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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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 tychoplanktonic 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 fultoportulae 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 (Armburst et al. 2004, Theriot et al. 2006, Alverson et al. 2007).

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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 °C (1992–2004 average) reported from Kangiqsujuaq (61°35′N, 71°55′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 (26–35°) 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 ± 0.261 mg L⁻¹; conductivity below instrument detection limits of 20 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 percussion 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 ¹⁴C 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 ± 9 ka BP (Guyard et al. 2011). DR3 sediments have ¹⁴C AMS ages ranging between 29 280 ± 630 and 35 670 ± 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$_2$O$_2$ 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 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 Antoniades 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 Serieyssol (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. *nivalis* (W. Smith) Haworth, *Aulacoseira* sp. 2, *A. perglabra* (Ostrup) Haworth and *Tabellaria flocculosa*, and small periphytic fragilarioid species (range of 4–25%, average 11%) including *Brachysira pseudostelligera* 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). Anastamosing 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 μm (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 μm, 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, radially 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 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 taxa includes Cyclotella kuetzingiana Thwaites, Cyclotella kuetzingiana var. radiosa Fricke, Cyclotella rossii Hákransson, Cyclotella polymorpha Meyer & Hákransson, Cyclotella ocellata Pantocsek, Cyclotella wuethrichiana Drur & Straub, Cyclotella delicatula Hustedt and Cyclotella andancensis Ehrlich (Table 1), of which several taxa were sympatric with Cyclotella pingualuitii.

Cyclotella kuetzingiana (Syn: Cyclotella kuetzingiana var. radiosa Fricke, Cyclotella rossii Hákransson, Cyclotella polymorpha Meyer & Hákransson, Cyclotella ocellata Pantocsek, Cyclotella wuethrichiana Drur & Straub, Cyclotella delicatula Hustedt and Cyclotella andancensis Ehrlich) (Håkansson 1990a, b) differs from Cyclotella pingualuitii as the former has a larger central area, more regular branching of the interstriae, more closely spaced marginal fultoportulae 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 fultoportulae and triangular satellite pore covers with Cyclotella pingualuitii, but differs in its more closely spaced marginal fultoportulae, wider central area and more regular striae pattern (Houk et al. 2010). Cyclotella rossii has a wider central area, fewer central fultoportulae and only weakly branched striae compared with Cyclotella pingualuitii. Cyclotella polymorpha has complex branching of its striae, but differs from Cyclotella pingualuitii because it has a broader central area and fewer central fultoportulae. Cyclotella ocellata has only one to four central fultoportulae, may have multiple rimoportulae in larger specimens and its well-spaced marginal fultoportulae are placed at the abvalvar edge of the alveolar foramina (Hákransson & Regnell 1993, Tanaka 2007, Houk et al. 2010). In contrast to Cyclotella ocellata, the marginal fultoportulae are positioned well outside the ring of alveolar foramina in Cyclotella pingualuitii. Cyclotella tripartita is smaller than Cyclotella pingualuitii, has a radially sculpted central area and has only one to three central fultoportulae. Cyclotella wuethrichiana is smaller than Cyclotella 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 Cyclotella delicatula differs from Cyclotella pingualuitii by having only one (rarely none) central fultoportula. Although not known in the SEM, Cyclotella andancensis, which was described from French Miocene deposits by Ehrlich (1966), bears a strong resemblance to Cyclotella pingualuitii with its similar size, striae patterns and small central area. However, Cyclotella andancensis has a slightly eccentric central area and few obvious central fultoportulae; a more detailed study with the SEM is warranted.

As with most centric diatoms (Theriot 1988), morphological variation within the new diatom species Cyclotella pingualuitii is strongly size- or diameter dependent. The diameter of the Cyclotella 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’gygytgyn is a crater lake located at 67°N in northeastern Siberia and preserves a sediment record potentially extending back 3.5 Ma. Paleoecological analysis of sediments from the last 250 ka show interglacials dominated by the Cyclotella species complex with Holocene sediment codominated by Pliocaenicus costatus (Cherapanova et al. 2007).

The Cyclotella 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.

<table>
<thead>
<tr>
<th>Genus</th>
<th><em>Cyclotella pingualuitii</em>&lt;sup&gt;a&lt;/sup&gt;</th>
<th><em>Cyclotella rossii</em> Håkansson&lt;sup&gt;a&lt;/sup&gt;</th>
<th><em>Cyclotella tripartita</em> Håkansson&lt;sup&gt;a&lt;/sup&gt;</th>
<th><em>Cyclotella krammeri</em> Håkansson&lt;sup&gt;a&lt;/sup&gt;</th>
<th><em>Cyclotella ocellata</em> Pantocsek</th>
<th><em>Cyclotella kuetzingiana</em> Thwaites</th>
<th><em>Cyclotella kuetzingiana v. wuethrichiana</em> Fricke</th>
<th><em>Cyclotella wuethrichiana</em> Druart &amp; Straub</th>
<th><em>Cyclotella delicatula</em> Hustedt</th>
<th><em>Cyclotella andancensis</em> Ehrlich</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diameter (μm)</td>
<td>9–21</td>
<td>5–18</td>
<td>2–18</td>
<td>8–40</td>
<td>5–22</td>
<td>8–45</td>
<td>8–45</td>
<td>3.5–6.5</td>
<td>4–15</td>
<td>8–16</td>
</tr>
<tr>
<td>Central area diameter (μm)</td>
<td>3.0–8.6</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1/2 to 1/3 diameter</td>
<td>1/2 to 1/3 diameter</td>
<td>1/2 to 3/5 diameter</td>
<td>2/3 of diameter</td>
<td>1.6–3.2</td>
</tr>
<tr>
<td>Central area description</td>
<td>Slightly undulate to flat</td>
<td>Flat, 2–5 radial striae, colliculate</td>
<td>Radially undulate, 6-sectored</td>
<td>Slightly undulate to flat</td>
<td>Flat, 3(–6) balls and depression</td>
<td>Slightly transversely undulate to flat</td>
<td>Slightly transversely undulate to flat</td>
<td>Slightly undulate to flat colliculate</td>
<td>Slightly undulate to flat colliculate</td>
<td>Excentric</td>
</tr>
<tr>
<td>Total costae</td>
<td>43–96</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Costae per 10 μm</td>
<td>11–17 (19)</td>
<td>16–18</td>
<td>19–22</td>
<td>12–18</td>
<td>14–20</td>
<td>12–18</td>
<td>12–14</td>
<td>18–26</td>
<td>16–20</td>
<td>14–16</td>
</tr>
<tr>
<td>No. rimoportulae, location</td>
<td>1, at end of short striae</td>
<td>1, at end of short striae</td>
<td>1, near openings of alveolae</td>
<td>1?</td>
<td>1 (usually)</td>
<td>1 (at least) to 3</td>
<td>1, close to edge of central area</td>
<td>1, on costa near margin</td>
<td>1 in striated area</td>
<td>?</td>
</tr>
<tr>
<td>No. central fulto-portulae</td>
<td>9–61; in loose radial rows</td>
<td>2–3 (5)</td>
<td>1–3</td>
<td>3–5</td>
<td>1–4 (5)</td>
<td>1–5 (7)</td>
<td>Many, radically arranged</td>
<td>1, near valve center</td>
<td>1 (0), near center, opposite rimoportule</td>
<td>?</td>
</tr>
<tr>
<td>Marginal fultoportula position</td>
<td>On costa, abvalvar to abarval foramen</td>
<td>On costa, at outside edge of foramen</td>
<td>On costa, at outside edge of foramen</td>
<td>On costa, abvalvar to foramen</td>
<td>On costa, abvalvar to foramen</td>
<td>On costa, abvalvar to foramen</td>
<td>On costa, at outside edge of foramen</td>
<td>On costa, at outside edge of foramen</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>No. satellite pores on marginal fultoportulae</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>?</td>
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</tbody>
</table>

Note: *Diatom species found in Pingualuit Crater Lake sediments.*
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 Pingualuit 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–psuedostelligera* 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 Pingualuit Crater Lake sediment, *C. pingualuitii* is present only in Pingualuit’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 zonations 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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