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## Small freshwater thalassiosiroid diatoms from Pleistocene sediments of Pingualuit Crater Lake, northern Québec (Canada), including description of *Cyclotella pingualuitii* sp. nov.

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Arctic and sub-arctic lake sediment sequences from the Pleistocene are uncommon due to multiple glacial–interglacial cycles and the associated advances and retreats of Pleistocene ice sheets. Pleistocene strata are preserved in a 9-m-long sediment core recovered from Pingualuit Crater Lake, Nunavik, northern Québec (Canada). In addition to tycho planktonic *Aulacoseira* species, the Pleistocene planktonic flora comprises representatives from the thalassiosiroid genera *Cyclotella*, *Discostella* and *Puncticulata*, of which most species are extant in perennially ice-free sub-arctic and arctic lakes. One *Cyclotella* species, *C. pingualuitii* is described as new and is characterized by a small central area, multiple central and scattered marginal fuloportulae with triangular satellite pore covers, a single large submarginal rimoportula and alveolate striae of unequal length. *Cyclotella pingualuitii* is the most prominent species during the oldest diatom-rich interval (DR3) recovered, which was deposited during the Late Quaternary (29–36 ky BP). This species has not been observed above 400 cm in Pingualuit Crater Lake sediments, or elsewhere in Pleistocene or Holocene sequences or modern collections, and is considered extinct.

**Keywords:** *Cyclotella*, Pingualuit Crater Lake, Pleistocene, diatom, sub-arctic lakes

### Introduction

Lake sediments in high latitude regions are natural recorders of climate and environmental variability because they preserve archives of past physical and chemical conditions, as well as important biological indicators (Pienitz et al. 2004). Harsh environmental conditions include long winters, low temperatures, short growing periods, extremes in irradiance and low nutrient availability, which lead to low diversity and growth rates of biota (Blake et al. 1992, Smol 1988, Douglas & Smol 1999, Cremer & Wagner 2003). Diatoms (Bacillariophyceae), however, are one of the most diverse and abundant algal groups in arctic and sub-arctic lakes and have been demonstrated to respond quickly and sensitively to environmental change in these extreme environments (Douglas & Smol 2010, Lotter et al. 2010), making them powerful proxies to track past environmental and climate change in these systems. Furthermore, diatoms in lake sediments represent a spatially and temporally integrated sample of in-lake diatom productivity, giving researchers a snapshot of whole-lake biodiversity over time for examining ecological, floristic, taxonomic and systematic research questions (Round et al. 1990, Smol & Stoermer 2010).

Because of multiple ice sheet advances culminating in the Last Glacial Maximum, few Pleistocene sediment sequences are preserved for understanding arctic and sub-arctic lake responses to climate change (Axford et al. 2009). Pingualuit Crater Lake (61°17'N, 73°41'W), also called the 'Crystal Eye of Nunavik' because of its extreme transparency and almost perfectly circular shape, is located in the northernmost part of the Ungava Peninsula in Nunavik, northern Québec. A 9-m core retrieved from Pingualuit Crater Lake in 2007 recovered a full Holocene and Late Pleistocene sequence. An unknown *Cyclotella* species dominated the Late Pleistocene sediments. Here we report on the lake's planktonic flora during the Late Pleistocene, which was dominated by thalassiosiroid genera including *Cyclotella*, *Discostella* and *Puncticulata*, and formally describe one new species as *C. pingualuitii* Black & Edlund sp. nov. Thalassiosiroid diatoms are a common component of modern plankton in high latitude large lakes (e.g., Rühland et al. 2003, Cremer & Wagner 2004), and their relevance to broader ecological, evolutionary and physiological research questions warrants the study of this unique fossil record (Armbrust et al. 2004, Theriot et al. 2006, Alverson et al. 2007).

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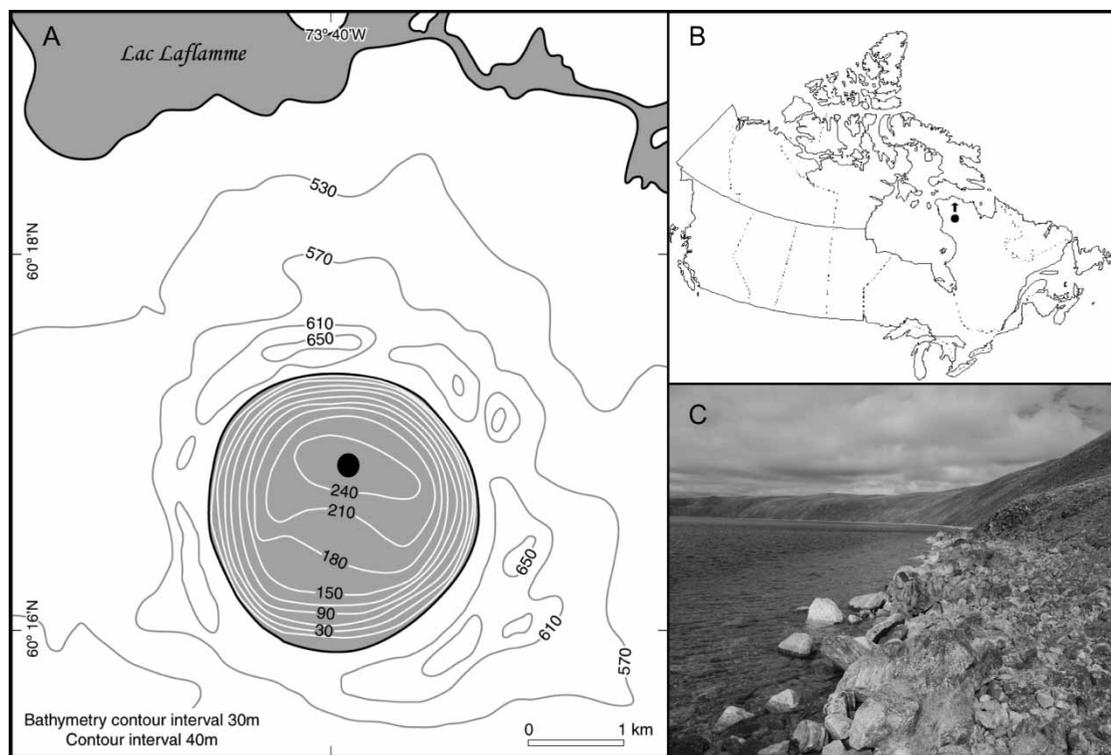
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**Fig. 1.** Pingualuit Crater Lake. (a) Bathymetric maps of Pingualuit Crater Lake adapted from Pienitz *et al.* (2008). Location of 2007 coring site marked with black dot in the deepest part of the lake. (b) Location of Pingualuit Crater Lake in Canada. (c) Photograph from the Pingualuit Crater Lake shoreline illustrating the steep basin walls and boulder terrain (photograph taken August 2010).

### Study area

Pingualuit Crater Lake is located in the Canadian subarctic and is currently ice-free for ca. 4–6 weeks a year in summer (R. Pienitz, pers. comm.). This region has an extreme cold climate with a mean annual air temperature of  $-6.3^{\circ}\text{C}$  (1992–2004 average) reported from Kangiqsuaq ( $61^{\circ}35'\text{N}$ ,  $71^{\circ}55'\text{W}$ ), and a short growing season (Environment Canada National Climate Archive 2005). Pingualuit Crater was the result of a meteorite impact ca. 1.4 million years ago (Ma) as determined by Ar/Ar dating of impactites collected at the site (Grieve *et al.* 1989). The crater is a perfectly circular depression hosting a lake that is currently 246 m deep and 2.7 km in diameter (Bouchard 1989, Grönlund *et al.* 1989, Fig. 1). Pingualuit Crater Lake has an extremely limited littoral zone due to its steep basin walls ( $26\text{--}35^{\circ}$ ) and boulder-strewn slopes. The lake is well-mixed during this ice-free period despite its great depth and can be considered an ultra-oligotrophic and cold-monomictic lake (Ouellet *et al.* 1989, Gantner *et al.* 2011). Pingualuit Crater Lake is one of the softest water environments (average salinity of  $2.070 \pm 0.261 \text{ mg L}^{-1}$ ; conductivity below instrument detection limits of  $20 \text{ mS cm}^{-1}$ ) on Earth and has an extremely deep euphotic zone (1% irradiance) of 115 m under ice-free conditions (Gantner *et al.* 2011).

### Material and methods

A coring expedition in May 2007 recovered 9 m of Pingualuit Crater Lake sediments using an Uwitec per-

cussion piston corer. Three separate diatom-rich intervals (DR1, DR2, DR3) recovered in the 9 m core were located at depths between 0 and 21 cm (DR1), 250 and 273 cm (DR2), and 700 and 800 cm (DR3). These intervals are diatom-rich, light brown in color and are thought to represent seasonally ice-free intervals in the lake's history. Diatom-poor intervals are a contrasting light-grey color, located between the brown diatom-rich levels and likely represent periods of semiperennial to perennial ice cover. DR1 and DR2 sediments have  $^{14}\text{C}$  Accelerator Mass Spectrometry (AMS) dates that correspond to the Holocene, following deglaciation at 6850 cal. yr BP (Bouchard 1989, Bouchard *et al.* 1987, Guyard *et al.* 2011). The DR2 sediments have a conflicting infrared stimulated luminescence (IRSL) age of  $74 \pm 9 \text{ ka BP}$  (Guyard *et al.* 2011). DR3 sediments have  $^{14}\text{C}$  AMS ages ranging between  $29\,280 \pm 630$  and  $35\,670 \pm 810$  cal. yr BP, but have multiple reversals (Guyard *et al.* 2011). Although a definitive age cannot yet be attributed to the oldest sediments recovered from Pingualuit Crater Lake, the sediments that contain the new diatom species *C. pingualuitii* are older than the Holocene deglacial ages published by Bouchard *et al.* (1987), Bouchard (1989) and Guyard *et al.* (2011), based on their stratigraphic position.

Fossil diatoms were subsampled from depths between 0 and 847 cm (subsampled contiguously in the DR3 interval every 0.5 cm between 755 and 774 cm depth) in the sediment cores recovered from Pingualuit Crater Lake. Sediment subsamples of a known volume were prepared

using H<sub>2</sub>O<sub>2</sub> digestion following the large batch waterbath method outlined by Renberg (1990). Samples were then spiked with a known quantity of microspheres for quantitative calculation of diatom concentrations. Aliquots of the samples were evaporated at room temperature on coverslips and then mounted on glass slides using Zrax<sup>®</sup> mounting medium. The diatom species were identified and digitally imaged under 1000× magnification using an oil immersion objective and condenser lens (NA = 1.4) on a Leica DM 2500 or Olympus BX51 microscope with differential interference contrast (DIC) optics. Diatom concentrations were generally low during DR3 and at least 100 diatoms were enumerated per slide. Where diatom concentrations declined (in the lowermost and uppermost portions of DR3 sediments and the surrounding sediment intervals between 400 and 730 cm and between 774 and 847 cm), at least 15 transects were counted per slide. Taxonomic assignments were made using Krammer and Lange-Bertalot (1986, 1988, 1991a, b), Grönlund et al. (1989), Camburn and Charles (2000), Fallu et al. (2000) and Antoniadou et al. (2008). For scanning electron microscopy (SEM), peroxide-cleaned material was first air-dried onto coverslips, which were then attached to aluminum stubs and coated in 20 nm of gold. Material was examined under a 15–20 kV accelerating voltage in a JEOL-JSM-6060LV SEM. Descriptive terminology follows Theriot and Serreyssol (1988).

## Results

The Pingualuit Crater Lake DR3 diatom assemblage comprises at least 118 diatom taxa. Not all the taxa could be identified to species level due to the fragmentary nature of the valves and some minor dissolution. In addition to the planktonic thalassiosiroid flora treated in this article, the DR3 diatom flora contained tychoplanktonic species including *Aulacoseira lirata*, *A. distans* var. *navalis* (W. Smith) Haworth, *Aulacoseira* sp. 2, *A. perglabra* (Østrup) Haworth and *Tabellaria flocculosa*, and small periphytic fragilarioid species (range of 4–25%, average 11%) including *Stauriosirella pinnata* (Ehrenberg) Williams & Round, *Pseudostauriosira pseudoconstruens* (Marciniak) Williams & Round, *P. brevistriata* (Grunow in VanHeurck) Williams & Round, *Stauriosira construens* Ehrenberg and *Stauriforma exiguiformis* (Lange-Bertalot) Flower, Jones & Round. Benthic taxa were rarely present at >1% and included *Achnanthes sensu lato*, *Amphora*, *Brachysira*, *Caloneis*, *Encyonema*, *Diademesis*, *Eunotia*, *Gomphonema*, *Navicula*, *Neidium*, *Nitzschia*, *Pinnularia* and *Tetracyclus* species (Black et al. 2010).

In contrast to many arctic and sub-arctic Pleistocene sequences (Edlund & Stoermer 2000, Cherapanova et al. 2007, Axford et al. 2009, Wilson 2009, Zimmermann et al. 2010), the most prominent taxa in DR3 sediments were planktonic thalassiosiroid species with a relative abundance range of 41–74% and an average abundance of 58%. The thalassiosiroid plankton comprised three taxonomic groups:

the *C. rossii*–*tripartita* complex (Figs 2–4), the *Discostella stelligera*–*pseudostelligera* complex (Figs 5–11) and a new *Cyclotella* species formally described below. *Puncticulata radiosa* (Fig. 12) was also present but very rare in the DR3 sediment sequence.

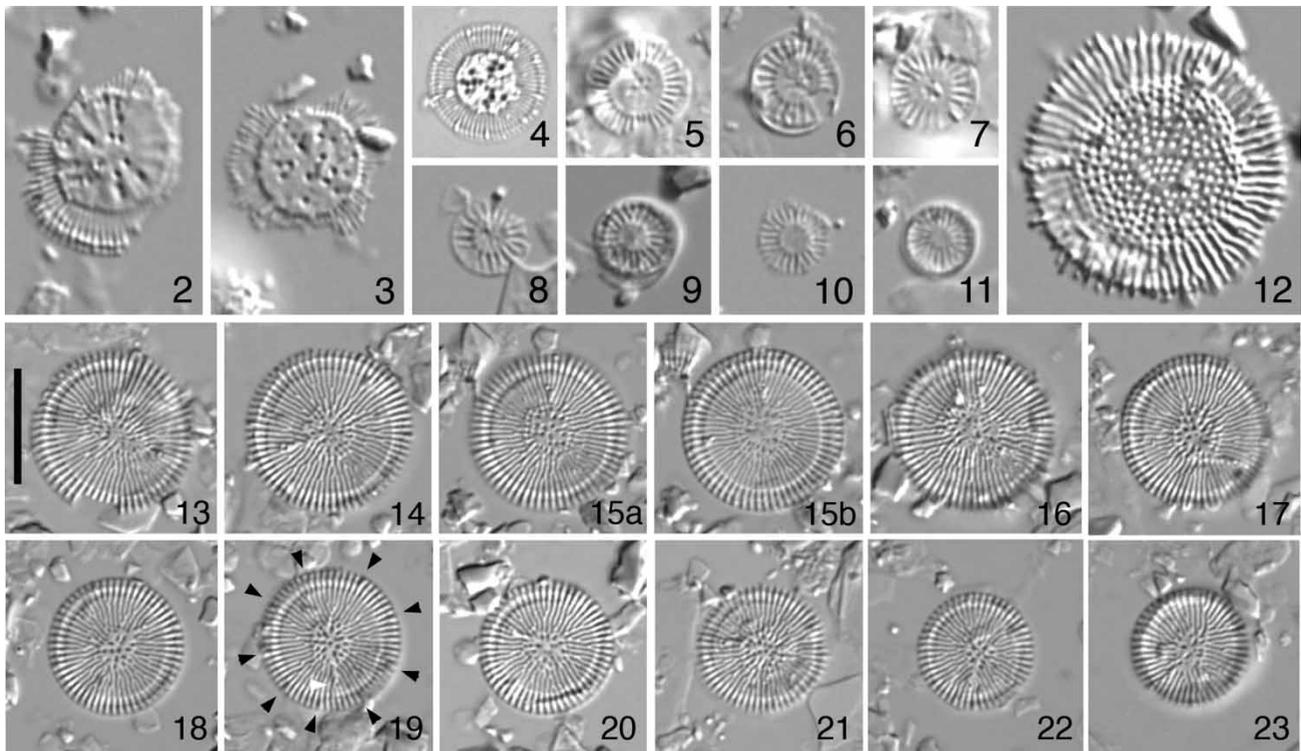
Within the *C. rossii*–*tripartita* complex, two morphotypes were common. Valves corresponding to the description of *C. rossii* varied in diameter from 7.1 to 16.4 µm and were characterized by a flat central area occupying approximately half the valve diameter and ornamented with four to eight radial rows of areolae. The central area is bounded by alveolate striae of equal length, with relatively small internal foramina. Marginal fultoportulae are separated by three to six costae. Valves corresponding to *C. tripartita* had a similar striae and marginal fultoportulae arrangement as *C. rossii*; however, the central area of *C. tripartita*, which occupies approximately half the valve diameter, is organized in six radial sectors with every other sector ornamented with wedge-shaped groups of areolae. *Cyclotella tripartita* had a diameter range of 7.8 to 11.4 µm. Transitional forms and rare specimens that contained valves of both types suggest these two species may represent a morphological continuum.

*Discostella* specimens in Pingualuit Crater Lake sediments from DR3 were present in a small size range (3.6–11.8 µm) and showed morphologies that varied along a continuum from *D. stelligera* forms (Figs 5–6) to *D. pseudostelligera* forms (Figs 7–11) and are treated here as the *D. stelligera*–*pseudostelligera* complex. Central areas on *D. stelligera* forms had short striae loosely arranged in floral patterns and surrounded circumferentially by a broad hyaline zone (Fig. 5), whereas *D. pseudostelligera* forms had central areas with more narrow hyaline zones and were variously ornamented with floral patterns of short striae (Figs 7–9) to lack of central area ornamentation (Figs 10–11).

The most abundant diatom in the lowermost diatom-rich sediments recovered was an undescribed *Cyclotella* taxon, described here as *C. pingualuitii*, with a relative abundance range of 5–67% (average 44%). *Cyclotella pingualuitii* is only found in the sediments between 400 and 847 cm core depth and is most abundant (33–67% relative abundance) in diatom-rich interval DR3 (between 730 and 774 cm depth). *Cyclotella pingualuitii* was not found in the upper core sediments between 0 and 400 cm, including the two more recent diatom-rich intervals DR1 and DR2.

*Cyclotella pingualuitii* Black & Edlund sp. nov.  
(Figs 13–31)

**Description.** Valve circular in outline, diameter 9–21 µm (Figs 13–23). Central part of the valve face slightly concentrically undulate to nearly flat (Fig. 24). Central area occupies one-third the diameter of the valve face (Figs 13–23). Anastomosing and dichotomously branching radial alveolate striae are of unequal length with some extending



**Figs 2–23.** Light micrographs of representatives of DR3. Pleistocene planktonic diatom flora from Pingualuit Crater Lake. **Figs 2–4.** Morphological and size variation within the *C. rossii*–*tripartita* complex including *C. rossii* forms (Figs 2–3) and *C. tripartita* forms (Fig. 4). **Figs 6–11.** Morphological and size variation within the *D. stelligera*–*pseudostelligera* complex including *D. stelligera* forms (Figs 5–6) and *D. pseudostelligera* forms (Figs 7–11). **Fig. 12.** *Puncticulata radiosa*. **Figs 13–23.** Size diminution series of *C. pingualuitii* type material. **Fig. 15.** Holotype specimen. (15a) High focus on central and marginal areas of holotype specimen. (15b) Mid-focus on marginal alveolae of holotype specimen. **Fig. 19.** Marginal fultoportulae (black arrowhead) visible around valve margin, single rimoportula located mid-radius (white arrowhead). Scale bar = 10  $\mu\text{m}$  (Fig. 13).

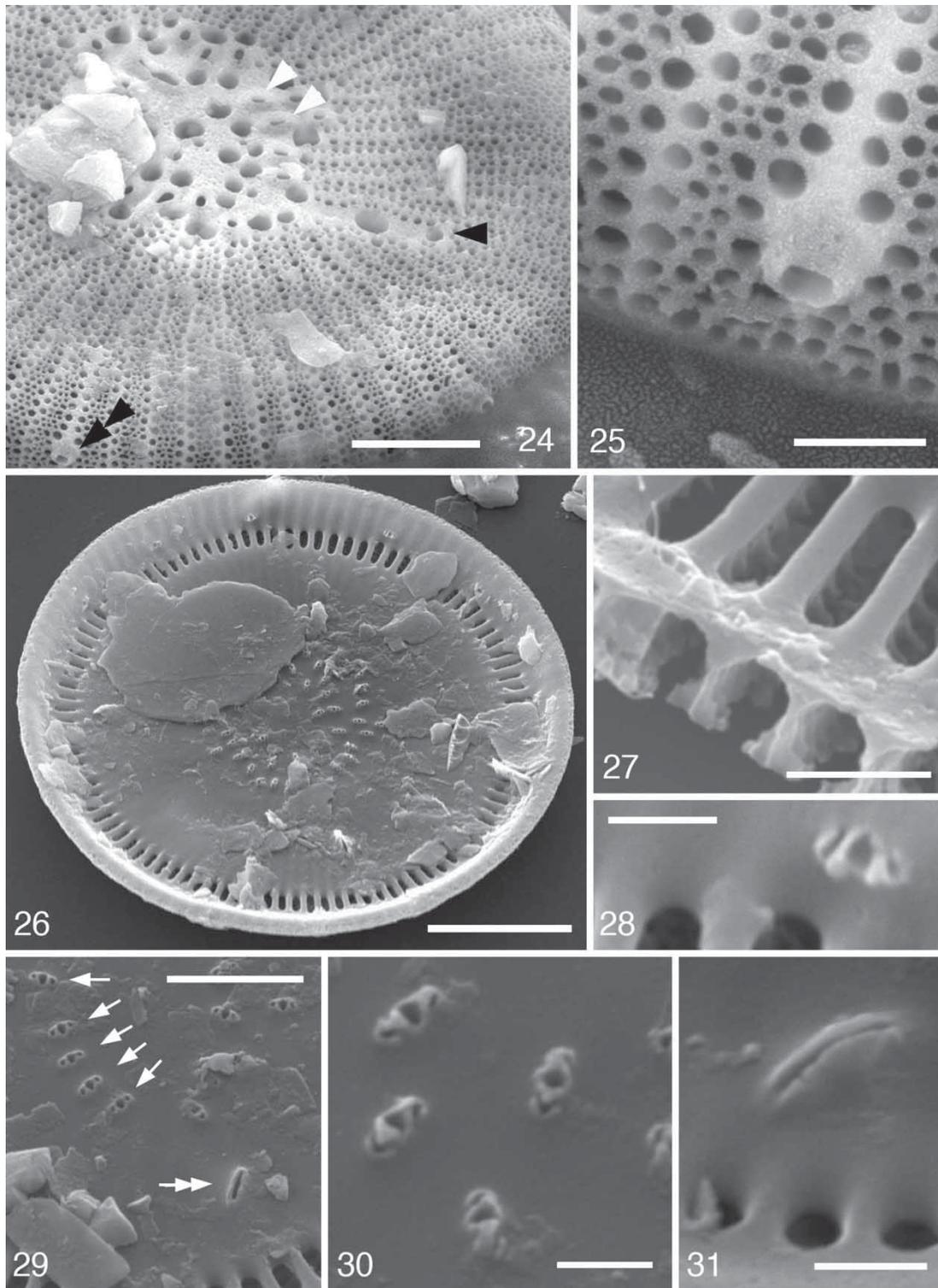
deep into the central zone and sometimes arranged in radial sectors (Figs 13–23). The alveolate marginal area has 11–17 (19) alveolae in 10  $\mu\text{m}$ , each consisting of three to five rows of areolae only loosely arranged in radial striae (Figs 11–24). Alveolae are separated by slightly elevated interstriae on the valve exterior with somewhat larger areolae bordering each interstria (Figs 24–25). Most interstriae/costae split into two or more branches on the valve face with shorter striae/costae between the primary and secondary branches of the interstriae (Figs 13–23). Alveolae open internally through oval to circular foramina separated by internal primary costae (Figs 26–27). Marginal fultoportulae are located on every fifth to tenth internal primary costa (Figs 18, 24–26). Marginal fultoportulae have short tube-like external openings arranged along a costa (Fig. 25) and internally have two satellite pores that are oriented circumferentially and rimmed by short raised cowlings (Fig. 28). The central tube splits internally and terminates in two, laterally oriented, triangular satellite pore covers (Fig. 28). The central area has 9–61 central fultoportulae aligned in loose radial rows (Figs 24, 26). Central strutted processes each have two satellite pores mostly oriented radially and rimmed by short raised cowlings (Figs 29–30). The external opening of each central fultoportula is a simple unornamented radially elongated pore (Fig. 24). The central tube of each

central fultoportula splits internally and terminates in two, radially oriented, triangular satellite pore covers (Fig. 30). A single rimoportula is located at the end of a shortened alveolus in the striated portion of the valve face, approximately halfway between the valve margin and the central area (Figs 26, 31). Internally, the rimoportula is a sessile labium variously oriented from radially to tangentially (Fig. 31); external opening is a simple unornamented pore (Fig. 24).

*Holotype.* Here designated as the circled specimen on the microscope slide marked GC59954, deposited at the Academy of Natural Sciences, Philadelphia, Pennsylvania, USA (ANSP) and illustrated in Fig. 15.

*Isotypes.* Here designated as the specimens on a microscope slide deposited at ANSP (GC58955), a slide deposited at the Canadian Museum of Nature (CANA 84189) and a slide deposited in the Edlund collection (Science Museum of Minnesota, MBE2121)

*Type material.* Cleaned and freeze-dried sediment of Pingualuit Crater Lake core sample 160 from core PING-PC-1-8 deposited at ANSP GCM4836, CANA 84189 and the Science Museum of Minnesota (MBE2121).



**Figs 24–31.** SEM images of *C. pingualuitii*. **Fig. 24.** External valve view of central area with scattered fultoportulae openings (white arrowheads), scattered occluded areolae, striated marginal area with opening of rimoportula (black arrowhead) and mantle with marginal fultoportulae openings (double arrowhead). **Fig. 25.** Mantle region of Fig. 24 showing external opening of a marginal fultoportula with short tube. **Fig. 26.** Internal valve view. **Fig. 27.** Internal view of broken marginal region showing alveolar structure with internal and marginal lamina, oval internal foramen and cross-section of alveolae. **Fig. 28.** Internal expression of marginal fultoportulae with short cowlings over satellite pores and split tube with laterally expanded triangular satellite pore covers. **Fig. 29.** Internal view of central area with a single rimoportula (double arrow) and scattered radially oriented central fultoportulae (arrows). **Fig. 30.** Internal view of central fultoportulae with short cowlings over satellite pores and split tube with radially expanded triangular satellite pore covers. **Fig. 31.** Internal view of sessile rimoportula that is oriented subradially. Scale bars = 2 μm (Figs 24, 29), 0.5 μm (Figs 25, 28, 30, 31), 5 μm (Fig. 26) and 1 μm (Fig. 27).

*Type locality.* Lacustrine sediments from Pingualuit Crater Lake, Nunavik, Québec, Canada (61°17'N, 73°41'W) at a core depth 765 cm below the sediment–water interface from core PING-PC-1-8, sample 160, coll: R. Pienitz, S. Hausmann, G. St-Onge, V.-P. Salonen and R. Niederreiter, May 2007.

*Etymology.* The specific epithet refers to Pingualuit Crater Lake.

*Geological range.* Unknown first occurrence but extinct in Late Pleistocene.

*Diagnosis.* *Cyclotella pingualuitii* is allied with a group of *Cyclotella* species that share a flat central area, multiple central fuloportulae with two satellite pores, a single sessile rimoportula located on the valve face, and broadly spaced marginal fuloportulae with two circumferentially oriented satellite pores that are positioned on primary costae outside the alveolar foramina. This group of taxa includes *C. kuetzingiana* Thwaites, *C. kuetzingiana* var. *radiosa* Fricke, *C. rossii* Håkansson, *C. polymorpha* Meyer & Håkansson, *C. ocellata* Pantocsek, *C. wuethrichiana* Druart & Straub, *C. delicatula* Hustedt and *C. andancensis* Ehrlich (Table 1), of which several taxa were sympatric with *C. pingualuitii*.

*Cyclotella kuetzingiana* (Syn: *C. krammeri* Håkansson 1990) (Håkansson 1990a, b) differs from *C. pingualuitii* as the former has a larger central area, more regular branching of the interstriae, more closely spaced marginal fuloportulae and very small, if any, triangular extensions on the satellite pore covers (Houk *et al.* 2010). *Cyclotella kuetzingiana* var. *radiosa* shares a similar arrangement of loose radial rows of central fuloportulae and triangular satellite pore covers with *C. pingualuitii*, but differs in its more closely spaced marginal fuloportulae, wider central area and more regular striae pattern (Houk *et al.* 2010). *Cyclotella rossii* has a wider central area, fewer central fuloportulae and only weakly branched striae compared with *C. pingualuitii*. *Cyclotella polymorpha* has complex branching of its striae, but differs from *C. pingualuitii* because it has a broader central area and fewer central fuloportulae. *Cyclotella ocellata* has only one to four central fuloportula, may have multiple rimoportulae in larger specimens and its well-spaced marginal fuloportulae are placed at the abvalvar edge of the alveolar foramina (Håkansson & Regnell 1993, Tanaka 2007, Houk *et al.* 2010). In contrast to *C. ocellata*, the marginal fuloportulae are positioned well outside the ring of alveolar foramina in *C. pingualuitii*. *Cyclotella tripartita* is smaller than *C. pingualuitii*, has a radially sculpted central area and has only one to three central fuloportulae. *Cyclotella wuethrichiana* is smaller than *C. pingualuitii*, and its rimoportula is often positioned on a costa (Houk *et al.* 2010). *Cyclotella delicatula* has dichotomously branched striae of unequal length and some valves

have a very small central area, but *C. delicatula* differs from *C. pingualuitii* by having only one (rarely none) central fuloportula. Although not known in the SEM, *C. andancensis*, which was described from French Miocene deposits by Ehrlich (1966), bears a strong resemblance to *C. pingualuitii* with its similar size, striae patterns and small central area. However, *C. andancensis* has a slightly eccentric central area and few obvious central fuloportulae; a more detailed study with the SEM is warranted.

As with most centric diatoms (Theriot 1988), morphological variation within the new diatom species *C. pingualuitii* is strongly size- or diameter dependent. The diameter of the *C. pingualuitii* cell is significantly correlated with the number of central strutted processes ( $r^2 = 0.78$ ), the central area diameter ( $r^2 = 0.73$ ) and the density of the costae ( $r^2 = 0.73$ ; Fig. 32).

## Discussion

Due to the erosional effects of multiple ice sheet advances, few sediment sequences have been preserved that offer the possibility to study Pleistocene plankton diversity and ecology in arctic and sub-arctic lakes or lake response to environmental and climate drivers. On Baffin Island (Nunavut, Canada), several sites with Pleistocene sediments have been investigated. Zimmermann *et al.* (2010) examined sediments associated with forest–tundra deposits and reported a tundra flora typically associated with low pH systems. Briner *et al.* (2007) proposed a mechanism for preserving sediments through multiple interglacials in arctic lakes and Axford *et al.* (2009) analyzed sediments from one of those sites on Baffin Island. Lake CR8 preserves sediments from at least three interglacials covering 200 ka, but in contrast to Pingualuit Crater Lake, the planktonic flora during the Pleistocene at Lake CR8 varies between a *Fragilaria* and an *Aulacoseira* flora common to modern, relatively shallow, arctic and sub-arctic lakes. Wolfe *et al.* (2000) found a similar flora in the Pleistocene sediments of another Baffin Island upland basin.

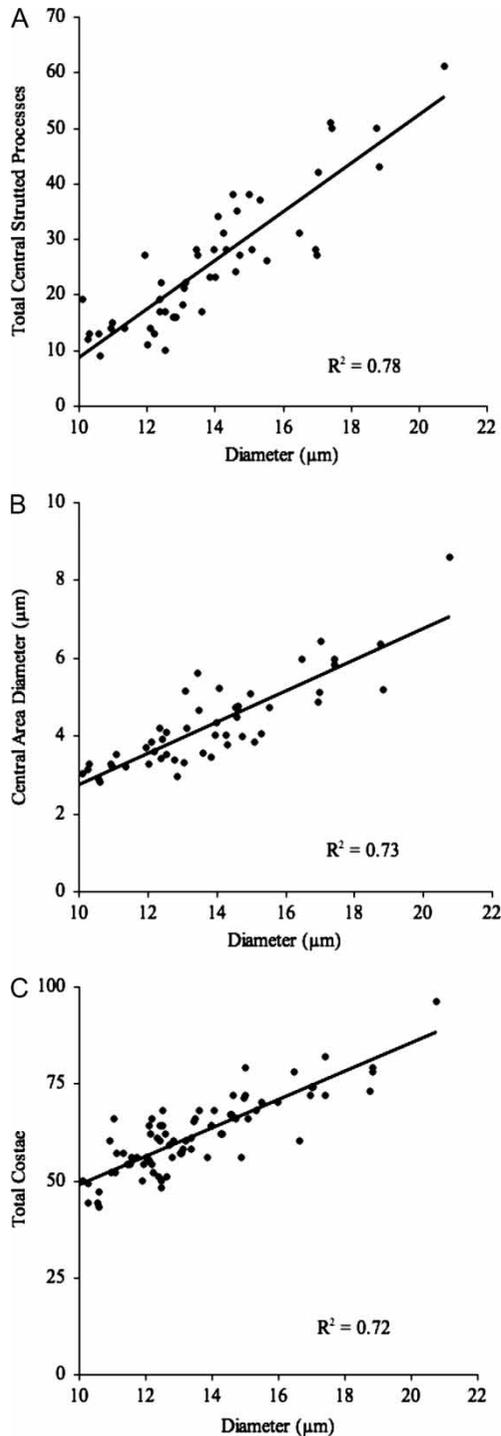
To find larger and deeper high latitude lakes with sediment records extending to the Pleistocene and potential analogues of Pingualuit Crater Lake, other crater and rift lakes must be considered. Lake Baikal's Pleistocene flora is dominated by endemic *Cyclotella*, *Stephanodiscus* and *Aulacoseira* species, and has no modern or Pleistocene analogues (Edlund & Stoermer 2000, Khursevich *et al.* 2001). Lake El'gygytyn is a crater lake located at 67°N in north-eastern Siberia and preserves a sediment record potentially extending back 3.5 Ma. Paleocological analysis of sediments from the last 250 ka show interglacials dominated by the *C. ocellata* species complex with Holocene sediment codominated by *Pliocaenicus costatus* (Cherapanova *et al.* 2007).

The *C. ocellata* species complex is common in the plankton of many modern temperate to arctic oligotrophic lakes and is widely regarded to have highly

**Table 1.** Observed morphological variation in *Cyclotella pingualuitii* compared with related centric diatom species.

Genus	<i>Cyclotella pingualuitii</i> <sup>a</sup>	<i>Cyclotella rossii</i> Håkansson <sup>a</sup>	<i>Cyclotella tripartita</i> Håkansson <sup>a</sup>	<i>Cyclotella krammeri</i> Håkansson	<i>Cyclotella ocellata</i> Pantocsek	<i>Cyclotella kuetzingiana</i> Thwaites	<i>Cyclotella kuetzingiana</i> v. <i>radiosa</i> Fricke	<i>Cyclotella wuethrichiana</i> Druart & Straub	<i>Cyclotella delicatula</i> Hustedt	<i>Cyclotella andancensis</i> Ehrlich
Reference	This study (Pingualuit Crater Lake)	Håkansson (1990a), Houk et al. (2010)	Håkansson (1990b, 2002)	Håkansson (1990a)	Houk et al. (2010)	Houk et al. (2010)	Houk et al. (2010)	Houk et al. (2010)	Houk et al. (2010)	Ehrlich (1966)
Diameter (µm)	9–21	5–18	2–18	8–40	5–22	8–45	8–45	3.5–6.5	4–15	8–16
Central area diameter (µm)	3.0–8.6	–	–	–	–	1/2 to 1/3 diameter	1/2 to 1/3 diameter	1/2 to 3/5 diameter	2/3 of diameter	1.6–3.2
Central area description	Slightly undulate to flat	Flat, 2–5 radial striae, colliculate	Radially undulate, 6-sectored	Slightly undulate to flat	Flat, 3(–6) balls and depression	Slightly transversely undulate to flat	Slightly transversely undulate to flat	Slightly undulate to flat colliculate	Slightly undulate to flat colliculate	Excentric
Total costae	43–96	–	–	–	–	–	–	–	–	–
Costae per 10 µm	11–17 (19)	16–18	19–22	12–18	14–20	12–18	12–14	18–26	16–20	14–16
No. rimoportulae, location	1, at end of short striae	1, at end of short striae	1, near openings of alveolae	1?	1 (usually)	1 (at least) to 3	1, close to edge of central area	1, on costa near margin	1 in striated area	?
No. central fulvo-portulae	9–61; in loose radial rows	2–3 (5)	1–3	3–5	1–4 (5)	1–5 (7)	Many, radially arranged	1, near valve center	1 (0), near center, opposite rimoportule	?
Marginal fulvoportula position	On costa, abvalvar to foramen	On costa, at outside edge of foramen	On costa, at outside edge of foramen		On costa, abvalvar to foramen	On costa, abvalvar to foramen	On costa, abvalvar to foramen	On costa, at outside edge of foramen	On costa, at outside edge of foramen	?
No. satellite pores on marginal fulvoportulae	2	2	2	2?	2	2	2	2	2	?
No. costae separating marginal fulvoportulae	5–10	2–3 (5)	(3) 4–6		2–5	2–4 (5)	2–4 (5)	3–6	(3) 4–5 (6)	4–5

Note: <sup>a</sup>Diatom species found in Pingualuit Crater Lake sediments.



**Fig 32.** Morphological binary plots of Pinguait Crater Lake *C. pingualuitii*. Linear regression lines (black) are shown for each plot together with their associated  $r^2$  values. (a) Total central strutted processes (fultoportulae) vs. valve diameter, (b) central area diameter vs. valve diameter, (c) total costae vs. valve diameter.

variable morphology both within and among populations. Forms have been variously classified as *C. ocellata*, *C. rossii*, *C. kuetzingiana*, *C. tripartita*, *C. comensis* and *C. ocellata-arctica* across regions, within individual lake histories, within collections and within heterovalvar

frustules (Kling & Håkansson 1988, Wunsam *et al.* 1995, Kiss 1996, Hegewald & Hindakova 1997, Cremer *et al.* 2001, Cremer & Wagner 2004, Cremer & Van de Vijver 2006, Cherepanova *et al.* 2010). Variability within these *Cyclotella* species has been hypothesized to reflect variation due to life history and ontogeny (Edlund *et al.* 2003), ecomorphological variability (Wunsam *et al.* 1995, Cremer *et al.* 2001), or evolutionary responses to climate change (Cherepanova *et al.* 2010).

In Pinguait Crater Lake sediments, the *C. rossii*–*tripartita* complex and the *D. stelligera*–*pseudostelligera* complex both showed continuous morphological variability making it difficult to clearly separate each complex's forms during counts. In sections of the core where the forms were separately tallied, forms within each complex showed concurrent variability in their relative abundances and thus we treat them here as the *D. stelligera*–*pseudostelligera* complex and the *C. rossii*–*tripartita* complex. Rühland *et al.* (2003) came to a similar conclusion regarding the *D. stelligera*–*pseudostelligera* complex in their analysis of surface-sediment diatoms from sub-arctic Canadian lakes. Cremer *et al.* (2001) identified a morphological continuum within the *C. rossii*–*tripartita* complex in a study of the sediment record from a Greenland lake. Few studies have been able to confidently separate these forms, which has limited their modern and paleoindicator value at the species level.

In contrast to these temporally (Julius 2000) and geographically widespread taxa that are common throughout much of the Pinguait Crater Lake sediment, *C. pingualuitii* is present only in Pinguait's Pleistocene sediments. This species has not been reported in the few known high latitude Pleistocene lake and wetland sequences (McLaughlin & Stone 1986, Wolfe *et al.* 2000, Cherepanova *et al.* 2007, Axford *et al.* 2009, Zimmermann *et al.* 2010) or in Holocene or recent collections from the arctic and sub-arctic (Pienitz & Smol 1993, Cremer *et al.* 2001, Fallu *et al.* 2002, Rühland *et al.* 2003, Cremer & Wagner 2004, Cremer & Van de Vijver 2006 and others). We therefore consider *C. pingualuitii* extinct; however, we recognize that future discovery and analysis of other Pleistocene lake sediments that experienced seasonal ice-free conditions may reveal additional distributions of *C. pingualuitii*.

The genus *Cyclotella* has long been recognized as an unnatural group and both phylogenetic and phenetic efforts have tried to ascertain relationships among 'Cyclotella *sensu lato*' species (Julius 2000, Håkansson 2002, Houk & Klee 2004, Alverson *et al.* 2007, among others). Among *Cyclotella sensu lato*, *C. pingualuitii* is closely allied with a group of taxa that share characters of a flat central area, multiple central fultoportulae with two satellite pores, a single sessile rimoportula located on the valve face, and broadly spaced marginal fultoportulae with two circumferentially oriented satellite pores that are positioned on primary costae outside the alveolar foramina. This group of species includes commonly recognized *Cyclotella* species such as *C. kuetzingiana* and varieties *C. ocellata*,

*C. tripartita* and *C. rossii*, as well as poorly known species such as the Miocene fossil *C. andancensis* (Ehrlich 1966). Although few of its allies, nor *C. pingualuitii*, have been included in phylogenetic analyses, Julius (2000) gathered evidence for a monophyletic clade containing *C. ocellata*, *C. michiganiana*, *C. ornata* and *C. pseudocomensis*; it is this clade where we believe *C. pingualuitii* would be placed. Julius (2000) further suggested that to address the current non-monophyletic state of *Cyclotella sensu lato*, several clades, including the *C. ocellata* clade, were deserving of generic recognition, a task we will leave to those taxonomists treating a larger number of *Cyclotella* species.

Because *C. pingualuitii* is an extinct taxon, knowledge of its ecology must remain speculative. However, certain inferences can be made by examining the general ecological preferences of *Cyclotella* and *Discostella* species complexes in arctic/sub-arctic lakes and within the context of the diatom populations that existed concurrently with *C. pingualuitii*. Smol et al. (2005) in a survey of 55 circumpolar arctic lake records spanning the last ca. 150 years, found large increases in planktonic *Cyclotella* species in response to lengthening of the summer growing season, which results in reduced ice cover and/or enhanced thermal stratification due to climate warming (Sorvari et al. 2002, Rühland et al. 2003). The *Cyclotella* and *Discostella* species complexes present in the DR3 sediments are similarly thought to represent open-water conditions when they are the dominant genera, precluding the existence of an ice sheet covering the lake during DR3 or perennial ice cover. As lake ice cover is reduced, wind circulation creates environments that favor open-water centric planktonic diatoms (i.e., thalassiosiroid species). Assuming that modern species–environment relationships can be used as an analogue for the past, the *Cyclotella* and *Discostella* species that codominate the DR3 with *C. pingualuitii* likely reflect a deep, circumneutral, oligotrophic lake with near annual open-water conditions in the summer.

*Cyclotella pingualuitii* also has potential biostratigraphic significance in the Pingualuit Crater Lake sedimentary record. Future work in Pingualuit Crater Lake will likely target the recovery of a longer sediment record and *C. pingualuitii* may prove to be an index species for a particular stratigraphic range. Khursevich et al. (2001) similarly described extinct *Cyclotella* species from Lake Baikal sediments that had specific stratigraphic ranges with narrow age intervals. These *Cyclotella* species were designated index species for diatom zonation in the Lake Baikal sedimentary record for the last 5 Ma and are thought to be linked with large shifts in Pliocene–Pleistocene climate (Khursevich et al. 2001). In a similar manner, the extinction of *C. pingualuitii* after the DR3 interval may prove to have implications for determining climatic forcing mechanisms in this region of the arctic.

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