function in the *R Stats* package. Only external valves observed in SEM were used because of their high morphological variability compared to the internal valves. The loadings of the first three PC axes were evaluated to determine each variable's relative influence.



FIGURES 3–11: Representative light microscopy images of *Pantocsekiella* from the Lake El'gygytgyn prior to 650 ka. **Fig. 3**) Earliest occurrence at 2.53 Ma (DC4200), **Fig. 4**) 1.13 MA (DC1740) **Fig. 5**) 1102.9 ka (DC1700), **Fig. 6**) 1.06 Ma (DC1644), **Fig. 7**) 996.2 ka (DC1550), **Fig. 8**) 952.6 ka (DC1480), **Fig. 9**) 937.9 ka (DC1460), **Fig. 10**) 695.3 ka (DC990), **Fig. 11**) 653.1 ka (DC910).



FIGURES 12–16: Transitional phase in morphology moving towards generally larger valves through time. **Fig. 12**) 554 ka (DC770), **Fig. 13**) 543 ka (DC760), **Fig. 14**) 537 ka (DC750), **Fig. 15**) 519 ka (DC730), and **Fig. 16**) 513 ka (DC720).



FIGURES 17– 25: Representative images of the *P. elgygytgynensis* morphology during MIS Stages 8, 10 and 12. Figs **17–18 & 24**) Valves from 440.7 ka (DC620) with initial valve (**Fig. 24**), **Fig. 19**) Holotype valve from 424.1 ka (DC570) **Figs 20–22, 25**) Valves from 351.9 ka (DC460), **Fig 23**) Valve from 246.6 ka (LZ11-14).

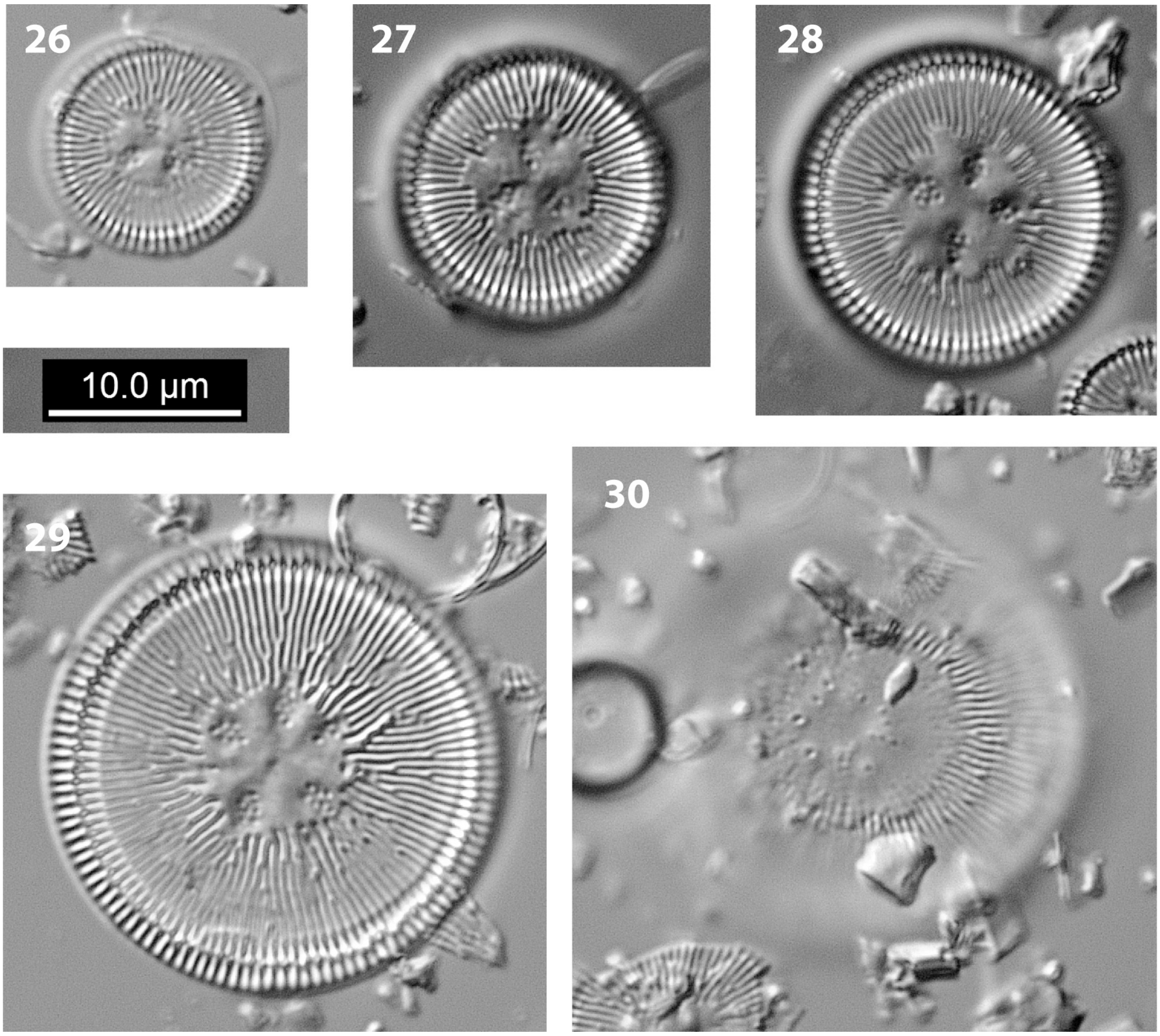
Valve diameter has a strong influence on other morphological features on the valve face, and for this reason *Pantocsekiella* valves were divided into size class including class 1 (0–5 µm), class 2 (6–10 µm), class 3 (10–15 µm), and class 4 (>15 µm). A PCA was subsequently run on each size class in the same fashion as outlined in the previous paragraph.

Results

Light microscope observations

Pantocsekiella valves from 2.5–1.2 Ma are relatively small, and co-occur with dominant genus *Pliocaenicus* (syn. *Lindavia)*. The first valves of *Pantocsekiella* observed in low abundance at ~2.5 Ma bear a striking resemblance to those observed from ~550-230 ka (**Figs. 3–4**). From 2.5-1.2 Ma *Pantocsekiella* valves display variable central area characteristics and are often poorly preserved. *Pantocsekiella* does not become a major component of the plankton until after 1.2 Ma, following the elimination of a species of *Pliocaenicus* during an inferred cold interval. Between 1.2 Ma and 550 ka, *Pantocsekiella* occurs sporadically, with each interval having a characteristic valve morphology (**Figs. 5–11**). At ~550 ka, *Pantocsekiella* becomes the dominant planktic species numerically, coeval with a decline in *Pliocaenicus seczkinae* (Stachura-Suchoples, Genkal & Khursevich) Nakov, Guillory, Julius, Theriot & Alverson

(2015: 258). From~550-510 ka the genus undergoes a morphological transition including a relative increase in valve diameter and formation of distinct clustered fultoportulae (**Figs. 12–16**). This transition culminates in a relatively stable morphology unique to the lake that persist from ~510-225 ka, exhibiting valve size fluctuations throughout the time interval (**Figs. 17–30**). Subsequent to an inferred cold event at ~225 ka, this long-lived species is replaced by a new morphology resembling *P. keutzingiana*, but with distinctively large numbers of fultoportulae scattered across the valve face (**Figs. 31–33**). The remainder of the record is characterized by varied morphologies previously described in the *P. ocellata* complex (**Figs. 34–39**). After 15 ka, *L. seczkinae* returns in abundance co-occurring with *P. ocellata*.



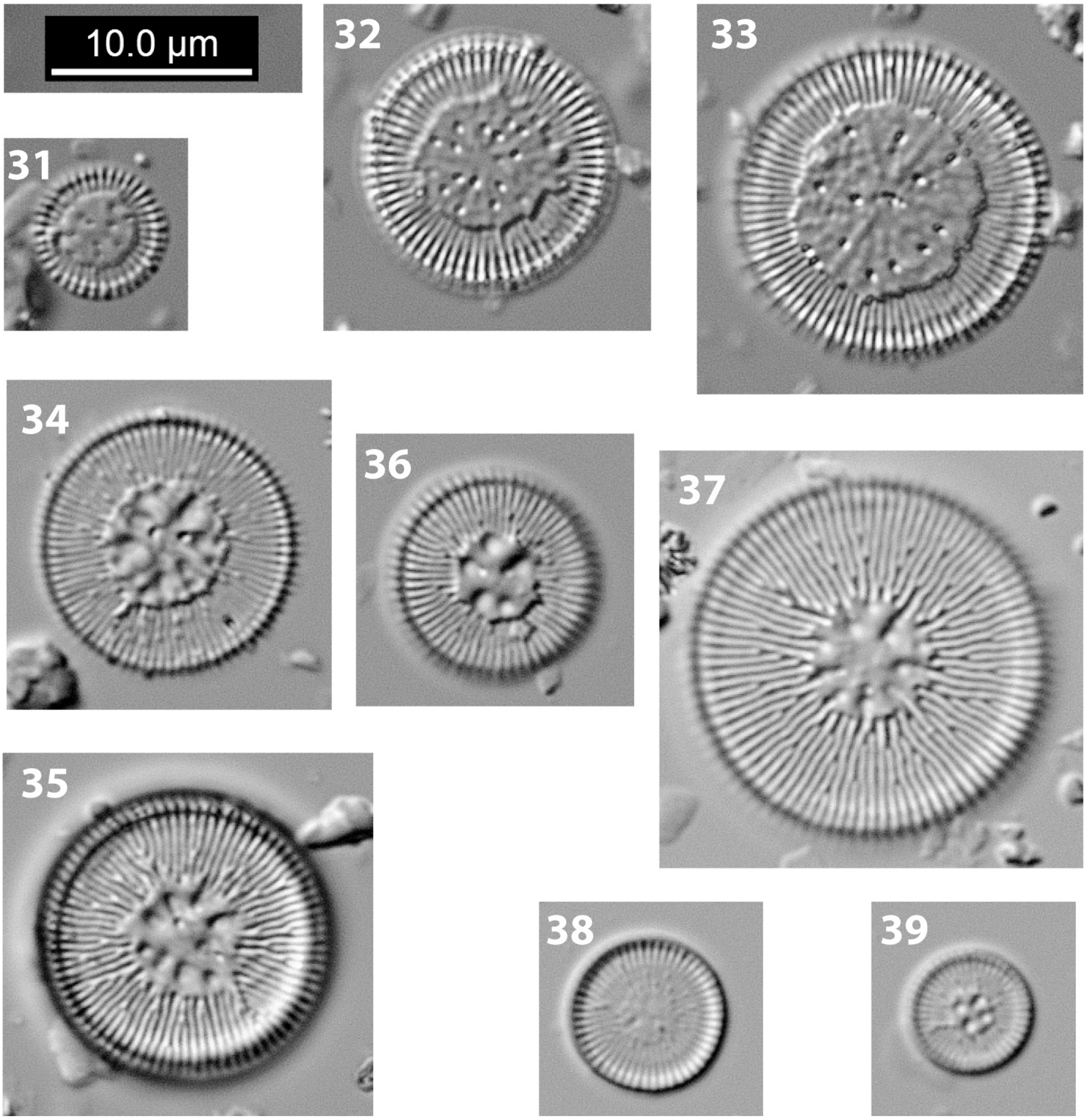
FIGURES 26–30: Representative valves of *P. elgygytgynensis* from MIS Stages 9 and 11. **Fig. 26**) Valve from 409.9 ka (DC548), **Figs. 27–28**) Valves from 401.5 ka (DC536), **Figs. 29–30**) Valves from 327.3 ka (LZ12-143) with initial valve (**Fig. 30**).

Valves of *Pantocsekiella* from the Lake El'gygytgyn record exhibit considerable size variability (**Fig. 40)**. VD ranges from 1.3–31.2 µm, and varies widely within samples. No significant difference is observed in mean VD between glacial and interglacial intervals across the whole record. However, from ~550-225 ka, as mean VD increases, several cycles of valve size correlate with inferred climate. Mean VD does not always capture the intervals with large valves because those same intervals have numerically abundant small valves. Mean diameter of initial valves is largest in peak interglacial intervals (**Fig. 40**).

Morphological Analysis SEM

Morphological characteristics for *Pantocsekiella* valves are highly variable (**Table 3, Figs. 41–70**). Measurements of CD range from 1.5–10.4 µm with a mean of 3.9 µm. The ratio of CD/VD ranges from 0.22–0.74, with a mean of 0.42. The number of striae/10 µm is highly variable with a minimum of 12 striae/10 µm and a maximum of 26 striae/10 µm.

Between these extremes, a majority of striae values reflected the mean of 19 striae/10 µm. The RD ranges from 0.5–5.2 µm, and the ratio of RD/VD ranges from 0.11–0.4 with a mean of 0.23. The number of CF on the valve face also is highly variable 1–33, with a mean of 3.



FIGURES 31–39: Representative light microscopy images of valves from ~230 ka to present. **Figs. 31–33**) The replacement *Pantocsekiella* morphology subsequent to an extreme cold event 214.2 ka (LZ10-65), **Fig. 34**) 159.7 ka (LZ8-67), **Fig. 35**) 128.2 ka (LZ6-130), **Fig. 36**) 24.7 ka (LZ477), **Fig. 37**) 70.2 ka (LZ688), **Figs. 38–39**) 0.075 ka (LZ23)

A total of 33 valves were observed from class 1 in SEM (**Table 3, Figs. 41–46**). Valves in this class have a CD range from 1.5–3.2 µm. The CD/VD ratio ranges from 0.33–0.72, with a mean of 0.48. Valves have 19–26 striae/10 µm, with a mean value of 23 striae/10 µm. The rimoportula is situated between 0.5–1.3 µm away from the valve margin, and the RD/VD ratio ranges from 0.12–0.28 with a mean of 0.22. Valves have 1–4 central fultoportulae, with a majority of valves observed having only one. External valves typically have a flat face with 2–4 depressions (**Figs. 42–43, 46**). Other valves in this size class have a flat face with less distinctive depressions, fovi, and no ornamentation present (**Figs. 41, 45**).

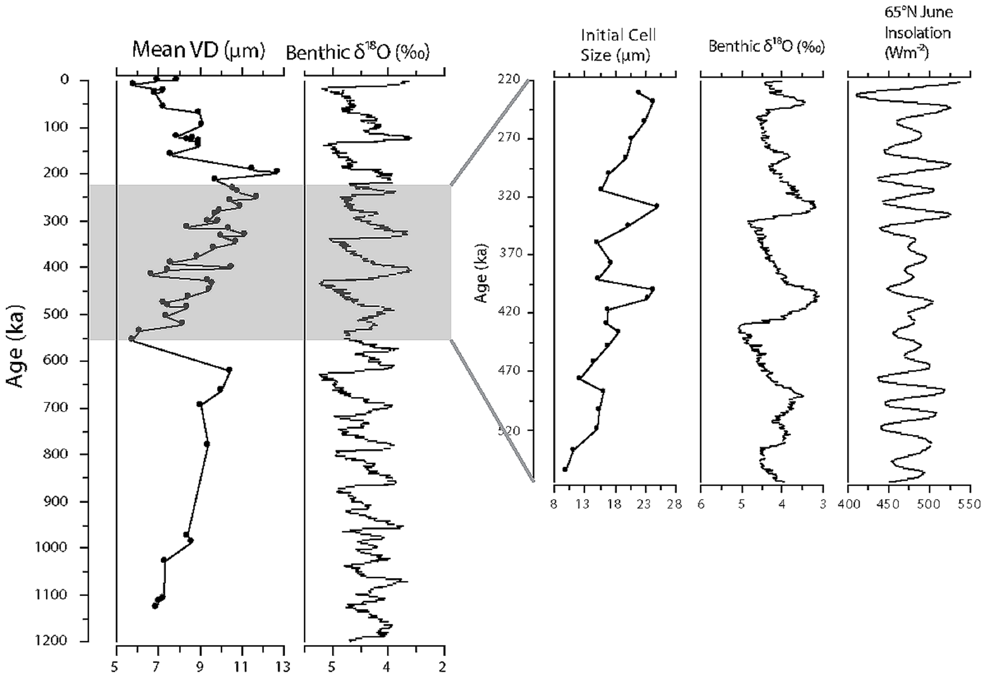
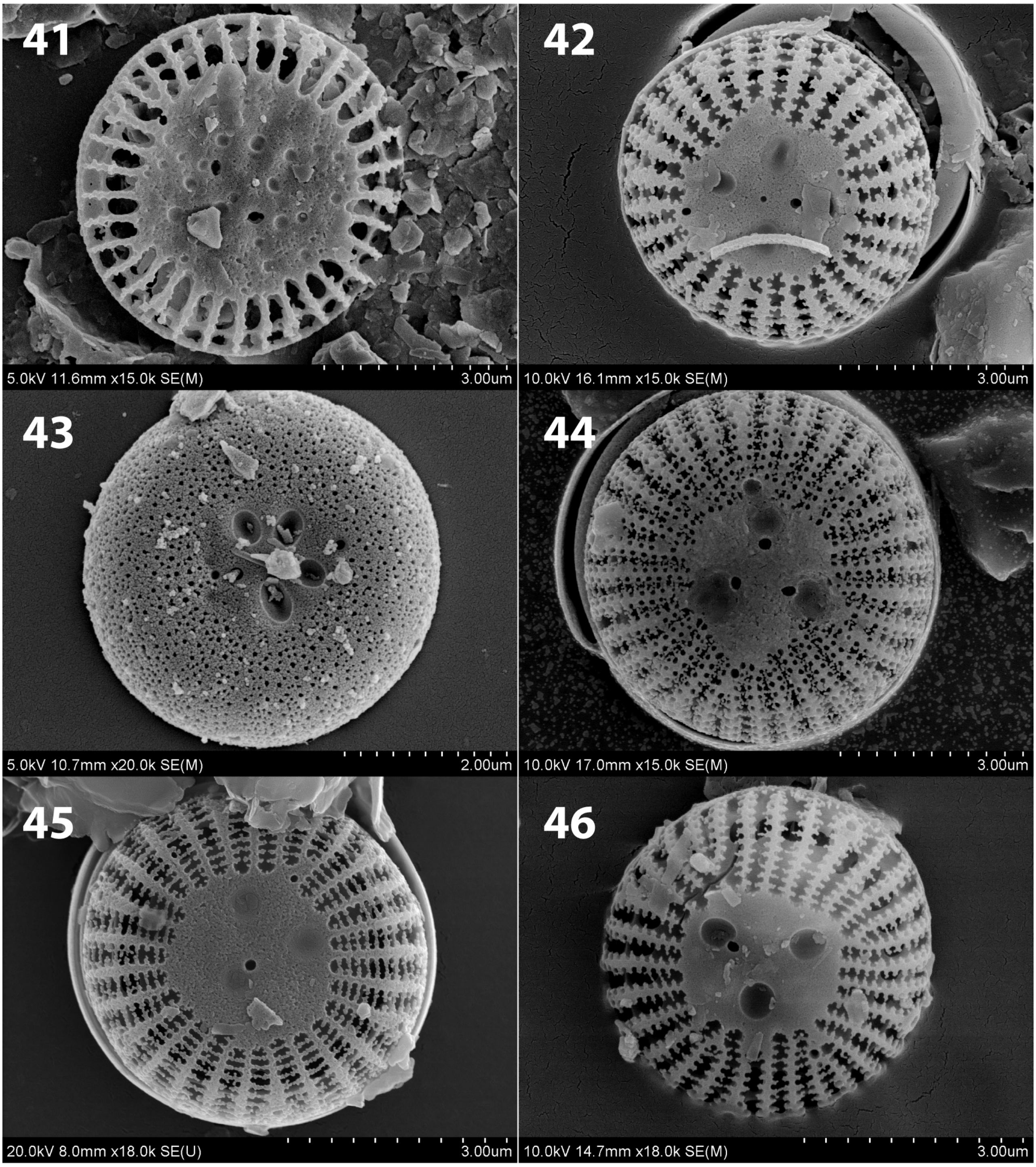


FIGURE 40: (Left) Mean valve diameter (VD) measured in LM and SEM for all valves spanning 1.2 Ma to present plotted next to the marine benthic stack from Lisiecki & Raymo (2005). The gray bar highlights the time between 550 to 220 ka. (Right) Mean initial cell size is plotted with the marine benthic stack and Northern Hemisphere summer insolation (Laskar *et al.*, 2004).

Size class 2 (5–10 µm) consists of 228 valves (**Table 3, Figs. 47–54**). Valves have a CD range from 1.5–6.3 µm. The CD/VD ratio ranges from 0.24–0.74, with a mean of 0.43. Valves have 14–28 striae/10 µm, with a mean value of 19 striae/10 µm. The rimoportula is situated 0.7–3.2 µm away from the valve margin, and the RD/VD ratio ranges from 0.14–0.4, with a mean of 0.23. Valves have 1–10 central fultoportulae; there is a clear temporal split between valves containing 1–2 central fultoportulae from present day to ~160 ka, valves containing >2 central fultoportulae from ~190 ka to ~1.03 Ma, and a return to valves containing 1–3 central fultoportulae from ~1.108-1.2 Ma. Similarly, the number of depressions and the pattern of these features on the valve exhibit corresponding temporal shifts. From present day to ~160 ka valves have 3–6 large depressions (**Figs. 47–48**). From ~190 to ~215 ka valves are flat to colliculate with small depressions (**Figs. 49–50**). From ~238 to ~504 ka valves consistently contain radially oriented 3–6 large depressions or grouped fovi (small depressions) with central fultoportulae situated as groups within the radial depressions (**Figs. 51–52**). Finally, from ~554 ka to ~1.2 Ma valves are flat with few to many fovi (**Figs. 53–54**).

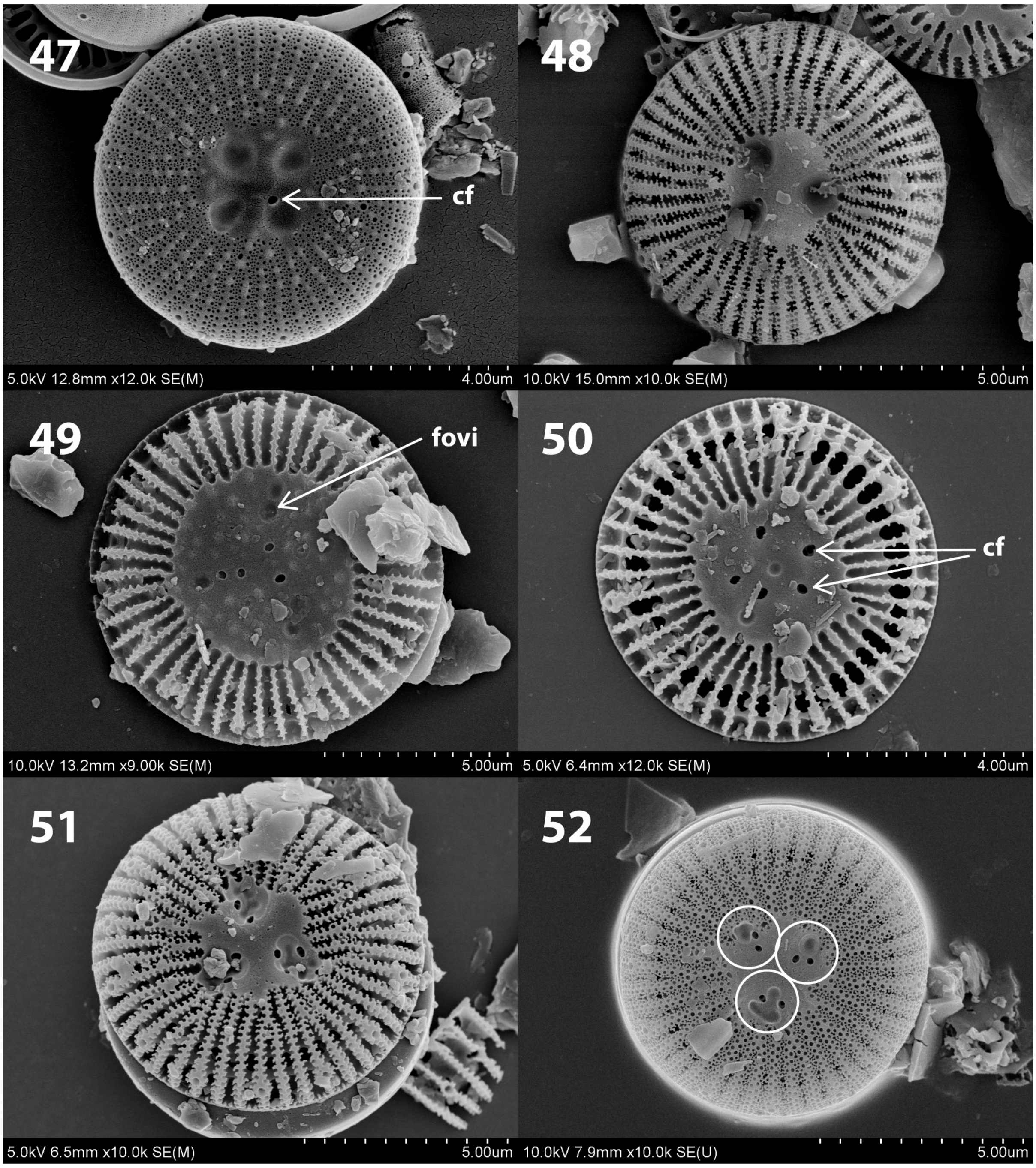
TABLE 3. Summary statistics of quantitative valve characteristics for the *different Panto*csekiella size classes. The mean value is reported for CD/VD, Striae/10 µm, and RD/VD. See Figure 2 for reference.

	CD/VD	**Striae/10 µm**	**RD/VD**	**CF**
Class 1 (3–5 µm)	0.34–0.72 x̄=0.48	19–26 x̄=23	0.12–0.28 x̄=0.22	1–4
Class 2 (5–10 µm)	0.23–0.73 x̄=0.43	14–26 x̄=19	0.13–0.40 x̄=0.23	1–10
Class 3 (10–15 µm)	0.22–0.66 x̄=0.41	13–25 x̄=17	0.11–0.33 x̄=0.23	1–15
Class 4 (>15 µm)	0.28–0.59 x̄=0.41	12–22 x̄=16	0.14–0.31 x̄=0.22	1–22



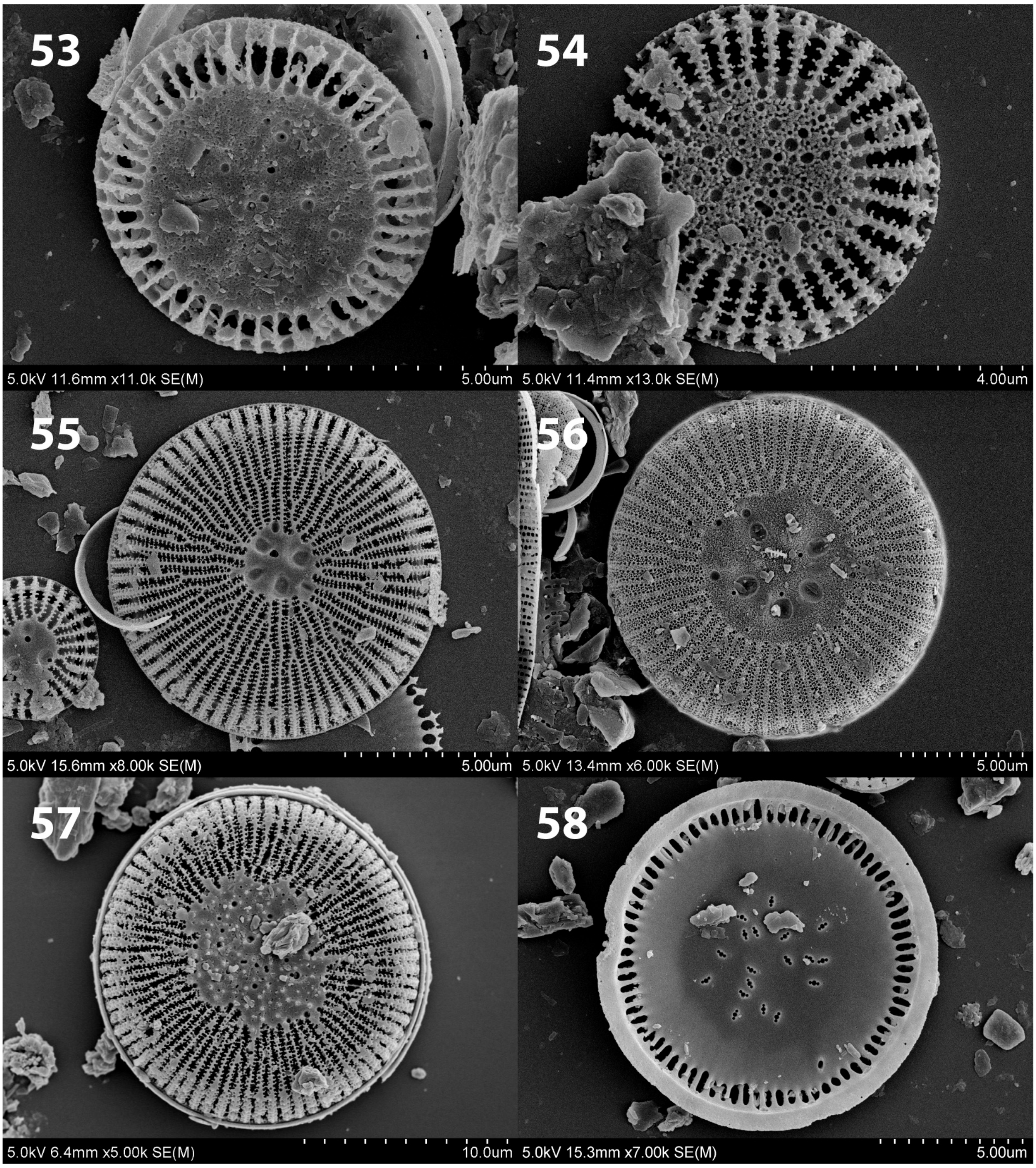
FIGURES 41–46. Representative external valves from size class 1 (3–5 µm). **Fig. 41**) Valve from 1.029 Ma (DC1600) showing numerous fovi and two central fultoportulae (cf), **Fig. 42**) Valve from 952.6 ka (DC1480) showing the rimoportula placement, **Fig. 43**) Valve of *P. elgygytgynensis* from 406.7 ka (DC550) showing the rimoportula placement, , **Fig. 44**) Valve of *P. elgygytgynensis* from 302.5 ka (LZ12-54) showing three depressions and three central fultoportulae, **Fig. 45**) Valve from 119.3 ka (LZ6-60) showing less distinct depressions, and **Fig. 46**) Valve from 8.28 ka (LZ366) showing *P. ocellata* morphology.

Size class 3 (10–15 µm) consists of 110 valves (**Table 3, Figs. 55–64)**). The CD ranges from 2.3–8.9 µm. The CD/VD ratio ranges from 0.22–0.66 with a mean value of 0.41. Striae range from 13–25 in10 µm with a mean of 17 striae in 10 µm. The rimoportula is situated 1.2–4.5 µm away from the valve margin, and the RD/VD ratio ranges from 0.11–0.33, with a mean of 0.23. Valves have 1–15 central fultoportulae; following similar temporal variability to those observed in size class 2 (**Figs. 55–64**). Valves also contain similar depressions and fovi patterns as observed in size class 2 (**Figs. 55–64**).



FIGURES 47–52. Representative external valves from size class 2 (5–10 µm). **Fig. 47**) Valve from 0.075 ka (LZ23) showing one central fultoportula (cf) and flat valve face with four depressions, **Fig. 48**) Valve from 29.12 ka (LZ491) showing flat valve face with three depressions, **Fig. 49**) Valve from 190.5 ka (LZ9-138) showing flat valve face with numerous fovi, **Fig. 50**) Valve from 198.2 ka (LZ9-155) showing flat valve face with five scattered central fultoportulae (cf), **Fig 51**) Valve of *P. elgygytgynensis* from 238.5 ka (LZ10-227), **Fig. 52**) Valve of *P. elgygytgynensis* from 417.4 ka (DC570) with white circles highlighting the clusters of central fultoportulae within the large depressions.

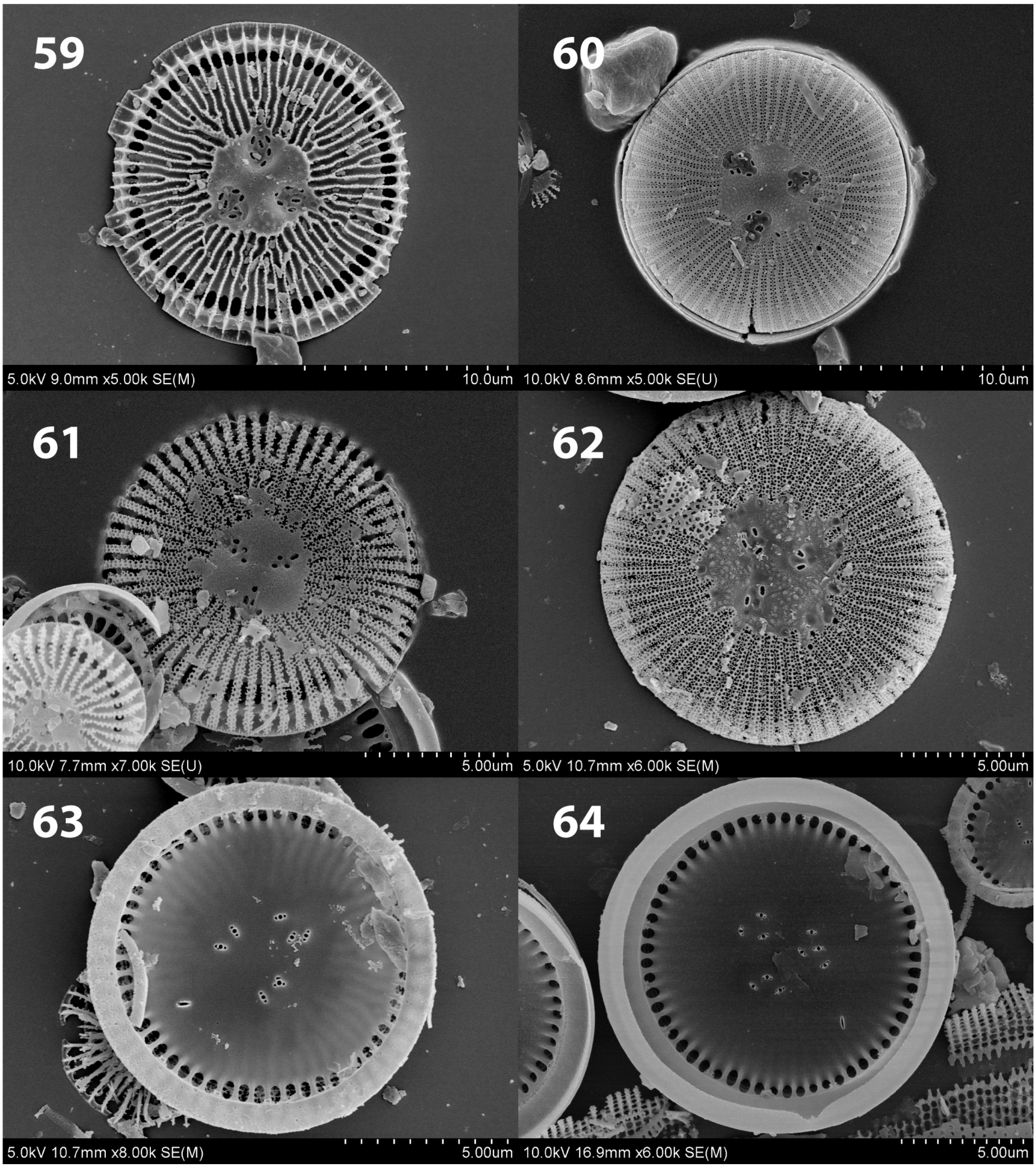
Size class 4 (15–20 µm) have 39 individual valves (**Table 3, Figs. 65–70**). Valves in this size class are observed from ~123 to ~953 ka, and the majority are observed in samples between ~390 to ~450 ka. The CD ranges from 4.4–10.4 µm, and the CD/VD ratio ranges from 0.29–0.6, with a mean of 0.41. The valves contain 12–22 striae/10 µm with a mean value of 16 striae/10 µm. The rimoportula is situated 2.5–5.2 µm away from the valve margin, and the RD/VD ratio ranges from 0.15–0.32, with a mean of 0.21. The central fultoportulae ranges from 1–20; the majority of large valves (20 valves of the 39) contain >10 central fultoportulae. Many small depressions are either randomly distributed across a flat valve face or clumped into groupings within the depressions (**Figs. 65–70**).



FIGURES 53–58. Representative valves from size class 2 (5–10 µm) and size class 3 (10–15 µm). **Fig. 53**) size class 2 external valve from 1.029 Ma (DC1600)showing flat valve face and large central area with many fovi, **Fig. 54**) size class 2 external valve 1126 ka (DC1750) with dissolution, **Fig. 55**) size class 3 external valve from 1.3 ka (LZ31) showing four depressions with small central area, **Fig. 56**) size class 3 external valve 70.2 ka (LZ688) showing five depressions, **Fig. 57**) size class 3 external valve 198.2 ka (LZ9-155) with flat valve face, granules, and scattered central fultoportulae, **Fig. 58**) size class 3 internal valve 214.2 ka (LZ10-65) showing scattered central fultoportulae.

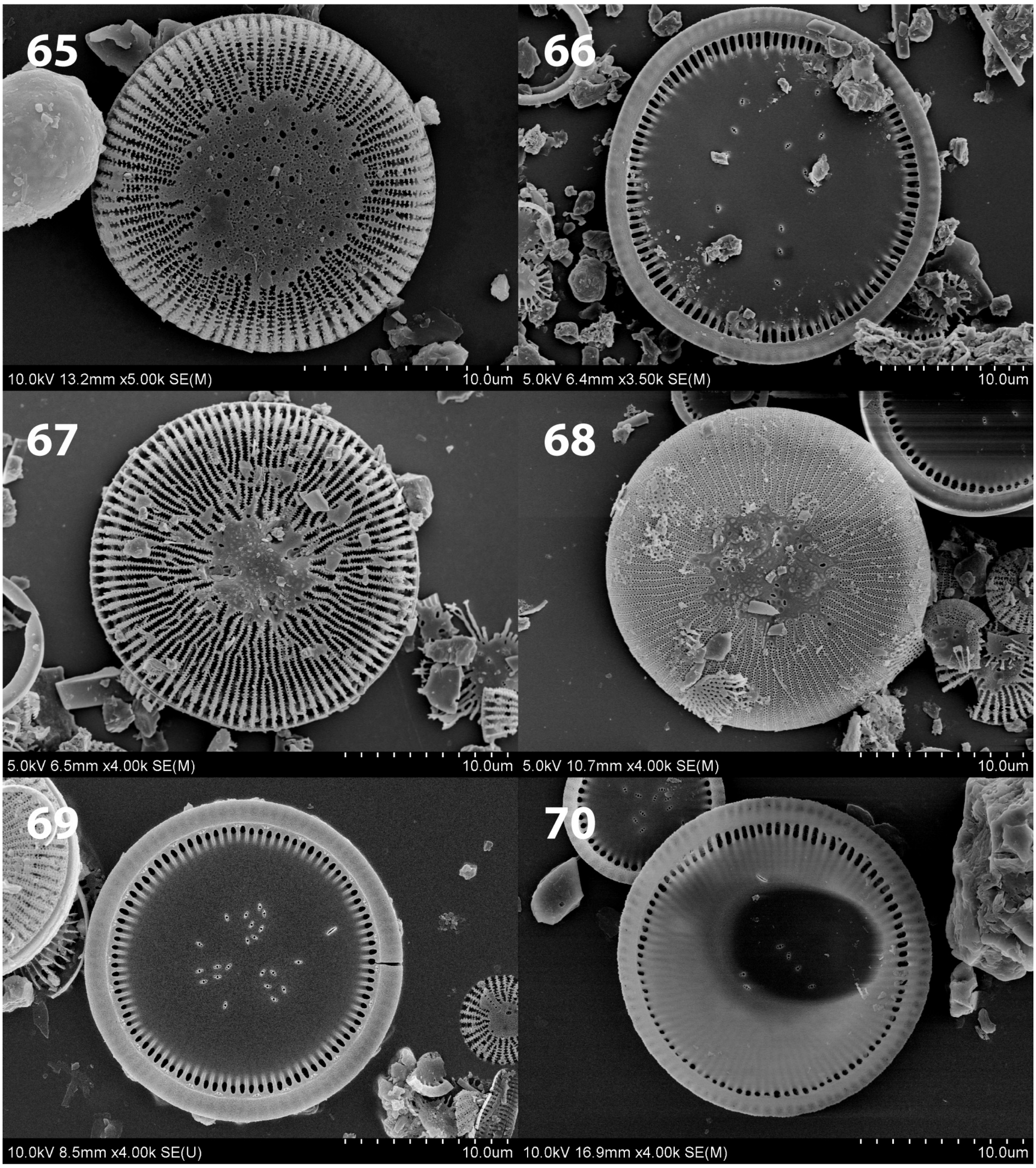
Principal components analysis results

The first two axes of the PCA performed on all valves accounts for 76.6% of the total variance (**Fig. 71A**). PC1 accounts for 53.1% of the total variance and is highly correlated with VD ($r^2 = 0.93$), as well as other size-dependent morphological variables. PC2 accounts for 21.5% of the total variance. This axis is more correlated with size-independent variables such as CD/VD ($r^2 = -0.81$). As expected, there is tremendous scatter and overlap between valve morphologies throughout the entire 1.2 Ma record. Despite this, valves from ~230 to 550 ka cluster more negatively on the PC2 axis.



FIGURES 59–64. Representative valves from size class 3 (10–15 µm). **Fig. 59**) external valve of *P. elgygytgynensis* from 278.8 ka (LZ11-125), **Fig. 60**) external valve of *P. elgygytgynensis* from 333.2 ka (LZ12-176), **Fig. 61**) external valve of *P. elgygytgynensi*s from 484.1 ka (DC680), **Fig. 62**) external valve of *P. elgygytgynensis* from 406.7 ka (DC550), **Fig. 63**) internal valve of *P. elgygytgynensis* from 406.7 ka (DC550), **Fig. 64**) internal valve of *P. elgygytgynensis* from 302.5 ka (LZ12-54).

To evaluate this relationship further, independent of size, an individual PCA was run on each different size class. For our purposes, only size class 2 and 3 are discussed further since a majority of the individuals belonged to these two size classes (**Fig. 71B & C**). The PCA for size class 2 accounts for 66.7% of the total variance (PC1 = 41.1%, PC2 = 25.6%) (**Fig. 71B**). The PC1 axis is correlated to the RD (r^2 = 0.95), the ratio of RD/VD (r^2= 0.66), and the number of striae/10 µm (r^2 = -0.64). Valves from 230-550 ka have a relatively wide scatter on the PC1 axis for size class 2. The PC2 axis is most correlated with the ratio of CD/VD (r^2 = -0.85). As valve size increases, valves observed between 230-550 ka cluster more tightly. For instance, the PCA performed on size class 3, accounts for 69.9% of the total variance (PC1 = 39.3%, PC2 = 30.6%) (**Fig. 71C**). PC1 is also correlated to the number of striae/10 µm (r^2 = -0.71) and the ratio of RD/VD ($r^2 = 0.77$). Valves from 230-550 ka, although still exhibiting some overlap, cluster more tightly together along the PC1 axis consisting of valves with larger RD/VD ratios with a mean of 0.24, which is significantly higher ($p < 0.001$) than valves from present to 220 ka with a mean of 0.20. The PC2 axis, like the results of size class 2, is also correlated to the ratio of CD/VD ($r^2 = -0.84$).



FIGURES 65–70. Representative valves of size class 4 (>15 μm). **Fig. 65**) external valve from 190.5 ka (LZ9-138), **Fig. 66**) internal valve from 198.2 ka (LZ9-155), **Fig. 67**) external valve of *P. elgygytgynensis* from 238.5 ka (LZ10-227), **Fig. 68**) external valve of *P. elgygytgynensis* from 406.7 ka (DC550), **Fig. 69**) internal valve of *P. elgygytgynensis* from 333.2 ka (LZ12-176), **Fig. 70**) *P. elgygytgynensis* initial valve internal view 302.5 ka (LZ12-54).

Qualitatively, valves observed from 230 to 550 ka also exhibit unique characteristics. These are related to the orientation of the depressions and the central fultoportulae compared with *Pantocsekiella* valves found elsewhere in the record. Specifically, valves during this interval have 3–6 orbicular depressions, with up to 22 central fultoportulae grouped within these large depressions. These morphological observations complimented by the PCA results constitute the naming of a new species unique to the Lake El’gygytgyn.

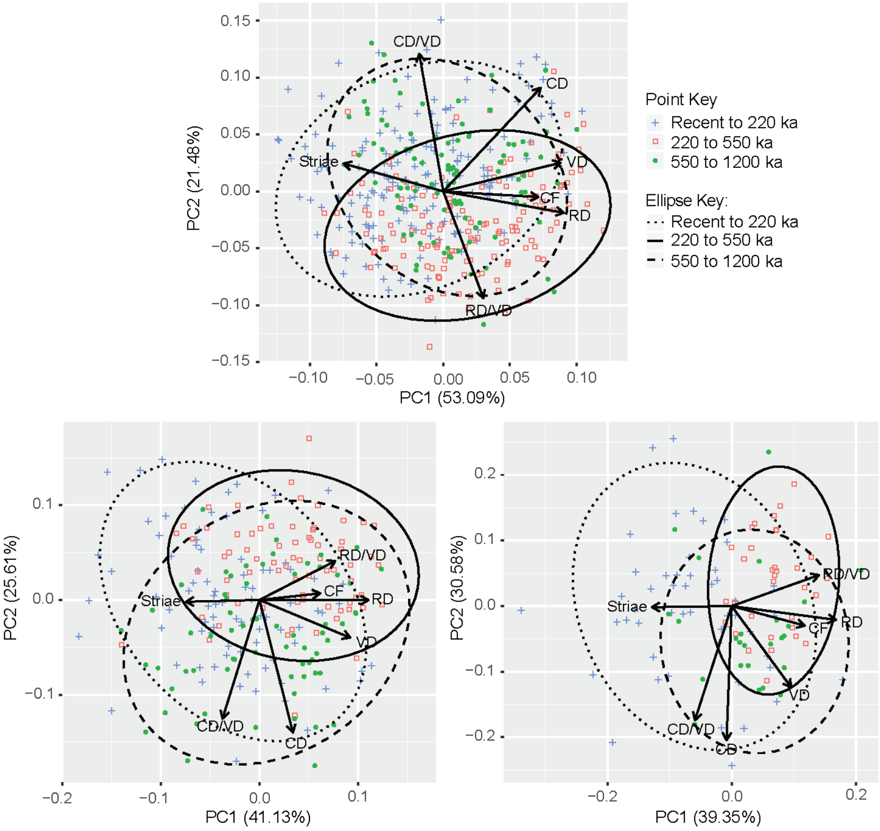


FIGURE 71. Principle components analysis (PCA) biplots of A) all valves, B) size class 2, and C) size class 3. Colors represent valves from a specific time range including green (1.2 to 550 ka), red (550 to 230 ka), and blue (230 ka to present).

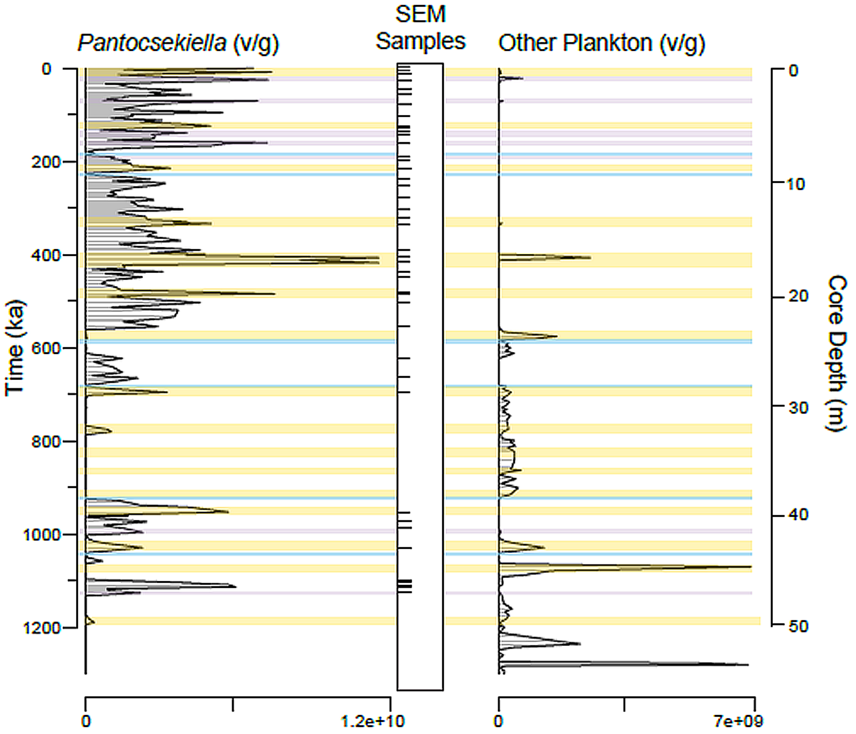


FIGURE 72. Summary figure showing the concentration (valves/gram) of *Pantocsekiella* valves (left) and other plankton (right) in Lake El'gygytgyn through the last 1.2 Ma. SEM samples taken for this study are indicated by the central column. Geochemically (Melles *et al.*, 2012) and diatom abundance (Snyder *et al.*, 2013) inferred climate events in the lake are indicated by the colored lines (yellow = warm productive, purple = cold productive, blue = extreme cold unproductive).

***Pantocsekiella elgygytgynensis* sp. nov.**
Figs. 17–30, 43–44, 51–52, 59–64, 67–70

Description:

Valves circular, valve faces nearly flat. Valve diameter (n = 139): 3.8–21.3 µm in SEM, 3–24 µm in LM. Initial valves dome-shaped, 9–27 µm in diameter (**Figs. 24, 30, 70**). Central area of valve flat to radially undulate, smooth to colliculate. Central area 25–75% of the valve diameter. Radial orbicular depressions 3–6 in number, occasionally with many fovi (small depressions). Central fultoportulae clustered within radial orbicular depressions and fovi. A single rimoportula present near marginal striae, approximately 0.8–5.2 µm from valve margin. Rimoportula distance from the valve margin 15–40% of the valve diameter. Marginal fultoportulae openings visible externally and internally, every 3–6 costae. Striae multiseriate composed of two outer rows of large areolae and 1–3 inner rows of small areolae. Striae density irregular, 12–25 striae /10 µm, with a mean of 18 striae/10 µm. Internally, valve face flat. Central fultoportulae 1–22 in number. Central fultoportulae robust, appearing as short tubules with 2–3 satellite pores. Costae bearing marginal fultoportulae slightly depressed. Internal openings of marginal fultoportulae with 2 satellite pores. The single rimoportulae visible as a sessile labium with a wide slit with variable orientation.

Etymology: The species named here (elgygytgynensis) has only been observed in the Lake El'gygytgyn sedimentological record and is therefore named after the lake.

Type locality: Lake El'gygytgyn, Russia, material from the Lake El'gygytgyn Scientific Drilling Project composite core 5011-1 and LZ1024

Holotype: Composite core 5011-1, sample DC570 (424.1 ka), ANSP GC 36369, slide housed at the Diatom Herbarium, National Academy of Sciences, Drexel University, U.S (**Fig. 19**).

Isotypes: ANSP GC 36370, slide housed at the Diatom Herbarium, National Academy of Sciences, Drexel University, U.S, and CANA 128930, slide housed at the Canadian Museum of Nature, Canada.

Taxonomic notes:

Pantocsekiella elgygytgynensis shares the circular valve shape, the flat valve face, the arrangement and position of the marginal striae, costae, and rimoportula with other members of the *P. ocellata* species complex (**Table 2**). The newly named species is distinct from other members of the *P. ocellata* complex in having up to 22 central fultoportulae that are oriented in radial groups, having a larger range in striae density from 12–25, and marginal fultoportulae on every 3–6 costae.

P. elgygytgynensis appears to be similar to the *P. ocellata* morphology, with a similar size range (5–22 µm for *P. ocellata* and 3–24 µm for *P. elgygytgynensis*), and unequal striae length, a flat smooth to colliculate central area, and 1 rimoportula. However, it differs from *P. ocellata* in the number of striae in 10 µm (14–20 in *P. ocellata* and 12–25 in *P. elgygytgynensis*), fovi grouped within the depressed concentric undulations, a higher number of central fultoportulae (1–5 in *P. ocellata*, and 1–22 in *P. elgygytgynensis*), central fultoportulae grouped in the depressed concentric undulations, and position of the marginal fultoportulae (each 2–5 costae in *P. ocellata* and each 3–6 costae in *P. elgygytgynensis*).

The new species also resembles *P. polymorpha* in that both exhibit radial undulation and a variable number of depressions and fovi. However, the two differ in a number of morphological features. They have different valve sizes (4.5–16 µm in *P. polymorpha* and 4–21 in *P. elgygytgynensis*), a different range of striae in 10 µm (20–24 in *P. polymorpha* and 12–25 in *P. elgygytgynensis*), a higher number of central fultoportulae (1–5 in *P. polymorpha* and 1–22 in *P. elgygytgynensis*), different pattern of the central fultoportulae, and a different position of the marginal fultoportulae (each 2–5 costae in *P. polymorpha* and 3–6 in *P. elgygytgynensis*).

P. tripartita valves exhibit radial undulation, are colliculate, and have a similar valve diameter range to *P. elgygytgynensis* valves. Valves of *P. elgygytgynensis* can be distinguished from *P. tripartita* valves by the absence of triangular punctate fields (present in *P. tripartita*), different number of striae in 10 µm (19–22 in *P. tripartita*, and 12–25 in *P. elgygytgynensis*), a higher number of central fultoportulae (2–3 in *P. tripartita* and 1–22 in *P. elgygytgynensis*), and the position of the marginal fultoportulae (each 5–7 costae in *P. tripartita* and each 3–6 costae in *P. elgygytgynensis*).

Discussion

The present study is the longest analysis of *Pantocsekiella* morphological variability within the Lake El'gygytgyn record, documenting multiple transitions in morphology throughout the last ~1.2 Ma. This study corroborates previous findings (Cremer *et al.*, 2005; Cherepanova *et al.*, 2010; Snyder *et al.* 2013) and the length of the record allows for extensive observations on *Pantocsekiella* morphological evolution and the connection of these changes to known climate (warm-cold) events in the lake. The detailed analysis of morphological traits allows for comparison with other lakes (e.g. Lake Ohrid).

Pantocsekiella valve size fluctuates widely throughout the last 1.2 Ma. One particularly striking observation is the relationship between climate and valve size in the newly proposed *P. elgygytgynensis,* which thrives from 550-230 ka (**Fig. 40**). Specifically, our data suggest that during warm interglacial climate maximum valve size increases, while during cold glacial climate maximum valve size decreases in *P. elgygytgynensis*. Similar results were seen in *Pliocaenicus* (syn. Lindavia) valve size, which was also significantly related to climate in the earlier record from 3.5-2.2 Ma, exhibiting larger valve size during warm interglacials (Phillips, 2013). Diatom valve size can be influenced by a number of environmental factors. For example, planktic diatoms that live in the pelagic zone of lakes are strongly affected by lake mixing regimes, which alters valve buoyancy, nutrient availability, and light availability (Passy *et al.*, 2007; Saros *et al.*, 2012; Spanbauer *et al.*, 2016). One explanation for the relationship between *P. elgygytgynensis* valve size and climate is variability in the extent of the ice-on season in the lake. Interglacial warmth would reduce the length of the ice-on season. Extended open water conditions would facilitate a longer lake-mixing period, sufficient for larger valves to thrive. Glacial cooling would increase the length of the ice-on season, resulting in less lake mixing, and thus creating conditions more conducive for smaller valve sizes. Alternatively, longer open water conditions could influence nutrient availability to the lake, which could also have an influence on valve size with increased nutrient availability yielding increased valve sizes (Hoffman *et al.*, 2002; Litchman *et al.*, 2008).

The trend towards larger valve sizes during inferred warm intervals in the lake is not consistent through time, suggesting that climate is not the only influence on *Pantocsekiella* valve size in the lake. Interspecific competition or niche partitioning between other members of the planktic diatom assemblage may partially explain this observation. For instance, the large *Pliocaenicus* co-occurs with *Pantocsekiella* from 1.2-550 ka and in the more recent history of the lake from ~35 ka to present. The presence of this larger genus may have a limiting effect on the size of the other. In Lake Baikal, investigations on larger *Lindavia baicalensis* (Skvortzov & Meyer 1928: 5) Nakov *et al.* (2015: 254) and smaller *Lindavia minuta* (Skvortzov 1937:305) Nakov *et al.* (2015: 256) found that the timing of their life cycles and peak cell abundances varied, allowing for co-existence and partitioning of resources (Jewson *et al.*, 2015). The increased valve size, and speciation of *P. elgygytgynensis* coincides with an absence of *Pliocaenicus* in the lake, and relatively stable climate conditions absent of cold, sparse diatom events. These favorable environmental conditions, and absence of competition would have allowed the development of large valves, which then reduced after the reestablishment of *Pliocaenicus* in the lake.

Morphological variability independent of size is also evident in Lake El'gygytgyn and appears to be connected to climate. Shifts in *Pantocsekiella* species morphologies are consistently associated with inferred "extreme cold" events in the lake (**Fig. 72**). Extreme cold events are defined by geochemical and sedimentological proxies, as well as an absence or low abundance of diatoms (see Melles *et al.*, 2012; Snyder *et al.*, 2013; Wennrich *et al.*, 2016). *Pantocsekiella* was first introduced to the lake prior to 2.5 Ma. Extreme cold events lead to a decline in the dominant *Pantocsekiella* morphology, allowing for the introduction of new morphologies either from external sources or alternatively from a reemergence of a small local remnant population. Sporadic external introductions are supported by observations of different planktic genera during favorable times co-occurring with the long-lived dominant genera in the lake. At times, introduced *Pantocsekiella* forms may co-occur with morphologies derived from ancient lineages in the lake, suggesting that previously described morphotypes in the recent lake record may actually be multiple co-existing species.

The PCA reveals that size independent variables including the ratio of the central diameter to the total valve face (CD/VD) and the ratio of the distance of the rimoportula from the valve margin to the total valve face (RD/VD) were most influential in differentiating between morphological groups. The distance of the rimoportula from the valve margin has been shown to be an important variable differentiating between centric species in previous research. For instance, the recent separation of the genus *Cyclotella* into *Lindavia* was based on the placement of the rimoportula (Nakov *et al.*, 2015). Similarly, Theriot *et al.* (1987) determined that the rimoportula characteristics represented a natural classification of species between *Cyclotella*, *Cyclostephanos* Round in Theriot *et al.* (1987: 346), and *Stephanodiscus*

(Ehrenberg 1845: 80). Therefore, the rimoportula distance from the margin appears to be an important differentiating feature between species within the Lake El'gygytgyn *Pantocsekiella* population.

Unique morphology has been observed in centric diatoms from other ancient lake systems. In subarctic Lake Baikal, the diatom species *L. baicalensis* reaches valves sizes of 135 µm (Jewson *et al.*, 2015). Lakes Ohrid and Prespa in Macedonia exhibit a wide range of morphologic variability (Cvetkoska *et al.*, 2012) and contain another unique species now named *Pantocsekiella paraocellata* (A.Cvetkoska *et al.* 2014: 317) K.T. Kiss & E. Ács (2016: 68) . *Stephanodiscus yellowstonensis* Theriot et Stoermer (1984: 41) experienced directional evolution from *S. niagarae* (Ehrenberg 1845: 80) coinciding with a shift towards warmer conditions in Yellowstone Lake (Theriot *et al.*, 2006). Similarly, in the high mountain Lake Titicaca the endemic diatom *Cyclostephanos andinus* (Theriot, Carney et Richerson 1985: 383) Tapia, Theriot, Fritz, Cruces et Rivera (2004: 324) experienced valve size fluctuations related to lake environmental variability (Spanbauer *et al.*, 2018). The current polyphyletic nature of cyclotelloid taxa and recent taxonomic revisions suggests that not only a within-lake phylogenetic analysis, but a phylogenetic analysis on all so-called members of cyclotelloid taxa would be beneficial to understand how these valve morphology changes are related to the environment.

Acknowledgements

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