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Morphology of some fossil lacustrine centric species from the western United States assigned to the genus *Cyclotella* (Bacillariophyta), including four described as new

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Abstract

During consideration of fossil centric diatoms from a variety of non-marine localities in the western USA, we encountered four new species and two previously known taxa that should be assigned to the genus *Cyclotella* (F.T. Kützing) A. de Brébisson. We detail the morphological features of these species, and discuss their relevance to other members of the *Cyclotella*. These fossil species are studied in light and scanning electron microscopes, and can be assigned to several morphological groups with respect mainly to the structure of alveolae as well as positon(s) of rimoportula(e) and marginal fultoportulae. Presence of loculate areolae with internal domed cribra and external foramina, or both areolae and valve face fultoportulae in the central area are characteristics found in all of these *Cyclotella* taxa.

Introduction

The diatom genus *Cyclotella* (F.T. Kützing) A. de Brébisson (1838: 19) has been investigated intensively with light and scanning electron microscopy, Gaul *et al*. (1993) and Henderson and Reimer (2003) document investigations with electron microscopy on over 165 species, in over 200 papers, were published on the genus until 2003. Many of the authors who examined multiple species of *Cyclotella* noted the diversity of forms, and suggested informal morphological groups (e.g. Lowe 1975; McFarland & Collins 1978; Seriyiessol 1981; Servant-Vildary, 1986; Loginova, 1990). These works identified a set of criteria on which to establish morphological groups, including presence and spacing of marginal fultoportulae, presence and spacing of valve face fultoportulae, presence and number of rimoportulae, presence of spines, other special features such as granulae and the structure and distribution of striae and alveolae. Loginova (1990) identified 12 morphological groups based on 7 features.

Description of many new taxa have increased our knowledge of the diversity of *Cyclotella* (e.g. Jousé & Mukhina 1978; Chen & Zhu 1985; Kling & Håkansson 1988; Loginova 1989; Kozyrenko et al. 1992; Khursevich et al. 2001; Prasad & Nienow 2006; Khrusevich & Kociolek 2008). More recently, additional works have proposed new taxa based on this morphological diversity of forms for species assigned originally to *Cyclotella,* and genera such as *Pliocaenicus* Round & Håkannson (1992: 116); *Tertiarius* Håkannson & Khursevich (1997: 21) (Khursevich & Kociolek 2002)*, Puncticulata* Håkannson (2002: 21, 112) and *Discostella* Houk & Klee (2004: 204–205) were created for taxa previously assigned to *Cyclotella*.

Investigations of fossil material from Europe (Serieyssol 1981; Servant-Valdary 1986), Asia (Khursevich et al. 2001; Tanaka 2007) and western North America (Hanna 1932; Khursevich & Kociolek 2008) suggest the diversity of species assigned to *Cyclotella* is well represented in the stratigraphic record, extending from the Middle Eocene (Wolfe & Siver 2009), with a great radiation of species in the Pliocene. Many of the

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morphological (not necessarily phylogenetic) groups that have been recognized have representatives, or are known exclusively, by fossil taxa.

In this report we describe new species that would, in the current understanding of the genus, be referred to *Cyclotella* (*sensu* Houk et al. 2010). We compare these new species with previously described taxa, and comment on the morphological groups that have been identified within *Cyclotella*.

Methods and Materials

Our observations are based on primarily on diatomites housed at the Diatom Collection of the California Academy of Sciences (CAS). We took raw material and mixed it with distilled water, and settled and air-dried the slurry onto coverslips. The dried material was permanently mounted onto microscope slides with Naphrax and viewed with a Leica DMRB light microscope with 100X, 1.4NA , DIC optics. For SEM, the dried material was mounted onto aluminum stubs, sputter coated with gold-palladium, and observations were made with Leo 1450VP. Samples are archived at the Diatom Collection of the California Academy of Sciences, San Francisco.

Material used in this study included:

USA. Kansas: Wallace County, Diatom marl from center Sec. 11, T.11S., R38W, Marshall Ranch, North Fork Smoky Mill River, Ogallala Formation. *CAS Accession Number 2383*. This is the type material studied by Hanna (1932).

USA. Idaho: Payette County, north bank of Willow Creek, 20 km NE on Willow Road from its intersection with Idaho highway 52, near center sec. 4, T.8N., R.2W., coll. S. Van Landingham. Diatomite is from Poison Creek Formation in the lower portion of Idaho Group, age approximately 11 to 12 mya. Unaccessioned material at the Diatom Collection of CAS.

USA. Oregon: Christmas Valley, Fort Rock, OD Sections 7.9 m (Kociolek Collection at COLO Accession Number 0502) and 8.3 m (Kociolek Collection at *COLO Accession Number 0503a*) (Colbath & Steele 1982).

USA, Oregon: Klamath County, Sprague River, Drews Road, *CAS Accession Number 701883, Slide Number 1026029*. Oregon: Klamath County, NE Sprague River Bridge, *CAS Accession Number 600180*.

USA. Oregon: Klamath Co., Forest Road, No. 3683-A, 6.6 miles W of Beatty, N of highway 140. *CAS Accession Numbers 600120, 600121, 600122, Slide Numbers 436069, 436070, 436071, 436072, 436073, 436074*.

USA. Idaho: Owyhee County, USGS Diatom Locality 5244, Chalk Hills Formation (*CAS Accession Number 602190, Slide Number 381069*),

Results

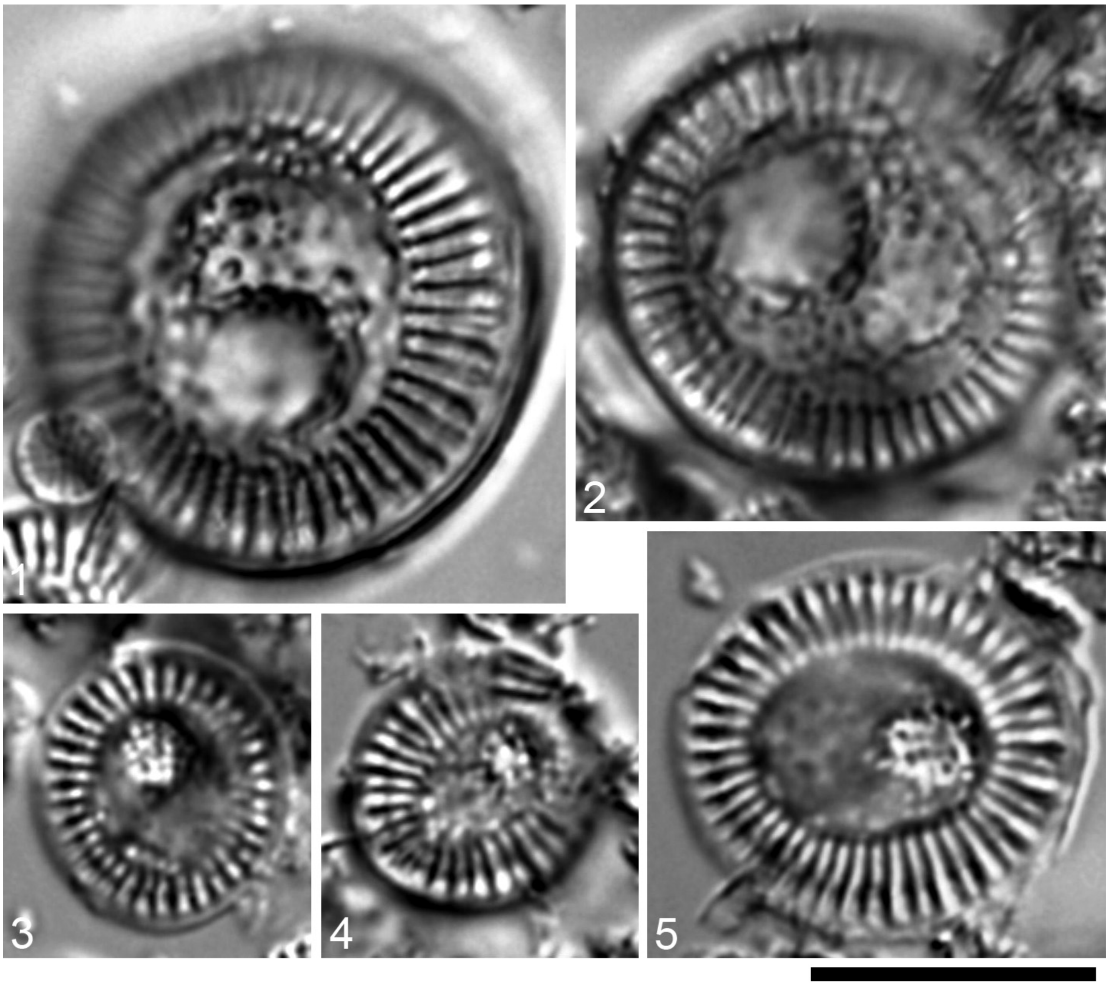
New species descriptions, observations and nomenclatural transfers

Division **Bacillariophyta**
Class **Coscinodiscophyceae** F.E. Round & R.M. Crawford in Round *et al.* 1990 emend. Medlin & Kaczmarska 2004
Order **Thalassiosirales** Glezer & Makarova 1986
Family **Thalassiosiraceae** Lebour 1930
Genus ***Cyclotella*** (Kützing) Brébisson 1838

Cyclotella idahica Khursevich & Kociolek, *sp. nov.* (Figures 1–9)

Type:—USA. Oregon: Christmas Valley, Fort Rock, 44° 10' N, 121° 48' W, OD Section 7.9 m (see Colbath & Steele 1982), diatomite, collected summer 1981 (Circled specimen (Fig. 2) on *Slide 019002*, material *Kociolek Collection 0502* (COLO!), **holotype, designated here**; duplicate slide of *COLO 019002* deposited in Khursevich Collection, Minsk, Belarus, **isotype, designated here**).

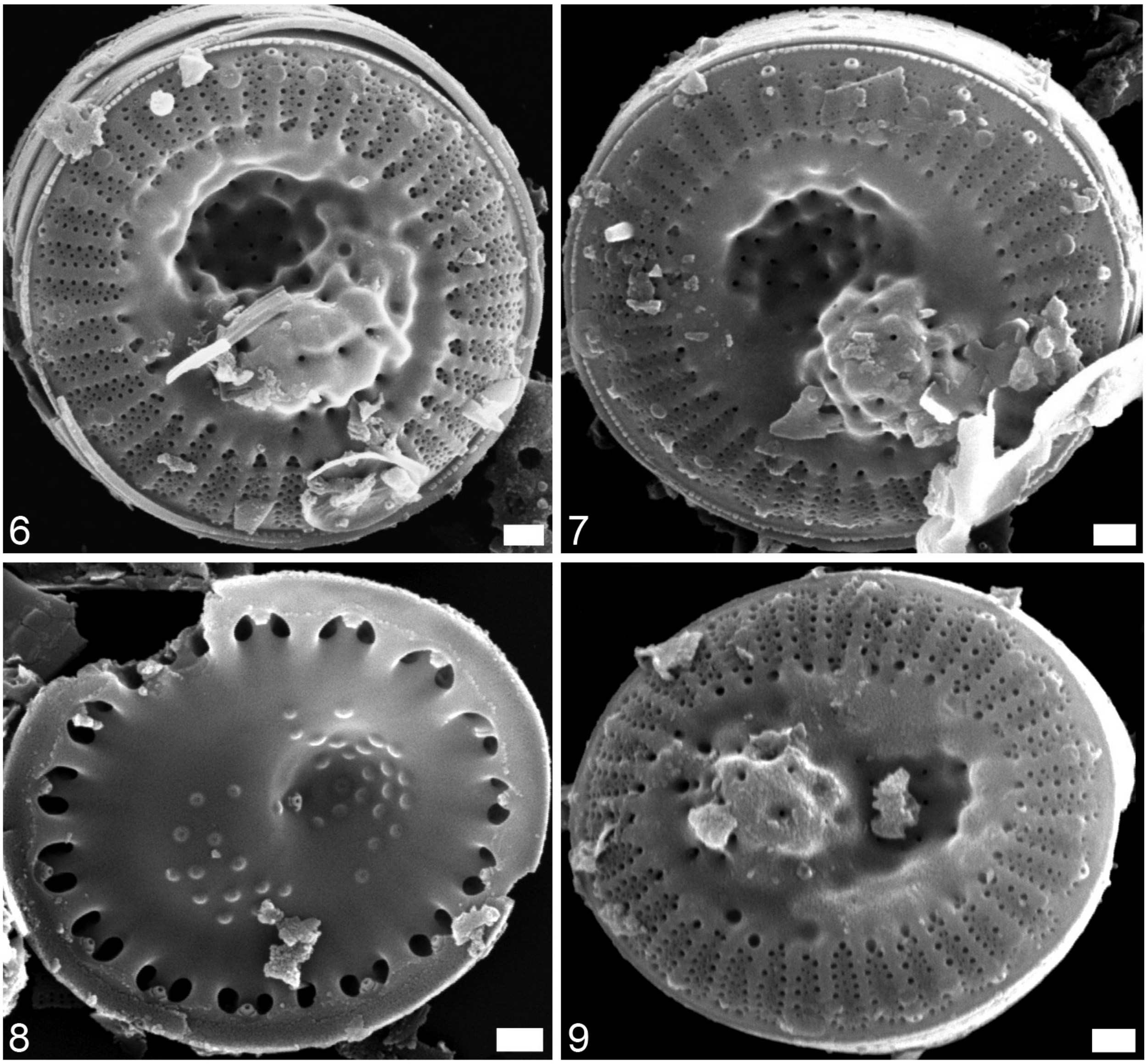
Additional material examined:—Idaho, Payette County, north bank of Willow Creek, 20 km NE on Willow Road from its intersection with Idaho highway 52, near center sec. 4, T.8N., R.2W., coll. S. Van Landingham. Diatomite is from Poison Creek Formation in the lower portion of Idaho Group, age approximately 11 to 12 mya.



FIGURES 1–5: *Cyclotella idahica*. LM. Valve views showing highly undulate valve face. Fig. 2. Holotype. Scale bar = 10 µm.

Description:—Valve outline oval-elliptical, sometimes nearly circular, with several girdle bands. Dimensions of the major axis 8.0–48.0 µm, minor axis 6.5–46.0 µm. Valve surface is divided into two distinct zones. Central zone oval to elongate, transversely undulate, with irregularly arranged areolae, becoming more or less radiate, 7–10/ 10 µm in large specimens only. Areolae with internal domed velum and external foramina. Fultoportulae on the valve face have two to four satellite pores, but those with three satellite pores are located mainly in the concave part of the valve face internally. Fultoportulae with small aperatures externally. External valve face is often covered with bumps. Marginal zone extends from 1/3 to 1/2 of the valve radius, and consists of alveolate striae in fascicles, 7–10/ 10 µm, separated by hyaline interfascicles. Each fascicle consists of 3–4 parallel or slightly wavy rows of small puncta. Puncta number 40–60 in 10 µm measured radially, in small specimens. In large specimens, 5–6 puncta at the margin become bi- or triseriate on the valve face. Striae fascicles are all of the same length. A ring of marginal chambers can be observed internally. Adjacent chambers are divided by thicker costae. Each chamber encompasses mostly 2 or 3 alveolar openings separated by thinner costae bearing marginal fultoportulae with 3 satellite pores, 4–6/ 10 µm. Externally marginal fultoportulae are represented by short tubes, which are often broken. A single rimoportula with a slit oriented radially or subradially occurs in association with a thinner costa. The rimoportula has a small external opening. Spines are irregular in number, being located on the interfascicles at the margin. Granules occur along the mantle edge.

Cyclotella idahica differs from *C. jonesii* McLaughlin (1992: 96, figs 1–11; see Figs 70–77 herein) by the smaller size of the valves, circular or oval valve shape, consistently having valve face fultoportulae, and having more pronounced bumps and granules on the valve face. Despite these differences, the two species share many features and appear to have close phylogenetic affinities.

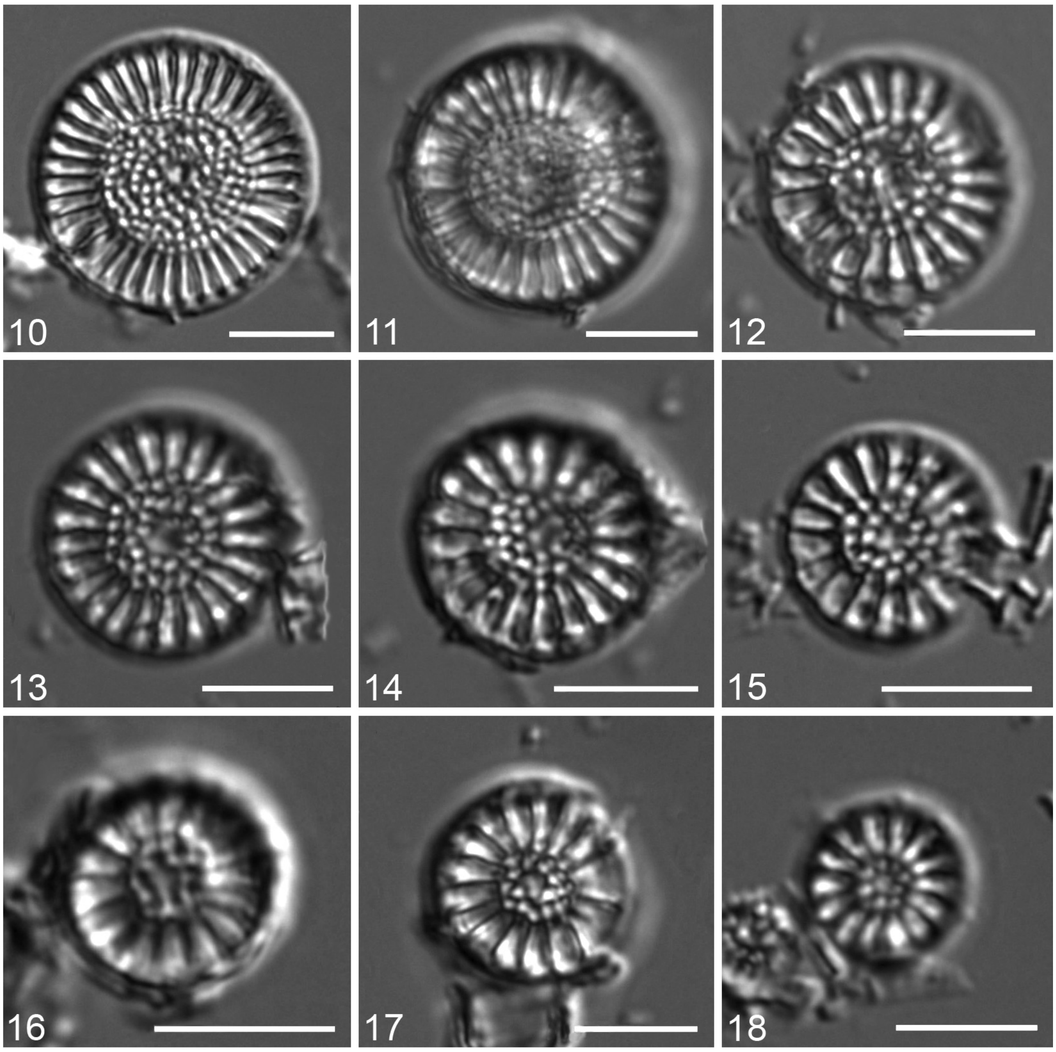


FIGURES 6–9: *Cyclotella idahica*. SEM. Figures 6, 7, 9. external views. Valve views showing transversely undulate central area with irregularly arranged areolae and covered by bumps. Present are external openings of areolae and short tubes of marginal fultoportulae. Spines and/or spines bases are found on the valve face/mantle junction. Scale bars = 1 µm. Figure 8, internal view. Valve view showing location of one fultoportula on the valve face. Arrow indicates position of the rimportula. Scale bar = 1 µm.

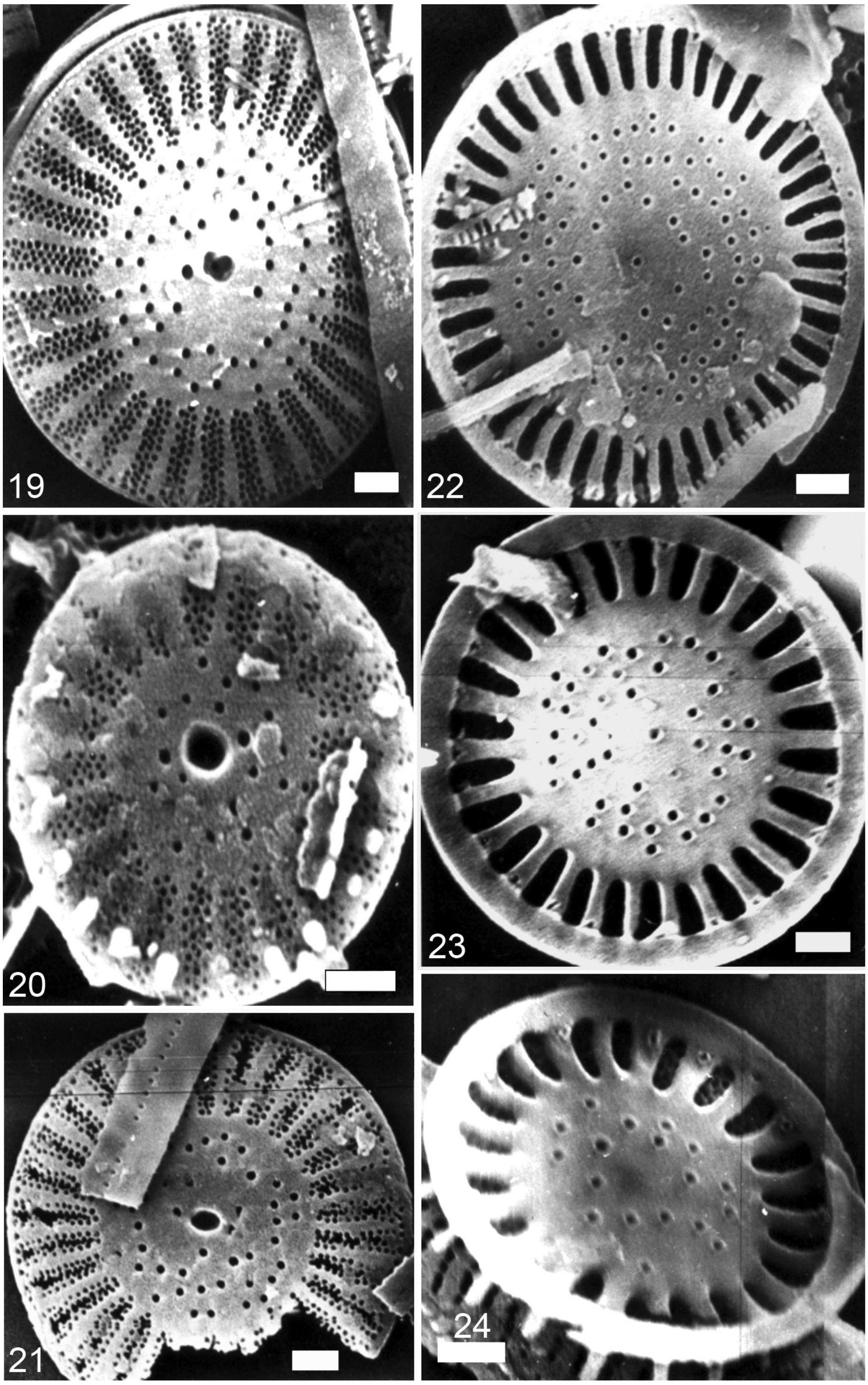
Cyclotella kansasica Hanna (1932: 376) (Figs 10–24)
Hanna 1932. University of Kansas Science Bulletin 20: 376, pl. 31, fig. 6.

Material examined:—USA. Kansas: Wallace County, Diatom marl from center Sec. 11, T.11S., R38W, Marshall ranch, North Fork Smoky Hill River, Ogallala Formation. *CAS Accession Number 2383* (CAS!). This is the type material studied by Hanna (1932). USA. Kansas: Wallace County, Sec. 12, T.11S., R38W. *CAS Accession Number 604437, Slide numbers 423092, 423093* (CAS!).

Description:—Valves are circular, nearly flat, 4.5–16.5 µm in diameter, with several girdle bands and a well-defined border between the central area and the marginal alveolate zone. Central area with one more or less well-developed depression at the center and a variable number of areolae which are arranged irregularly or in short radial rows. Marginal zone extending a little over 1/3 of the valve radius consists of alveolate striae fascicles, 8–12 in 10 µm, separated by hyaline interfascicles. Striae fascicles are of equal length. They contain 3–4 rows of puncta, 40–60 in 10 µm. Alveoli are simple. Length of alveolar openings is almost equal to the length of striae fascicles. Marginal fultoportulae with 3 satellite pores are located on every costa or every second costa separating alveolar openings internally. A single rimoportula occurs at the marginal ends of one of the costae. Spines are present at the junction of the valve face and mantle at every interfascicle, but they may be broken.



FIGURES 10–18: *Cyclotella kansasica*. LM. Valve views showing flat valve face and size diminution series. Scale bars = 5 µm.



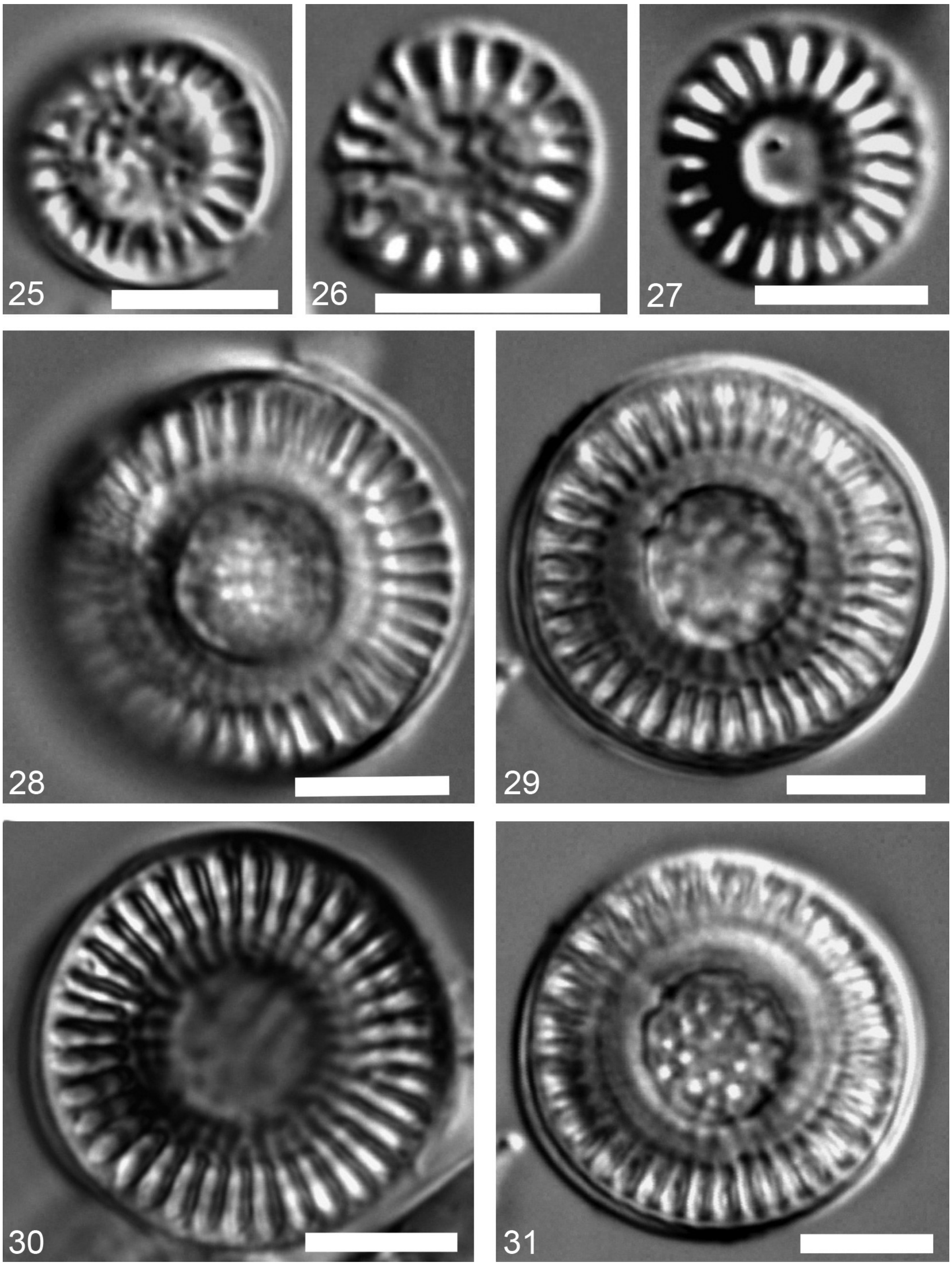
FIGURES 19–24: *Cyclotella kansasica*, SEM. Figures 19–21, external views. Flat valve face has striae with 3–4 rows of areolae towards the margin, and scattered areolae in the center, usually with one enlarged depression. Openings of the marginal fultoportulae occur on every rib. Thick spines or bases are visible on the margin of the valve. Scale bars = 1 μm. Figures 22–24, internal views. Marginal fultoportulae occur on every costa. A ring of simple alveolae is present on the mantle. Central fultoportulae are wanting. Central areolae do not reflect an enlarged opening seen externally. Scale bars = 1 μm.

Cyclotella discostelliformica Kociolek & Khursevich, *sp. nov.* (Figs 25–39)

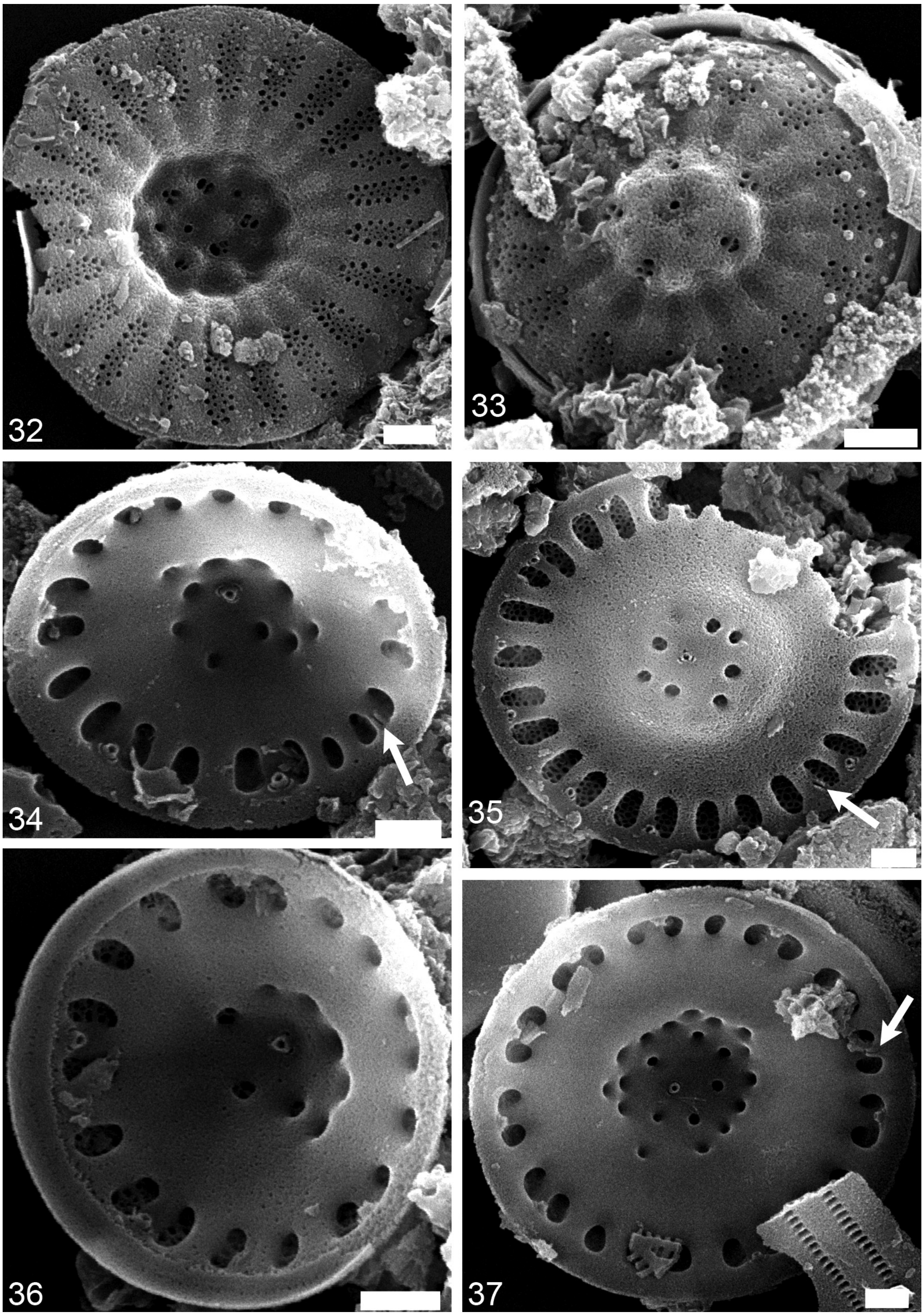
Type:—USA. Oregon: Klamath County, Sprague River, Drews Road, diatomite, (Circled specimen (Fig. 31) on *CAS Slide Number 1026029*, material *CAS Accession Number 701883* (CAS!), **holotype, designated here**; duplicate of *CAS Slide Number 1026029* deposited in Khursevich Collection, Minsk, Belarus, **isotype, designated here**).

Additional material examined:—USA. Oregon: Klamath County, NE Sprague River Bridge, *CAS Accession Number 600180, Slide Number 433093* (CAS!)

Description:—Valve outline nearly circular, with several girdle bands, 5.0–17.0 µm in diameter. Valve surface is divided into two distinct zones with different morphologies. The central area is distinctly concave or convex with irregularly arranged areolae (5 to 17) and one to three valve face fultoportulae. The latter have three satellite pores internally and open by small aperatures externally. This central zone is separated from the marginal zone by a wide hyaline ring. Small specimens have simple alveolae. Marginal fultoportulae are located in small fovae on the gentle slope of costae. A single rimoportula has internal elongated slit and is positioned within the alveolar opening close to one of the costae. The marginal zone extends from 1/3 to ½ of

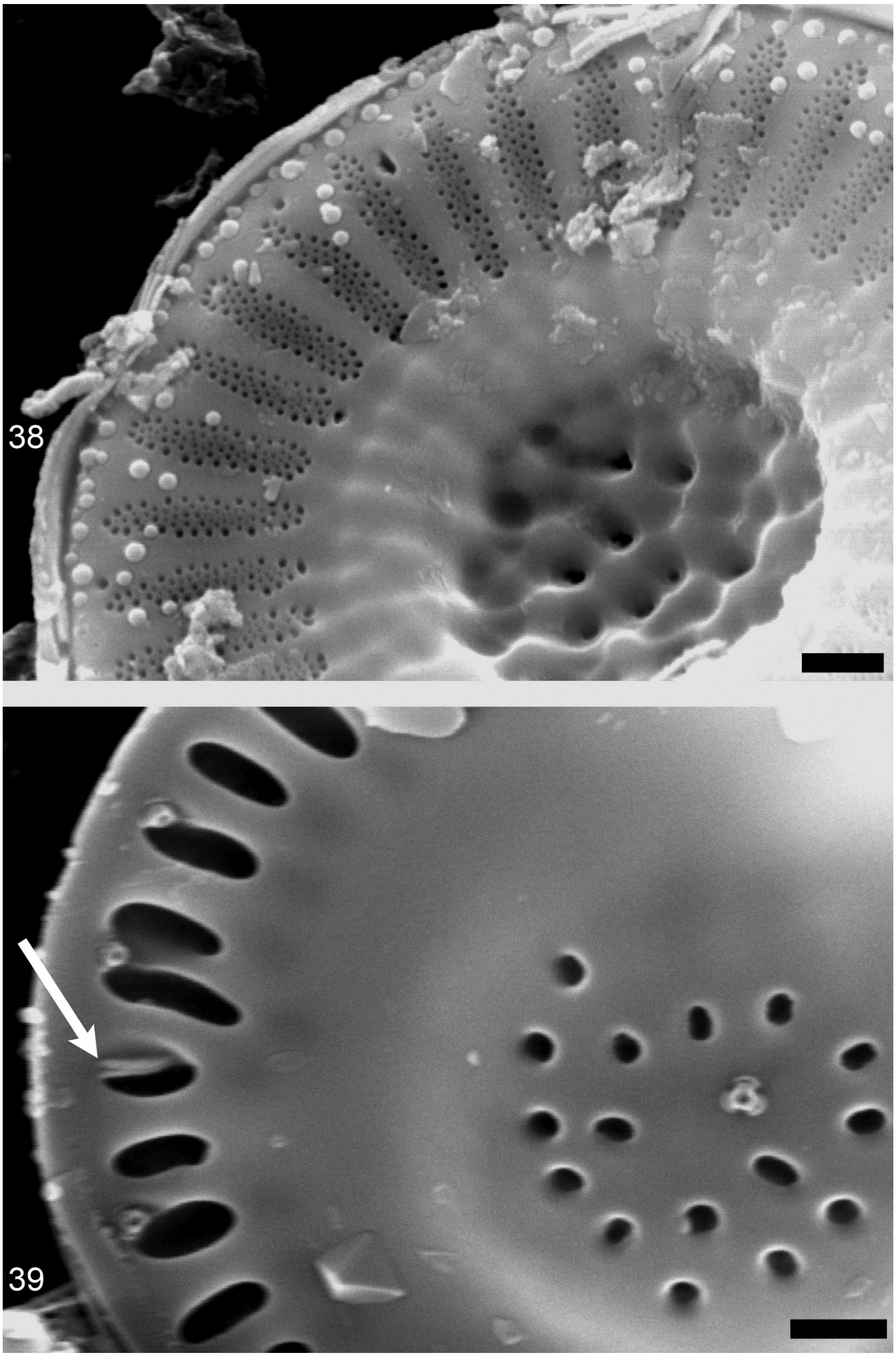


FIGURES 25–31: *Cyclotella discostelliformica*. LM. Valve views showing highly undulate valve face. Fig. 31. Holotype. Scale bar = 5 µm.



FIGURES 32–37: *Cyclotella discostelliformica*. SEM. Figures 32, 33. External views showing valves with sunken and elevated central areas, respectively. Fascicles are composed of 2–5 rows of areolae. Openings of the marginal fultoportulae are located at or near the thickened ribs. They lack tubes or thickenings. The central portion of the valves have isolated areolae, that are larger than those of the fascicles. Scale bars = 1 µm. Figures 34–37. Internal valve views showing a single central fultoportula with 3 satellite pores, and marginal fultoportulae at every costa or every second costa. The rimoportula is located on or near a costa (arrows). Scale bars = 1 µm.

the valve radius and consists of alveolate and fasciculate striae, 8–10/10 µm, divided by hyaline interfascicles. Interfascicles become broader towards the margin. Each fascicle has one-two rows of smaller puncta, which have a row of larger puncta on each side. Striae fascicles are of equal length. A ring of marginal chambers, separated by thicker costae, is evident internally. Alveolar chambers appear simple and complex in larger specimens. Complex alveolae are comprised of alveolar openings divided by thinner costae. The thinner costae bear marginal fultoportulae. Each fultoportula has three satellite pores, and number 4 in 10 µm. Externally, marginal fultoportulae are represented by small, circular openings. A single rimoportula is located on a thinner costa or along the slope of one of the costae. External rimoportula opening is a small, but distinct, slit. Granules may occur along the edge of the mantle.



FIGURES: 38–39: *Cyclotella discostelliformica*. SEM. Figure 38. External view showing opening of rimoportula and fine nature of the areolae. Scale bar = 1 µm. Figure 39. Internal view showing large rimoprotula (arrow) located on the side of a costa. Central fultoportula with 3 satellite pores is evident. Scale bar = 1 µm.

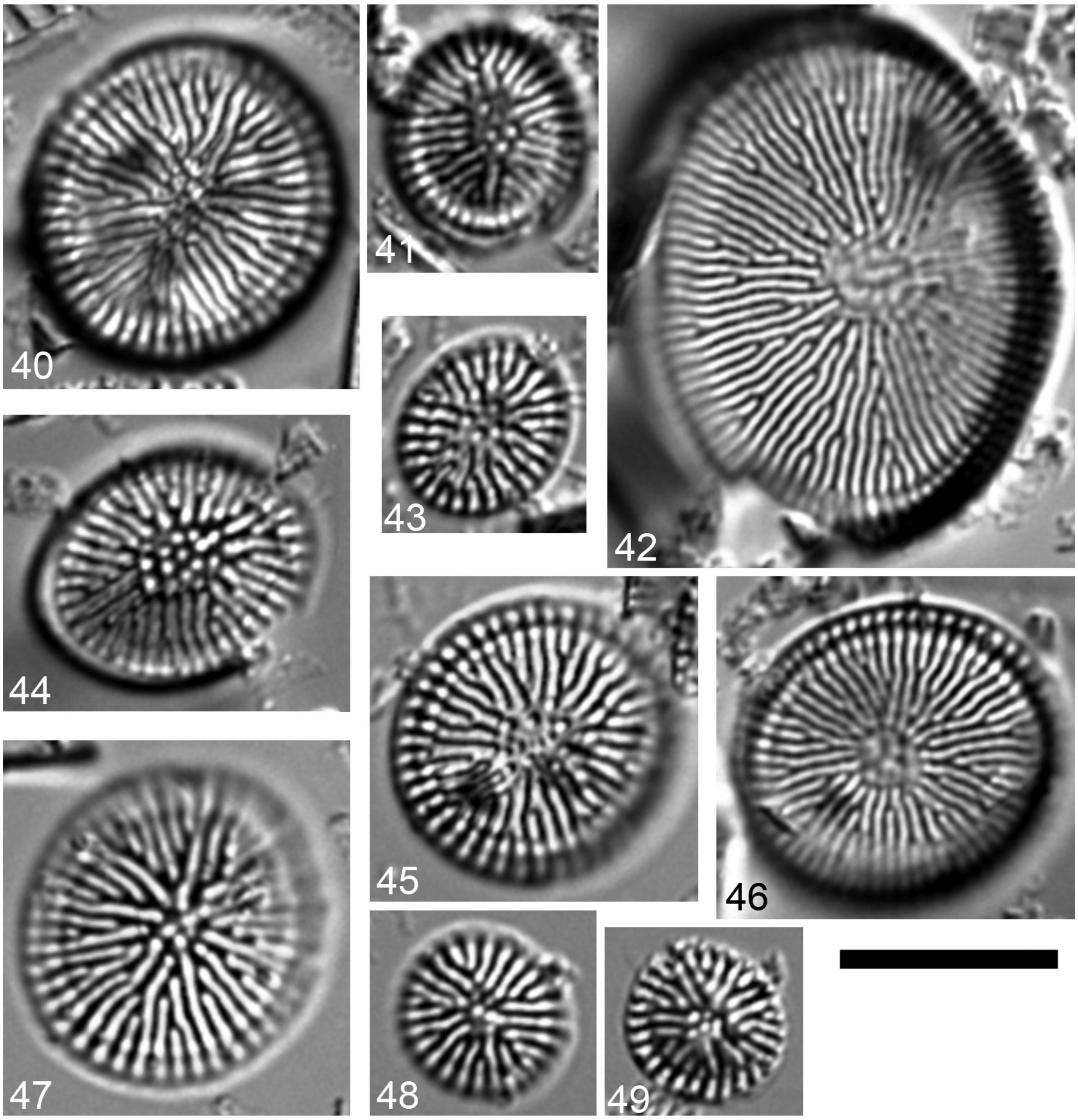
Cyclotella discostelliformica differs from *C. idahica* by its smaller size, presence of strongly concave or convex central area, external expression of the rimoportula (a distinct slit in *C. discostelliformica*; a small circular opening in *C. idahica*) and the absence of spines.

This new species appears in the light microscope to resemble *Discotella stelligera* (Cleve & Grunow) Houk & Klee (2004: 209, figs 23, 24) but differs in the position of the rimoportula and marginal fultoportulae, (between two costae in *D. stelligera* and on thinner costae in *C. discostelliformica*). Moreover, marginal fultoportulae in *C. discostelliformica* have three satellite pores; *D. stelligera* has marginal fultoportulae with two satellite pores.

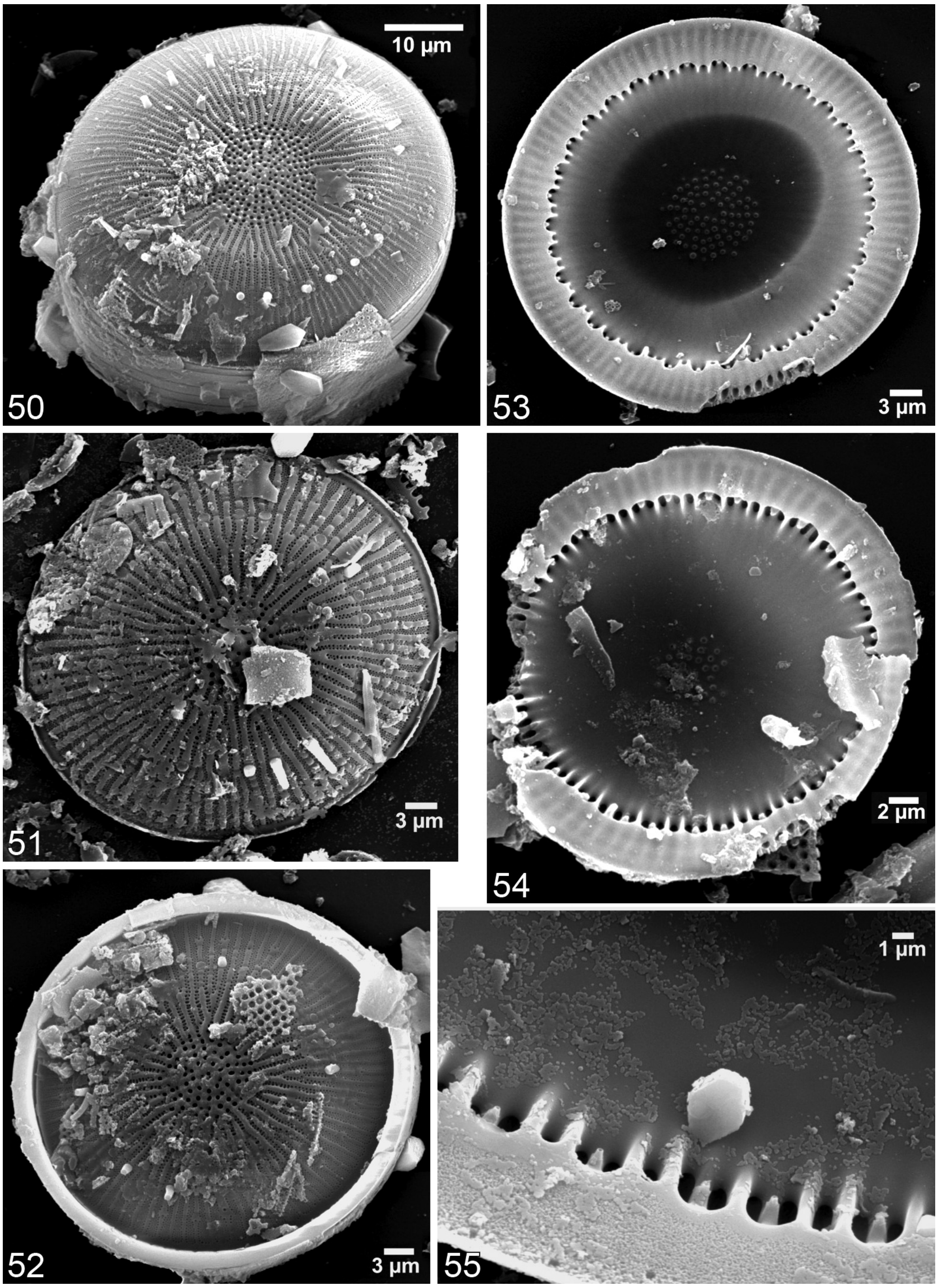
Cyclotella stoermeri Khursevich & Kociolek, *sp. nov*. (Figs 40–55)

Type:—USA. Oregon: Klamath County, Sprague River, Drews Road, diatomite, (Circled specimen (Fig. 40) on *CAS Slide #433091,* material *CAS Accession Number 600179* (CAS!), **holotype, designated here**).

Additional material examined:—Oregon, Klamath County, Sprague River, Drews Road, *CAS Accession Numbers 600175, 600176, 600181, 701883, Slide Number 1026029* (CAS!).



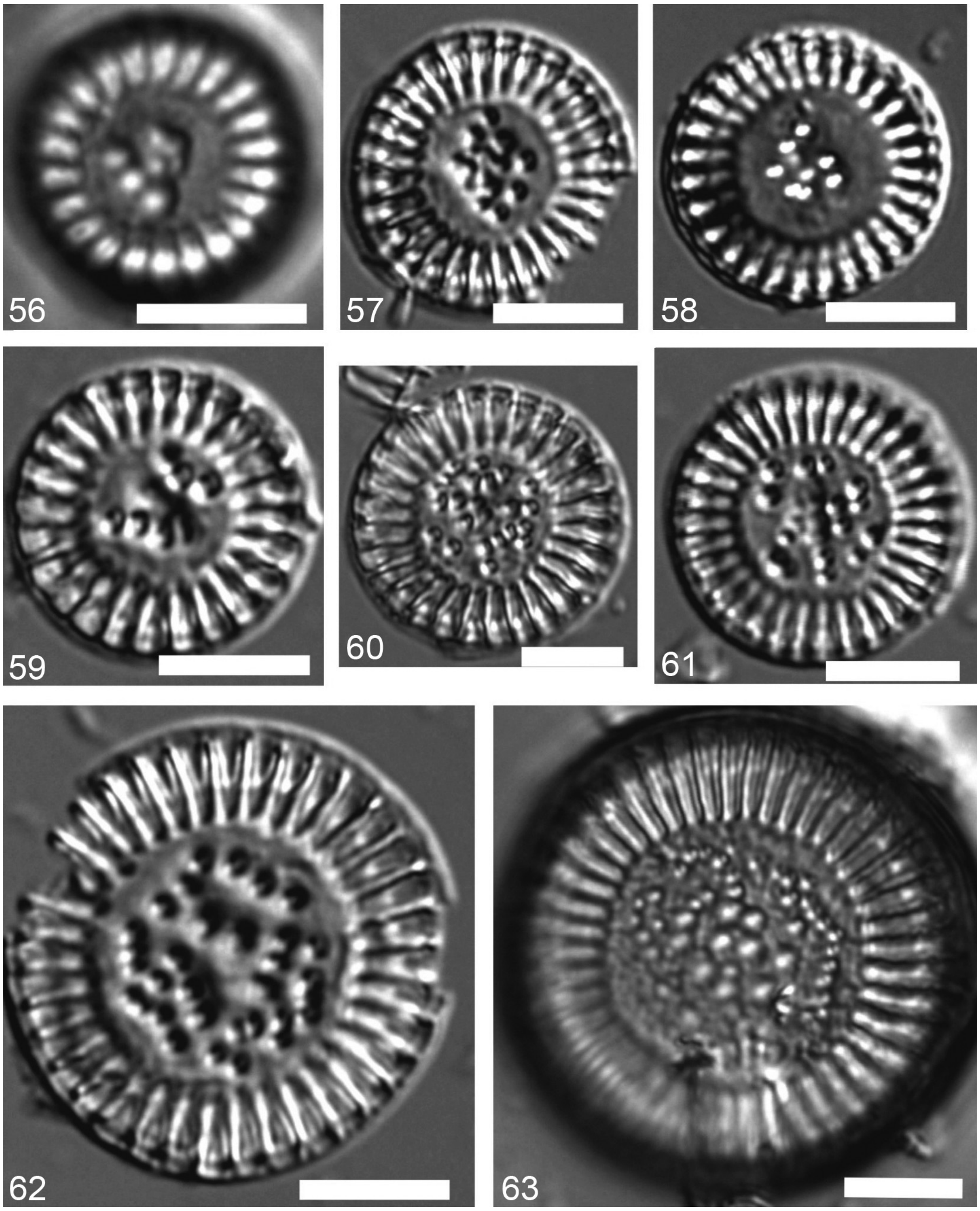
FIGURES 40–49: *Cyclotella stoermeri*. LM. Valve views showing size diminution series. Note dissimilar lengths of striae. Fig. 40. Holotype. Scale bar = 10 µm.



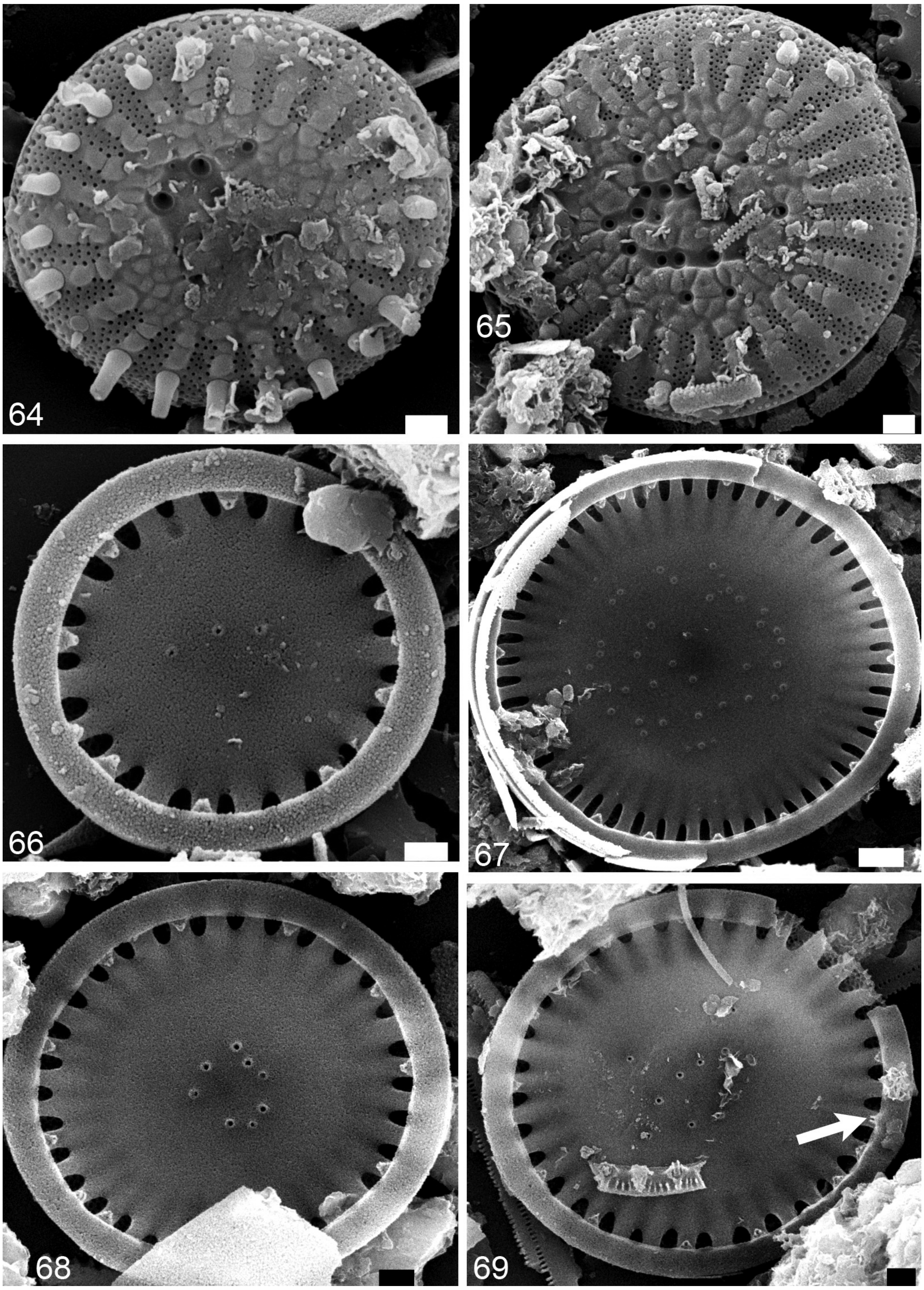
FIGURES 50–55: *Cyclotella stoermeri*. SEM. Figures 50–52. External valve views . Fascicles are comprised of 1–3 rows of small areolae. The ribs are thickened and elevated, becoming thinner on the valve mantle. The valve center has enlarged areolae. Scale bars = 10 and 3 µm, respectively. Figures 53–55, internal valve views. Complex and simple alveolae are positioned around the perimeter of the valves. Thick and thin costae are evident, and marginal fultoportulae are evident on the recessed costae. Rimportulae are positioned also on the recessed costae. Areolae with domed cribra are evident in the center of the valves. Scale bars = 3, 2 and 1 µm, respectively.

Description:—Frustules solitary, round or circular in valve view, 7–100 µm in diameter, short cylindrical in girdle view with several intercalary bands. Valve face is nearly flat. The valve center has one-several areolae surrounded by hyaline ring, rarely it is structureless. Central area contains loculate areolae with internal domed cribra and external foramina, arranged in more or less short radial rows (from 2 to 17 small areolae in row). Central area fultoportulae have never been observed. The striated zone occupies 1/2 to 3/4 the length of the valve radius. Striae, 7–12 in 10 µm, are radial, of unequal length, slightly undulate towards the center of the valve. They consist of two rows of small puncta on the valve face surface and of three-five small puncta on the valve margin. The striae are divided by costae dichotomously branched from the central area towards the valve margin. Alveolae are complex and simple. Marginal fultoportulae with three satellite pores are located on all recessed costae within marginal chambers. They are represented by small openings externally. One-several raised rimoportulae are positioned also on the recessed costae internally. They are marked by small round apertures on the external valve surface. Solid conic spines are present irregularly at the valve face/mantle junction.

Remarks:—*Cyclotella stoermeri* differs from *C. elgeri* Hustedt (1952: 374, fig. 31) by the wider striated zone, the smaller central area, as well as by the different structure and location of marginal fultoportulae (they have two satellite pores and are placed on all thick costae on the mantle in *C. elgeri*, while marginal fultoportulae in *C. stoermeri* possess three satellite pores and occur only on thin recessed costae). This species is dedicated to our friend and colleague, Dr. E.F. Stoermer of the University of Michigan, Ann Arbor.



FIGURES 56–63: *Cyclotella pseudokansasica*. LM. Valve views showing size diminution series. Fig. 61. Holotype. Scale bar = 5 µm.



FIGURES 64–69: *Cyclotella pseudokansasica.* SEM. Figures 64, 65. External valve views. Prominent spines or spine bases are located about the periphery of the valves. Multiseriate fascicles alternate with thick costae. Openings of the marginal fultoportulae are located near the base of the mantle. Scale bars = 1 µm. Figures 66–69. Internal valve views. The valves have a few to several scattered central areolae, and marginal fultoportulae positioned on every second or third costa. Scale bars = 1 µm (in figs 64–66, 68, 69). Scale bar = 2µm (in fig. 67).

Cyclotella pseudokansasica Khursevich & Kociolek, *sp. nov.* (Figs 56–69)

Type:—USA. Idaho: Owyhee County, Chalk Hills Formation, USGS Diatom Locality 5244, (Circled specimen (Fig. 61) on *CAS Slide #381069*, material *CAS Accession Number 602190* (CAS!), **holotype, designated here**).

Description:—Valves are circular, nearly flat, 10–23 µm in diameter, with a well-defined border between the central area and the marginal alveolate zone. Central area with a variable number of irregularly arranged areolae. Marginal zone extending from 1/3 to 1/2 of the valve radius consists of alveolate striae fascicles, 8–12(14) in 10 µm, separated by hyaline interfascicles or costae. Striae fascicles are of equal length. They contain 3–4 rows of puncta, 40–60 in 10 µm. Alveoli are simple. Length of alveolar openings is not equal to the length of striae fascicles. Marginal fultoportulae with 3 satellite pores are located on every second–fourth costa separating alveolar openings internally. A single rimoportula occurs at one of the costae. Spines are present at the junction of the valve face and mantle at every interfascicle or costa.

Remarks:—*Cyclotella pseudokansasica* is similar to *C. kansasica* in the structure of alveolae, in the location of rimoportula and marginal fultoportulae, but differs by the absence of one more or less well-developed depression at the center, as well as by the shorter length of alveolar openings as compared with the length of striae fascicles.

Cyclotella jonesii McLaughlin (Figs 70–77)
McLaughlin 1992, *Diatom Research* 7: p. 96, figs 1–11.

Materials examined:—Oregon, Klamath Co., Forest Road, No. 3683-A, 6.6 miles W of Beatty, N of highway 140. *CAS Accession Numbers 600120, 600121, 600122, Slide Numbers 436069, 436070, 436071, 436072, 436073, 436074* (CAS!)

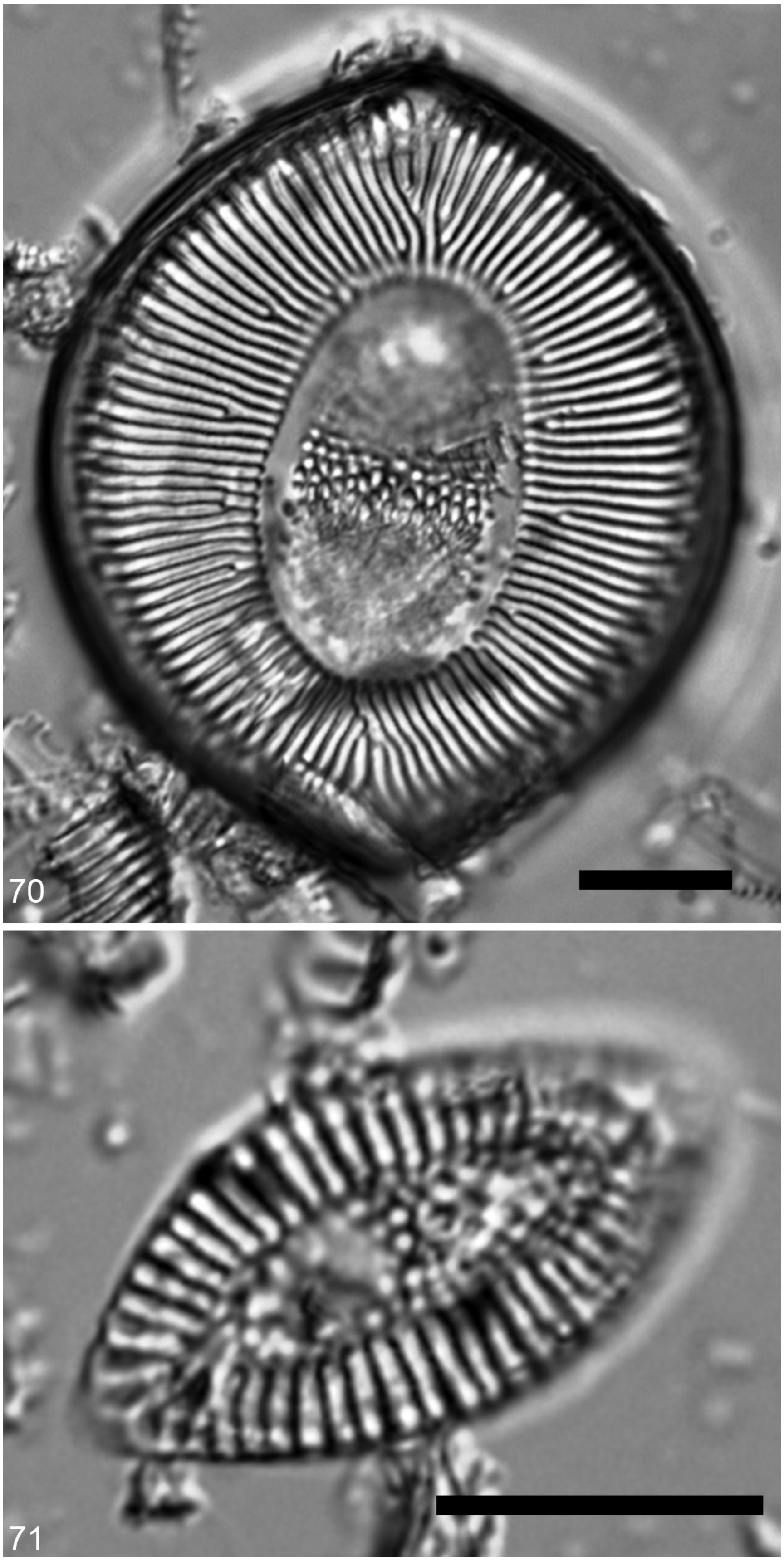
We observed two morphotypes in populations we examined. They are almost exactly the same except for size and valve outline. We present descriptions for both morphotypes even though at this time we recognize them as the same taxon, *C. jonesii*.

Morphotype 1 (Figs 70, 72, 73, 75)

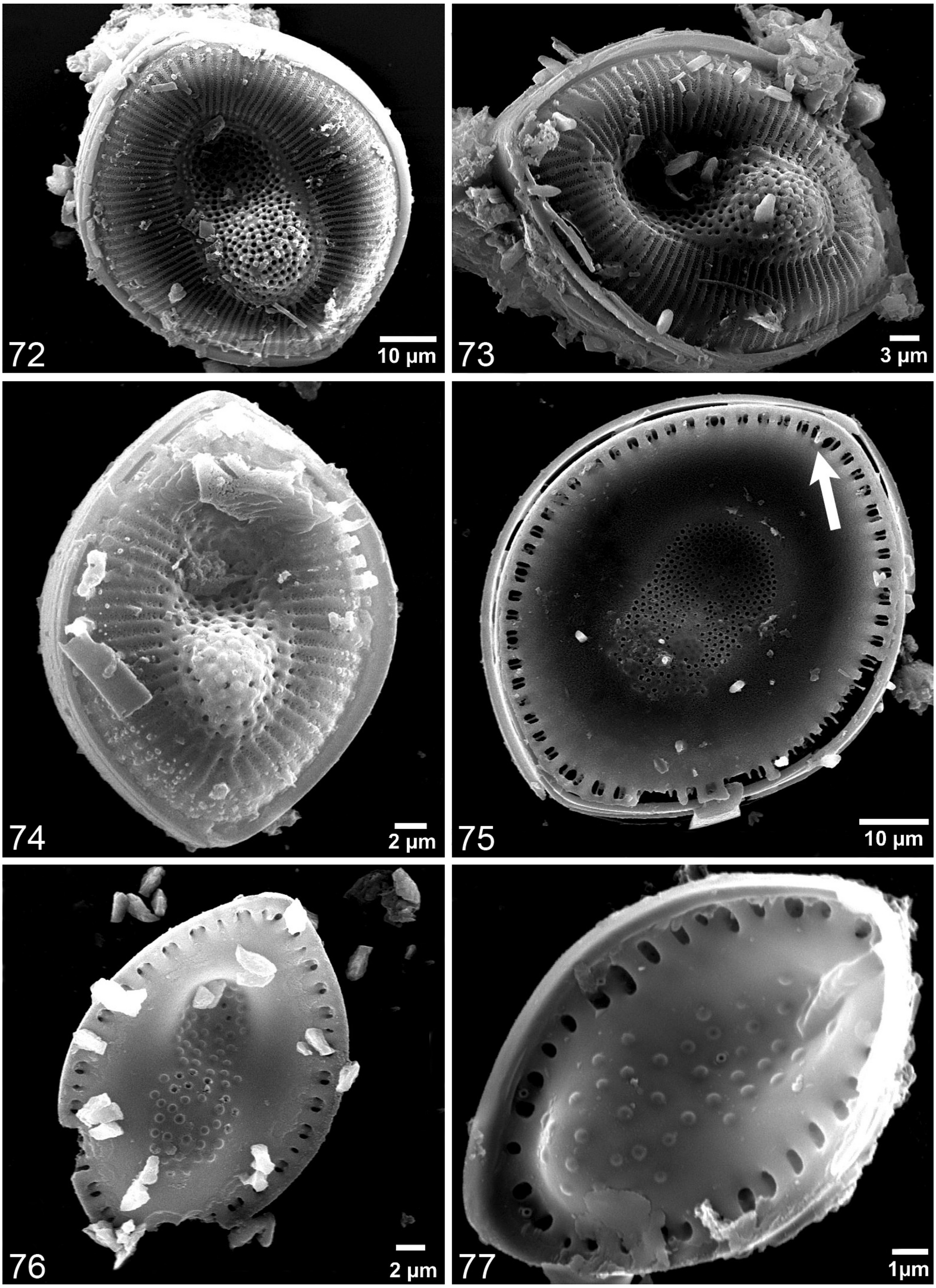
Description:—Valve outline rhomboid to ellipsoid, but large forms are nearly circular. Major axis is 20 to 95 µm, minor axis 11 to 93 µm. Central area is elongated, asymmetrically undulate with the depressed portion shallower than the rise of the elevated part. Central area occupies 1/3 to 1/2 of the total valve face and contains areolae arranged in more or less radial rows. Valve face fultoportulae are absent. Striae number 7–9/10 µm, consisting of 2–3 rows of small puncta (with up to 30 puncta in 10 µm measured radially), and separated by interstriae. Alveolae are complex and simple. Marginal fultoportulae have three satellite pores and are located on all recessed costae within alveolar chambers internally. They open by short tubes on the external valve surface. One or two rimoportulae are present also on recessed costae between two alveolar openings. A closed valvocopula and several open copulae without puncta are present.

Morphotype 2 (Figs 71, 74, 76, 77)

Description:—Frustules solitary, elliptical-lanceolate in valve view, with several girdle bands. A closed valvocopula has numerous plaques along the valve. Several open bands, as a valvocopula, lack areolae. Dimensions of major axis of valves vary from 11.7 to 42.7 µm, of minor axis from 7 to 30 µm. Valve face is distinctly divided into two zones: a marginal alveolate zone and a transversely undulate, elongated areolate central area. A narrow, irregular hyaline area separates these two zones. Central area is elliptical, symmetrically undulate: elevated and depressed parts are almost equal. Areolae with internal domed cribra and external foramina are arranged mainly irregularly. One valve face fultoportula with two satellite pores internally and a round thickened aperture externally can be seen within the central area, rarely can be absent. Striae, 10–12 in 10 µm, are slightly radiate in the middle part of the marginal zone and strongly radiate towards the valve ends. Striae consisting of two-four rows of small puncta (40–50 puncta in 10 µm) are divided by interstriae (costae). Alveolae are complex and simple, 10–12 in 10 µm. Marginal fultoportulae have three satellite pores internally and open by short tubes externally. They are positioned on all recessed costae within alveolar chambers on the internal valve surface. One or two rimoprtulae are sessile internally, and each is located on a costa between two alveolar openings in the pole area. Rimoportulae open by a round apertures externally. Spines can be present on the valve face/mantle junction, but they are often broken.



FIGURES 70–71: *Cyclotella jonesii*. LM. Figure 70 is of Morphotype 1. Figure 71 is of Morphotype 2. Scale bars = 10 µm.



FIGURES 72–77: *Cyclotella jonesii*. SEM. Figures 72, 73. External valve views of Morphotype 1. Fascicles are comprised of fine areolae, while the tangentially undulate center has larger areolae. Marginal fultoportulae have tubular external openings, located on or about every other costa. Scale bars = 10 µm, respectively. Figure 74. External valve view of Morphotype 2. Multiseriate fascicles are comprised of areolae much smaller than those in the center of the valve. Scale bar = 2 µm. Figure 75. Internal valve view of Morphotype 1. Thick and thin costa are present. Central areolae are numerous. Scale bar = 10 µm. Figures 76, 77. Internal valve view of Morphotype 2. Marginal fultoportulae are located on recessed costae, and have 3 satellite pores. Central fultoportula is present, situated among scattered areolae with domed cribra. Scale bars = 2, and 1 µm, respectively.

Discussion

Variation in *Cyclotella* morphology has been documented with light and electron microscopy over the past 35 years (e.g. Lowe, 1975; Serieyssol, 1981, 1993; Servant-Vildary 1986; Håkansson 2002; Tanaka 2007), and from this diversity a number of formal and informal groups have been identified and named. Most recently Houk et al. (2010) identified three morphological groups within *Cyclotella*:

Group 1: possess tangentially undulate to nearly flat valves, with the central part lacking areolae, and a single rimoportula within the ring of marginal fultoportulae (and contains the nomenclatural type of the genus *C. distinguenda* Hustedt (1927: 320))
Group 2: possess the valve face tangentially undulate or nearly flat, central area is without areolae and at least one rimoportula not within the ring of marginal fultoportulae (included here, for example, are the well known species *C. comensis* Grunow in Van Heurck (1882: pl. 93, figs 16, 17), *C. ocellata* Pantocsek (1902: 104) and others)
Group 3: possess the valve face tangentially undulate or nearly flat , a central area with areolae, one rimoportula not within the ring of marginal fultoportulae, but on the valve face, nearer to the center complex alveolae (*C. bodanica* Eulenstein in Grunow (1878: 126), *C. comta* (Ehrenberg) Kützing (1849: 20), etc.)

Observations on centric diatoms from western North America presented here suggest the presence of three additional morphological groups:

A. one group with *C. idahica, C. jonesii* and *C. stoermeri*; this group is closely related to *C. oregonica* Kociolek & Khursevich, though this last species lacks areolae in the center of the valve (Khursevich & Kociolek 2008);
B. the second group has *C. discostellaeformica*;
C. the third group is comprises *C. pseudokansasica* and *C. kansasica.* Also included here is *C. mahoodii* Kociolek & Khursevich in Khursevich & Kociolek (2008: 41), which also lacks central areolae (Khursevich & Kociolek 2008).

Presence of a variety of taxa with, and without, central areolae in other groups that are otherwise diagnosed by a variety of features, suggest the feature of presence/absence of areolae in the central area is homoplasious, and not helpful in diagnosing natural groups. Data on the morphology of *C. elgeri* supported the transfer of this taxon, first suggested by Khursevich & Kociolek (2002), to the genus *Tertiarius* (Houk et al. 2010).

The species of *Cyclotella* considered here can be separated into three morphological groups with respect mainly to the structure of alveolae and position(s) of rimoportula(e) and marginal fultoportulae. One of these groups is composed of 3 extinct species and distinguished by a variety of valve outlines, including circular to round (*C. idahica,* and *C. stoermeri*) to elliptical-lanceolate or even rhomboid-ellipsoid (*C. jonesii*). The central area is from almost flat or slightly concentrically undulate to strongly transversely undulate. The latter is characteristic of *C. idahica* and *C. jonesii*. The central area may consist of areolae only (*C. stoermeri* and *C. jonesii*), or of both areolae and valve face fultoportulae, internally surrounded by two or three or rarely four satellite pores (*C. idahica*). The position of rimoportulae in species from this group is one of recessed costae within marginal chambers that can be observed on the internal valve surface. Alveolae are complex and simple. Marginal fultoportulae with three satellite pores internally are located also on recessed costae within alveolar chambers. Spines may be present in this group.

Cyclotella idahica is very similar morpholgically to *C. jonesii*, differing mainly in valve outline, having smaller dimensions, presence of valve face fultoportulae and pronounced bumps on the face of the valve. *Cyclotella idahica and C. jonesii* may well be sister taxa and discreet character differences suggests they be recognized as separate taxa.

Cyclotella jonesii resembles *C. oregonica* Kociolek & Khursevich in Khursevich & Kociolek (2008: 44) in the outline of the valve and presence of other valve features described above for *C. jonesii*, but differs from *C. oregonica* in that the latter lacks valve face areolae.

Cyclotella stoermeri is similar to *C. iris* Brun & Heribaud (1893: 224) in the structure of the marginal striated zone, presence of simple and complex alveolae, position of the rimportula and marginal fultoportulae on the internal recessed costae and absence of valve face fultoportulae (Serieyssol 1984). These taxa differ in the lack of areolae in the central area and mainly flat or slightly convex valves in *C. iris*.

The second morphological group is represented by *Cyclotella discostelliformica* which resembles species of the genus *Discostella* (Houk & Klee 2004) in having well expressed concave-convex central area, slit-like external expression of the rimoportula and location of the rimoportula and marginal fultoportulae sometimes in the marginal part of the alveolae.

The third morphological group includes the extinct species *C. kansasica* and *C. pseudokansasica*, which is characterized by circular valves with a flat central areolar area. Valve face fultoportulae are absent within the central area. Alveolae are simple. A single rimoportula is positioned on one of the costae, marginal fultoportulae are located on costae separating alveolar openings on the internal valve surface.

Cyclotella kansasica is similar to *C nevadica* Khursevich & Kociolek (2008: 42) in the structure of alveolae, rimoportulae with radially-oriented internal slit and marginal fultoportulae located on costae, and absence of valve face fultoportulae. The two species differ in the relief of the valves, length of striated marginal zone, and lack of valve face areolae in *C. nevadica*.

With regard to *Puncticulata*, Houk et al. (2010, p. 4–5) write, "As for the genus *Puncticulata* Håkansson (Hakansson 2002), it was based on *Cyclotella comta* Kutzing 1849 (nom.cons.). However, there is *Puncticulata austriaca* (Peragallo) Håkansson also mentioned as a synonym of *Handmannia austriaca* Peragallo in Handmann (1913: 14). But this is the type of validly published genus *Handmannia* Peragallo in Handmann (1913: 14) and from this point of view the generic name *Puncticulata* Hakansson is illegitimate by the International Code of Botanical Nomenclature, Art. 52. So we preferred to retain the previous generic name *Cyclotella* for the *Puncticulata* taxa."

Our observations on these mainly Pliocene aged species suggest that there are close morphological similarities between them and *Puncticulata*, as diagnosed by Håkansson (2002). Some of the relationships seem very close, with the only difference differentiating between members of the three morphological groups we describe here and members of *Puncticulata* is the lack of valve face areolae in the *Cyclotella* taxa. If the primary feature used by Håkansson to distinguish *Puncticulata*, namely presence of valve face areolae (Håkansson 2002), would turn out to be primitive among this group of very closely related taxa, it might result in *Puncticulata* not representing a natural group (Houk et al. 2010).

Detailed phylogenetic analysis of this group of taxa, along with *Tertiarius* and *Pliocaenicus*, is required to sort out the complex set of features displayed among them. Interesting will be the fact that only a small subset of them have extant taxa, thus such an analysis will require and indicate the important role of fossil in understanding the relationships among this important group of freshwater diatoms.

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