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Fascinorbis gen. nov., a new genus of Stephanodiscaceae (Bacillariophyta) from a Late Miocene lacustrine diatomite

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We used light and electron microscopy to characterize a Late Miocene freshwater diatomite deposit in the Chalk Hills Formation, near Payette, Idaho, USA. The diatom assemblage from this sample was nearly monotypic, dominated by a single taxon with similarities to *Lindavia bodanica* (Thalassiosirales) but with several features uncharacteristic of the genus *Lindavia*, such as a rimoportula(e) on the valve mantle located on a costa, simple alveolar structure, and spines at the external valve face-mantle junction. A combination of other characters for this species complicate its placement into existing genera, including a lack of central fultoportulae, central area with loculate areolae with domed cribra, and a single ring of mantle fultoportulae with three satellite pores with well-developed cowlings and broad satellite pore covers. Based on this unique set of features, we have established a new genus, *Fascinorbis*, which appears to represent an important transitional form in the evolution of the *Lindavia* lineage.

Keywords: Lindavia*, fossil, taxonomy, extinct, Thalassiosirales,* Cyclotella

Introduction

The strutted process (fultoportula) is the defining feature, or synapomorphy, for the Thalassiosirales. Despite some losses, the labiate process (rimoportula) is an ancestral, or plesiomorphic, feature of all diatoms. The ancestral thalassiosiroid likely had a single rimoportula positioned within a ring of fultoportulae on the valve mantle. Modifications of this arrangement have been rare and, as a result, should be phylogenetically informative, i.e., that they can be used to diagnose monophyletic groups. The labiate process was repositioned off the valve mantle and onto the valve face twice over the course of Thalassiosirales evolution, in the marine genus *Shionodiscus* Alverson, Kang & Theriot (Alverson et al. 2006) and the freshwater genus *Lindavia* (Schütt) De Toni & Forti (sensu Nakov et al. 2015; referred to throughout as *Lindavia* sensu lato), both of which are well-supported monophyletic groups (Alverson et al. 2007). The position of the rimoportula has been useful in establishing more natural genus-level classifications of both *Thalassiosira* Cleve and *Cyclotella* (Kützing) Brébisson, two morphologically diverse and species-rich, but polyphyletic, genera within the Thalassiosirales (Theriot et al. 1987, Houk & Klee 2004, Alverson et al. 2006, Nakov et al. 2015).

The broad diversity of morphological forms in *Cyclotella*, as originally conceived, motivated numerous efforts to subdivide the genus into morphological groups (e.g., Lowe 1975; Serieyssol 1981; Khursevich and Kociolek 2012). Phylogenetically based interpretations of these groups and their morphological features, together with molecular phylogenetic analyses, have provided the framework necessary for creating a natural genus-level classification of ‘*Cyclotella*’, one in which the broad set of morphological characters within *Cyclotella* could be understood as either ancestral or derived. This, in turn, allowed subdivision of *Cyclotella* into a set of monophyletic genera. The locations and arrangements of labiate and strutted processes, and their positions relative to costae (the spoke-like thickened ribs of silica that radiate outward from the central area) have proven to be especially informative and useful in classifying *Cyclotella* species (Theriot et al. 1987, Houk & Klee 2004, Nakov et al. 2015). These features were used to resurrect the generic name *Lindavia* for cyclotelloid species with a rimoportula located on the

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valve face. Other cyclotelloids have retained the ancestral mantle-area rimoportula that is either on (*Cyclotella* s.s.), adjacent but adjoined to (*Tertiarius* Håkansson & Khursevich), or between (*Discostella* Houk & Klee) mantle costae (Håkansson & Khursevich 1997, Houk & Klee 2004, Nakov et al. 2015). Interpretation of these features within a phylogenetic framework supported the transfer of several cyclotelloid groups, including *Pliocaenicus* Round & Håkansson and the ocellatoid and bodanicoid species of *Cyclotella*, into *Lindavia* (Nakov et al. 2015). Subsequently, Kociolek et al. (2016) split the genus *Edtheriotia* Kociolek et al. from *Lindavia*, and Ács et al. (2016) separated ocellatoid species, those with no areolae in the central area and striae with unequal lengths, out of *Lindavia* and into a new genus, *Pantocsekiella* Kiss & Ács. *Lindavia* was emended and distinguished from *Pantocsekiella* and *Cyclotella* by 'complex' alveolar structure and two ancestral characters within Thalassiosirales, presence of areolae and fultoportulae in the central area (Ács et al. 2016).

Ancestral features are, by definition, not diagnostic of any particular group, so the use of ancestral characters as diagnostic features (i.e., putative synapomorphies) leads to confusion about how to classify and place taxa with a mix of 'diagnostic' ancestral and derived characters. This is evident, for example, in applying the *Cyclotella*/*Lindavia*/*Pantocsekiella* diagnoses of Ács et al. (2016) to fossil *Cyclotella* species from diatomites in the western USA. According to the emended diagnoses of Ács et al. (2016), loculate areolae and domed cribra on the valve face would place *Cyclotella kansasensis* Hanna and *Cyclotella pseudokansasica* Khursevich & Kociolek into their narrowed concept of *Lindavia* (*Lindavia* sensu stricto), but these species lack valve face fultoportulae (cf. *Pantocsekiella*), have a radially oriented rimoportula located on a mantle costa within the ring of marginal fultoportulae (cf. *Cyclotella*), and like many cyclotelloids have striae that are roughly equal in length (Kociolek & Khursevich 2013). Likewise, *Cyclotella stoermeri* Khursevich & Kociolek has most of the characteristics of *Lindavia* s.s., such as striae of unequal lengths, loculate areolae on the valve face with domed cribra and 'complex' alveolar chambers, but this species lacks fultoportulae on the valve face (Kociolek & Khursevich 2013). Although the character conflicts appear to confound placement of *C. kansasensis*, *C. pseudokansasica*, and *C. stoermeri* into any one genus, the characters showing apparent conflict are either phylogenetically widespread and ancestral (e.g., domed cribra and unequal striae) or highly variable (e.g., equal vs. unequal striae length) within the cyclostephanoids (sensu Theriot et al. 1987).

Many fossil diatoms possess a mix of ancestral and derived characters that place them outside extant genera and, as transitional lineages, reveal the temporal sequence and character order of morphological change through time. Miocene- and Pliocene-aged diatomite deposits from the western USA are rich in fossil Thalassiosirales and have, as a result, provided many insights into the evolution of this group (Theriot & Bradbury 1987, Bradbury & Krebs 1995). We characterized a diatom deposit located in the Chalk Hills Formation, near Fayette, Idaho, USA. The diatom assemblage from this sample was nearly monotypic (Fig. 1), dominated by a single cyclotelloid diatom with a novel combination of ancestral and derived morphological characters. The unique set of features led to the establishment of a new genus, *Fascinorbis*, which we suggest represents an important transitional form in the evolution of the *Lindavia* s.l. diatom lineage.

Materials and methods

A sample of diatomite was collected from an exposure at the Lower Ringer Gulch, 18 km east-northeast of Payette, Idaho (coordinates: 44.1134, −116.7052; NAD27). The diatomite was part of the Chalk Hills Formation (Late Miocene, ~9–5 Ma) and was collected by Renee Love and Reed Lewis of the Idaho Geological Survey (Sample 17RLB004b) in 2017 as part of a geologic mapping project involving the Lake Idaho diatomites (Idaho Geological Survey 2018, Lewis et al. 2018). Material from the site was shipped to the Indiana State University (ISU) Paleolimnology Laboratory for analysis.

We gently broke the sample into small pieces before treatment with 30% hydrochloric acid at room temperature for 15 days. We rinsed the samples four times, air dried the cleaned diatoms onto glass coverslips, and used Naphrax mounting medium (Brunell Microscopes, Chippenham, UK) to permanently mount the coverslips onto slides. Light microscope (LM) observations were conducted using a Leica DRM2500 light microscope with a digital camera at 1000 × magnification using differential interference contrast. For scanning electron microscope (SEM) observations, we air dried the cleaned diatoms directly onto aluminium specimen mounts, attached these to aluminium stubs with carbon tape, and coated the mounted specimens with gold using a Denton Desk V coater (Denton Vacuum, LLC) for 1.5 min at 50 amps (~500–1000 Å thick). We used a TESCAN Vega 3 (Tescan USA, Inc) at an acceleration voltage of 10 kV for SEM imaging.

Morphometric analysis of the population included LM measurements of 51 valves, selected to represent the full range of observed specimens within the sample. Morphometric analyses included the diameter of the valve (µm), diameter of the central area (µm), and costa density. Costa density (costae per 10 µm) was calculated according to Spaulding et al. (2019) as (the total number of costae on the valve * 10)/valve circumference (µm).

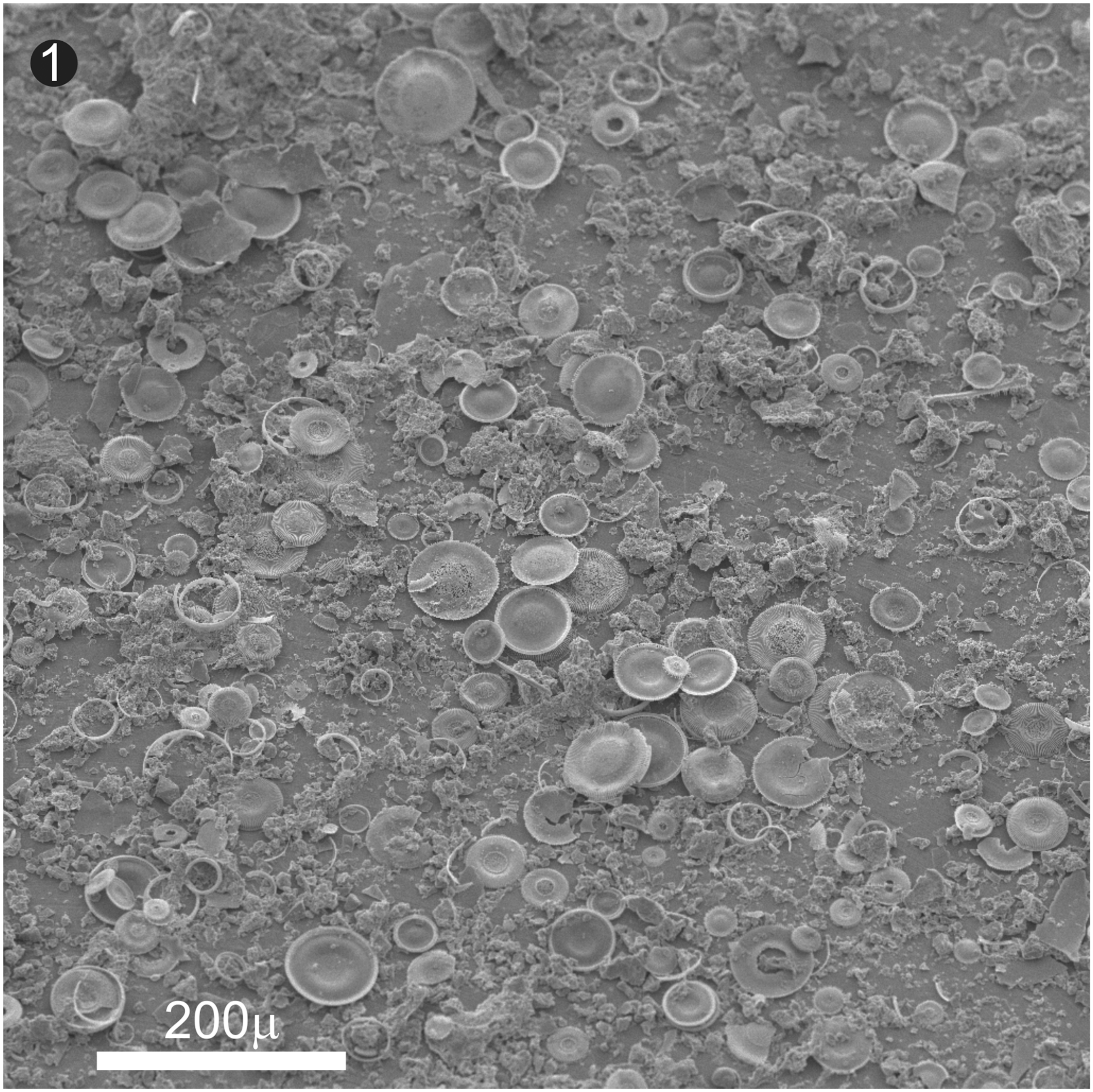


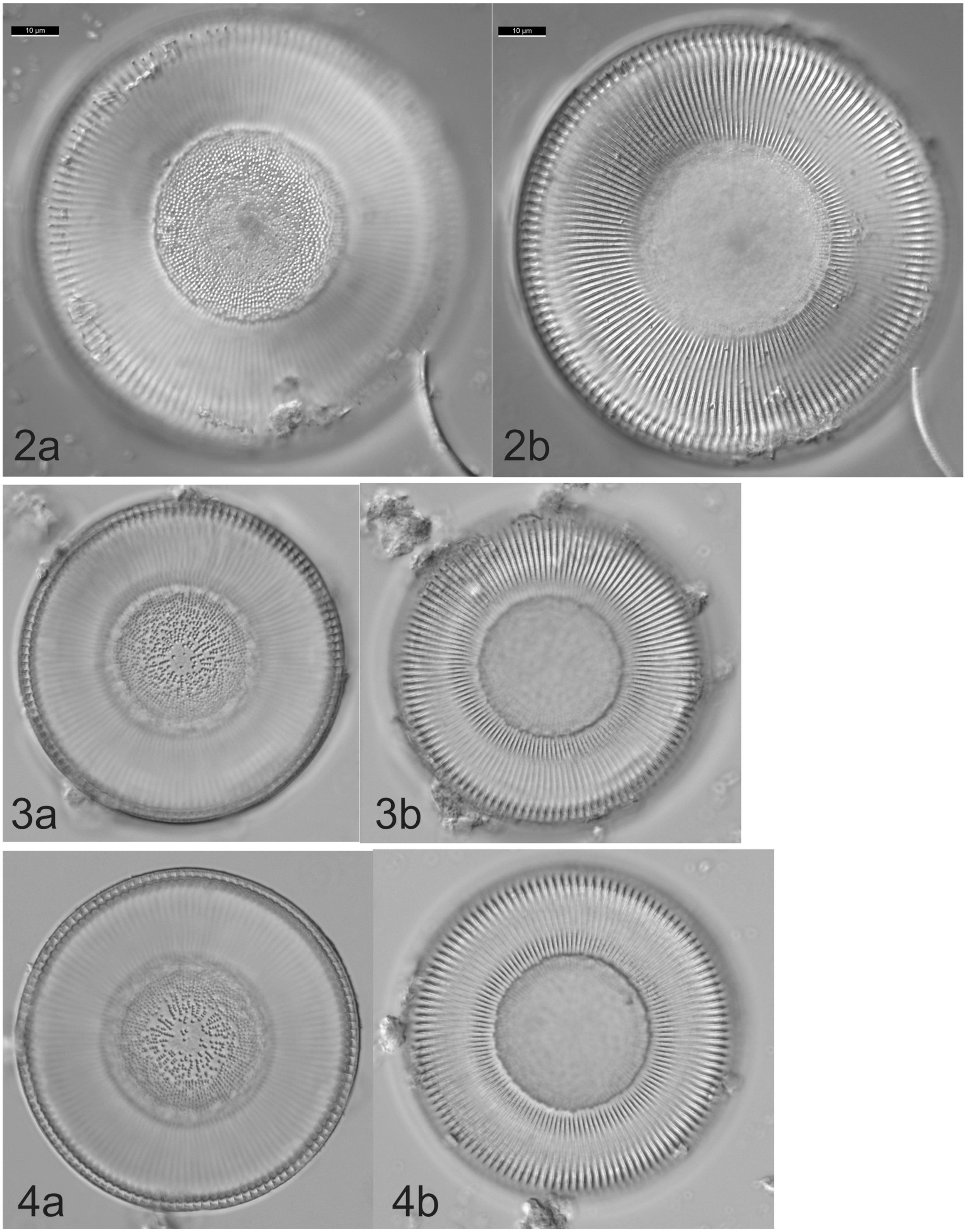
Fig. 1. Wide scanning electron microscope view of Sample 17RLB004b from the Chalk Hills Formation diatomite. Image collected with working distance 7 mm, 10 kV, 30° tilt. Scale bar 200 µm.

Results

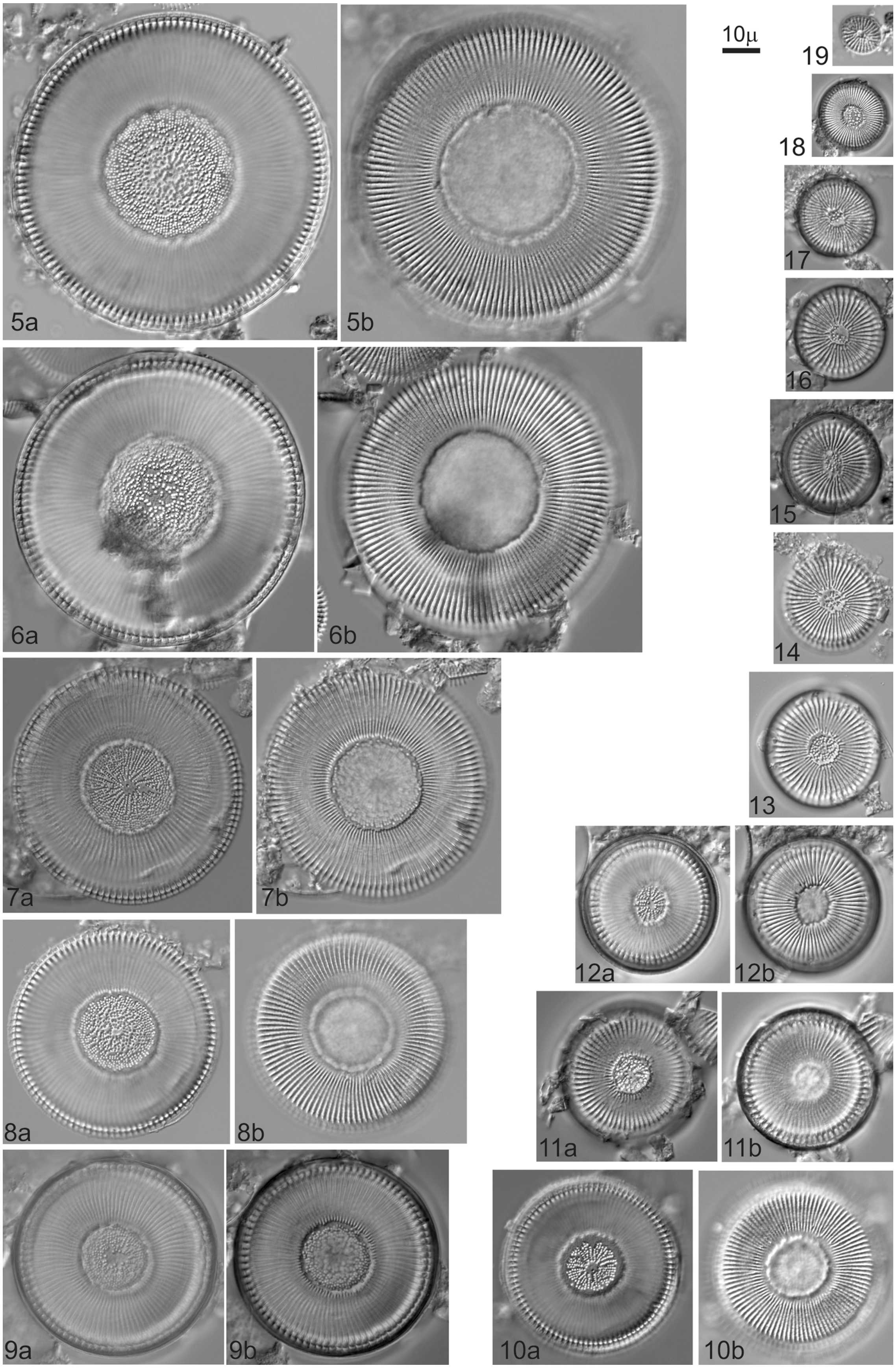
Fascinorbis Jeff.R.Stone, Edlund & A.J.Alverson gen. nov.

Description

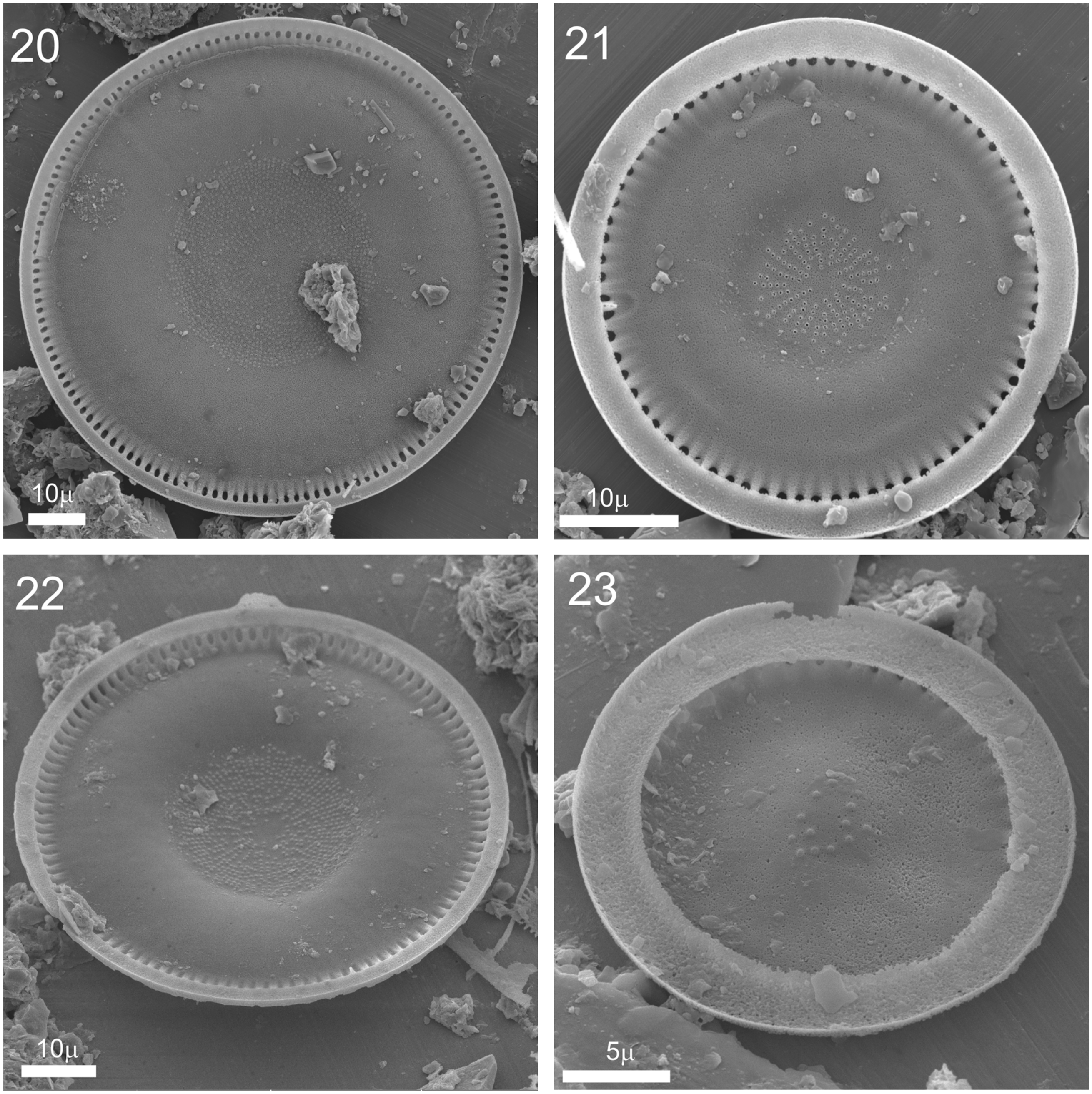
Valves circular, rarely oval, valve face concentrically undulate. Internally, the marginal zone extends from 1/3 to 1/2 of the valve radius and consists of radial alveolae with hyaline laminae covering the internal surface of the alveolae on the valve face. Alveolae open internally by oval foramina located at the face-mantle junction. Radiate alveolae are separated internally by costae, and multiseriate striae are visible within the alveolae, lining the outer siliceous layer of the valve. Central area areolate. Areolae occluded internally with domed cribra. Central fultoportulae absent. A single ring of fultoportulae on the valve mantle; marginal fultoportulae located on every second to third costa. Mantle fultoportulae bearing three satellite pores, with well-developed cowlings and broad satellite pore covers. One or two sessile rimoportulae located on the



Figs 2–4. Light microscope images of the type specimen (Figs 2a, 2b), and isotype specimens (Figs 3a, 3b, 4a, 4b) of *Fascinorbis illustris*, showing high and low focal elevations. All specimens scaled to the 10 µm scale bars in Figs 2a/2b.



Figs 5–19. Light microscope images of a size series of *Fascinorbis illustris* from Sample 17RLB004b. All images at the same magnification; scale bar 10 µm.



Figs 20–23. Scanning electron microscope images of *Fascinorbis illustris* displaying internal views of the valve. Images in Figs 20 and 21 collected with working distance 4 mm, 10 kV; images in Figs 22 and 23 collected with working distance 7 mm, 10 kV, 30° tilt. Scale bars 10 µm (Figs 20–22), 5 µm (Fig. 23).

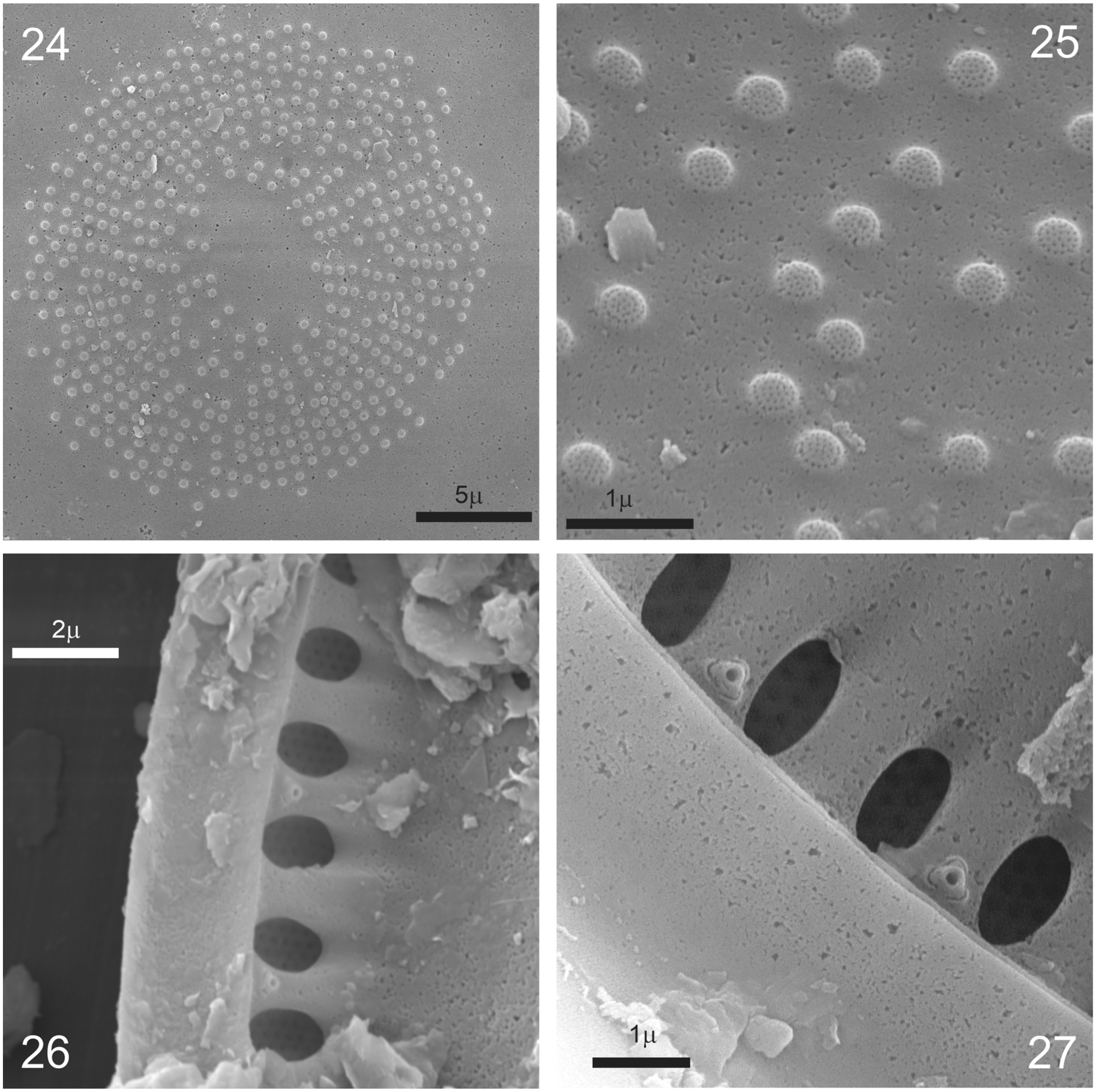
mantle on costae; rimoportulae opening oriented radially and just slightly advalvar to or within the ring of marginal fultoportulae.

Externally, mantle–face junction broadly sloped, usually marked by a single ring of cone-shaped spines, a spine on every costa. Costae mostly linear to lanceolate, may branch near central area on small valves; striated margin spans from central area to mantle edge; striae bi- to multiseriate and separated by costae. Central area thickened, areolae open externally with simple round foramina. Mantle fultoportula openings are distinct, occurring as a short, thickened tube; rimoportula openings slightly larger, external tube absent.

Type species: *Fascinorbis illustris* Jeff.R.Stone, Edlund, & A.J.Alverson

Etymology: Named for its charming appearance (*fascino*) and disk-shaped (*orbis*) valves

Comments: This genus is distinguished by the presence of simple marginal alveoli, spines usually on the external



Figs 24–27. Scanning electron microscope images of *Fascinorbis illustris* displaying characteristic interval valve features including the internally domed cribra in the central area without central fultoportulae (Figs 24, 25) and mantle fultoportulae located on costae with 3 satellite pores (Figs 26, 27). Images in Figs 24 and 27 collected with working distance 5 mm, 10 kV; images in Figs 25 and 26 collected with working distance 7 mm, 10 kV. Image in Fig. 25 with 30° tilt. Scale bars 5 μm (Fig. 24), 2 μm (Fig. 26), 1 μm (Figs 25, 27).

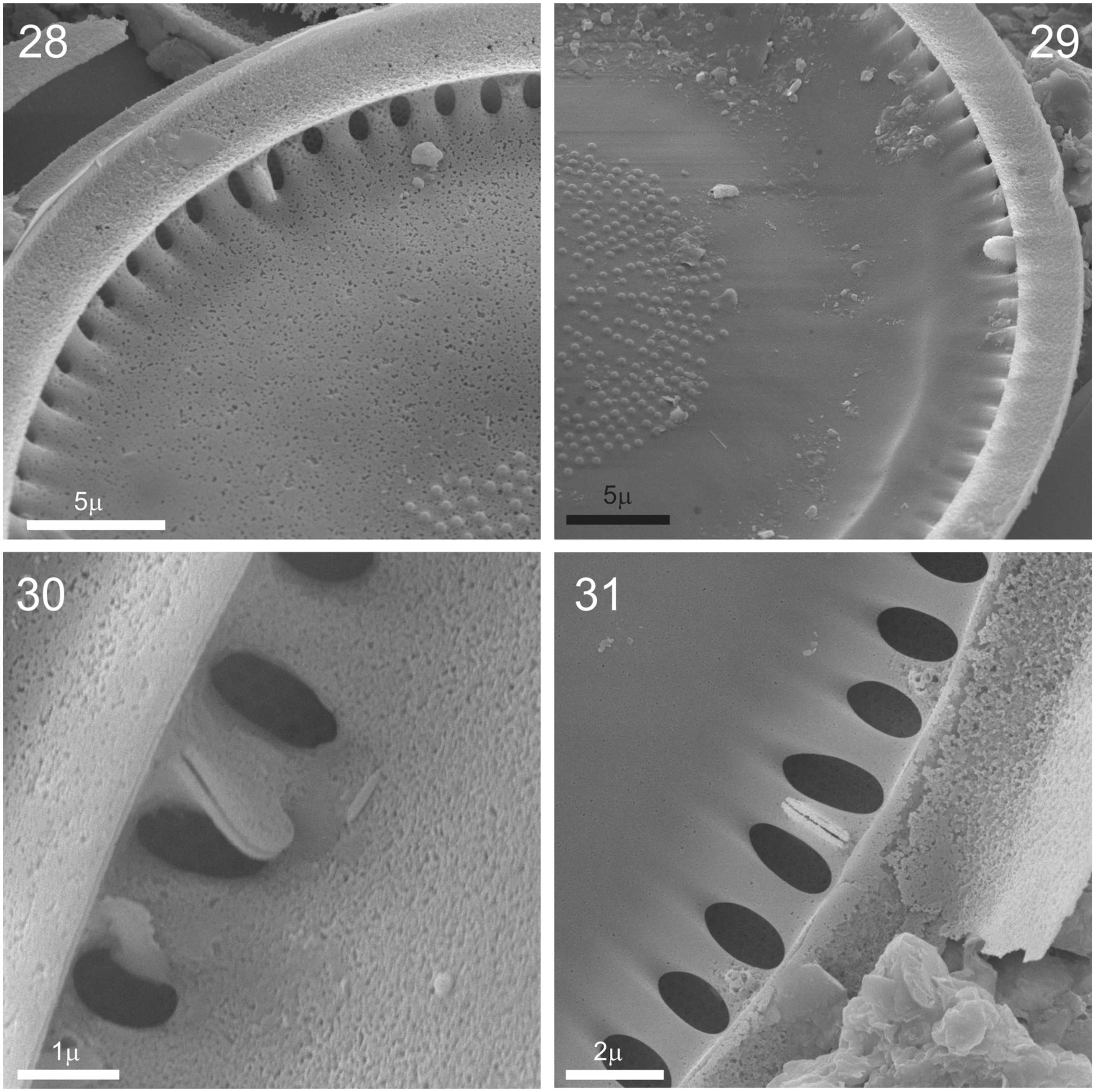
valve face-mantle junction, rimoportula(e) on the valve mantle located on a costa, lack of central fultoportulae, mantle fultoportulae with three satellite pores with well-developed cowlings and broad satellite pore covers, and a well-defined central area with loculate areolae bearing internal domed cribra.

Fascinorbis illustris Jeff.R.Stone, Edlund & A.J.Alverson, sp. nov.

Holotype: Circled specimen on slide ANSP GC-65330 (Fig. 2).

Isotypes: Circled specimen on slide CANA 128534 (Fig. 3). Circled specimen on slide ANSP GC-65331 (Fig. 4).

Type locality: Lower Ringer Gulch, Chalk Hills Formation (44.1134°, −116.7052°; NAD27), Payette County, Payette, Idaho, USA. Collected by Renee Love and Reed Lewis of the Idaho Geological Survey, 2017 (Sample



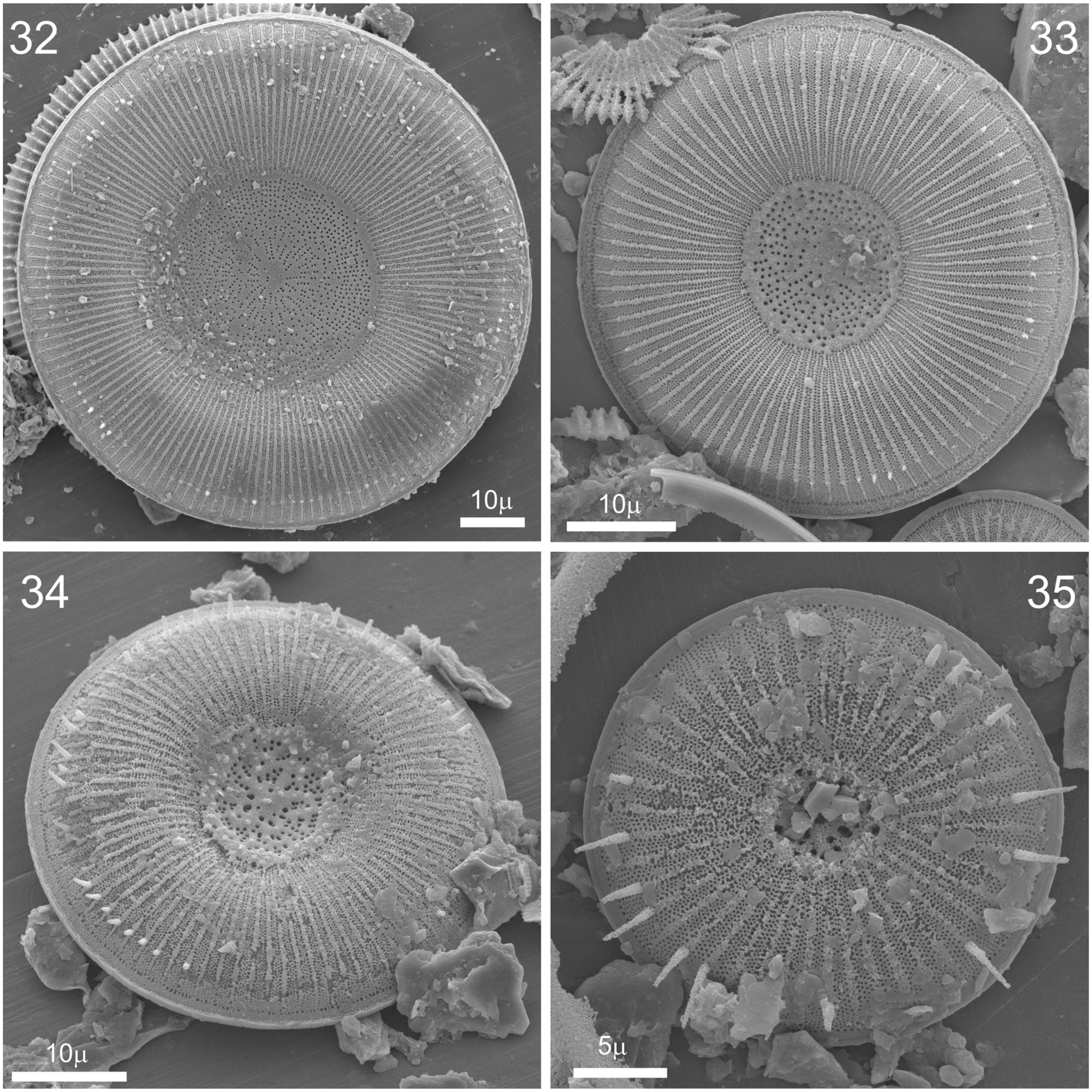
Figs 28–31. Scanning electron microscope images of *Fascinorbis illustris* displaying characteristic radially-arranged rimoportula (28–31), located on a costae and typically associated with a small depression on the valve face (28, 29). Images in Figs 28 and 29 collected with working distance 4 mm, 10 kV, 30° tilt. Image in Fig. 30 collected with working distance 5 mm, 10 kV; image in Fig. 31 collected with working distance 7 mm, 10 kV. Scale bars 5 µm (Figs 28, 29), 2 µm (Fig. 31), 1 µm (Fig. 30).

17RLB004b; ANSP material GC-5764, CANA material 128534).

Etymology: The species is named for the distinct and radiant structure of the costae.

Description:

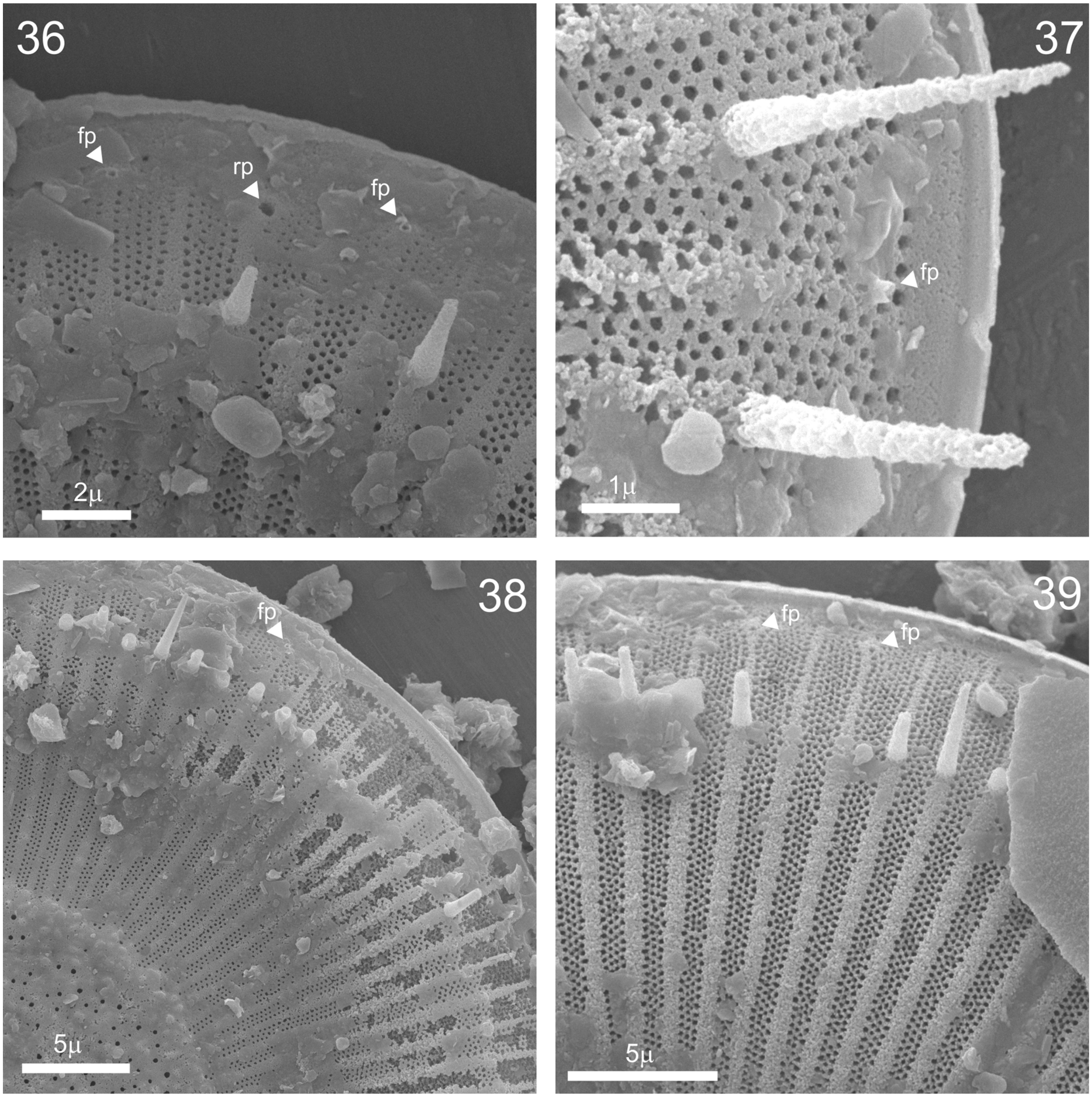
Valves circular, slightly oval in small specimens (Figs 16–19), valve face concentrically undulate, 11.6–93.5 μm in diameter (Figs 5–19). Internally, a wide unornamented area spans from face-mantle junction to a central area defined by undulation of the valve face and the presence of areolae occluded by domed cribra (Figs 20–25). Areolae of the central area arranged, sometimes loosely, in radiating rows (areolae 14–18/10 μm) of unequal length that stop before reaching the centre of the valve; centremost area of valve typically unornamented (Fig. 24). Central fultoportulae



Figs 32–35. Scanning electron microscope images of *Fascinorbis illustris* displaying characteristic external valve features, including concentric undulation (Figs 32–35) and a ring of spines at the mantle/face junction (Figs 34, 35). Images in Figs 32 and 35 collected with 10 kV, working distances 4 and 5 mm, respectively; images in Figs 33 and 34 collected with 10 kV, working distance 7 mm. Scale bars 10 μm (Figs 32 and 34), 5 μm (Fig. 35).

absent. Alveoli each open internally by a small foramen (typically 1–1.5 μm in diameter), slightly elongated toward the advalvar margin (Figs 26 and 27). Mantle fultoportulae with three satellite pores, well-developed cowlings, and broad satellite pore covers on the central tube; mantle fultoportulae occur on every other or every third costa, very close to valve margin (Figs 26 and 27). Rimoportulae (1 or 2) sessile, slit radially oriented, located on costae slightly advalvar to ring of fultoportulae, often associated with elongated adjacent alveoli and a slight depression on the valve face (Figs 28–31).

Externally, mantle–face junction broadly sloped, marked by a single ring of cone-shaped spines on every costa (spines often missing) (Figs 32–35). Costae mostly linear (costae density 5–6/10 μm, up to 7/10 μm in small valves), rarely lanceolate, branching near central area on small valves ($< 40\,\mu$m); striated area on valve face spans from central area to mantle edge. Striae



Figs 36–39. Scanning electron microscope images of *Fascinorbis illustris* displaying close views of the external expression of the mantle fultoportula (fp; Figs 36–39), including short extensions (Fig. 37) and the slightly wider opening of the rimoportula (rp, Fig. 36) located just slightly advalvar to the ring of mantle fultoportulae. Images in Figs 36–38 collected with 10 kV, working distance 5 mm; image in Fig. 39 collected with working distance 7 mm, 10 kV. Scale bars 5 µm (Figs 38, 39), 2 µm (Fig. 36), 1 µm (Fig. 37).

multiseriate and separated by costae, typically ranging from 2 or 3 decussate rows of areolae near central area to 5 or 6 rows of punctae near mantle edge (35–42/10 μm along a radius). Central area thickened, areolae with simple round openings. Mantle fultoportula openings are distinct, occurring as a short, thickened tube; rimoportula openings slightly larger, external tube absent (Figs 36–39).

Discussion

Fascinorbis has a novel combination of ancestral and derived characters that highlight it as a transitional stage in the evolution of the *Lindavia* s.l. lineage of cyclostephanoid diatoms. *Lindavia* species typically have complex marginal alveoli, a well-defined central area with domed cribra, unequal striae, and, most critically, all *Lindavia* s.l. species share the synapomorphy of a rimoportula

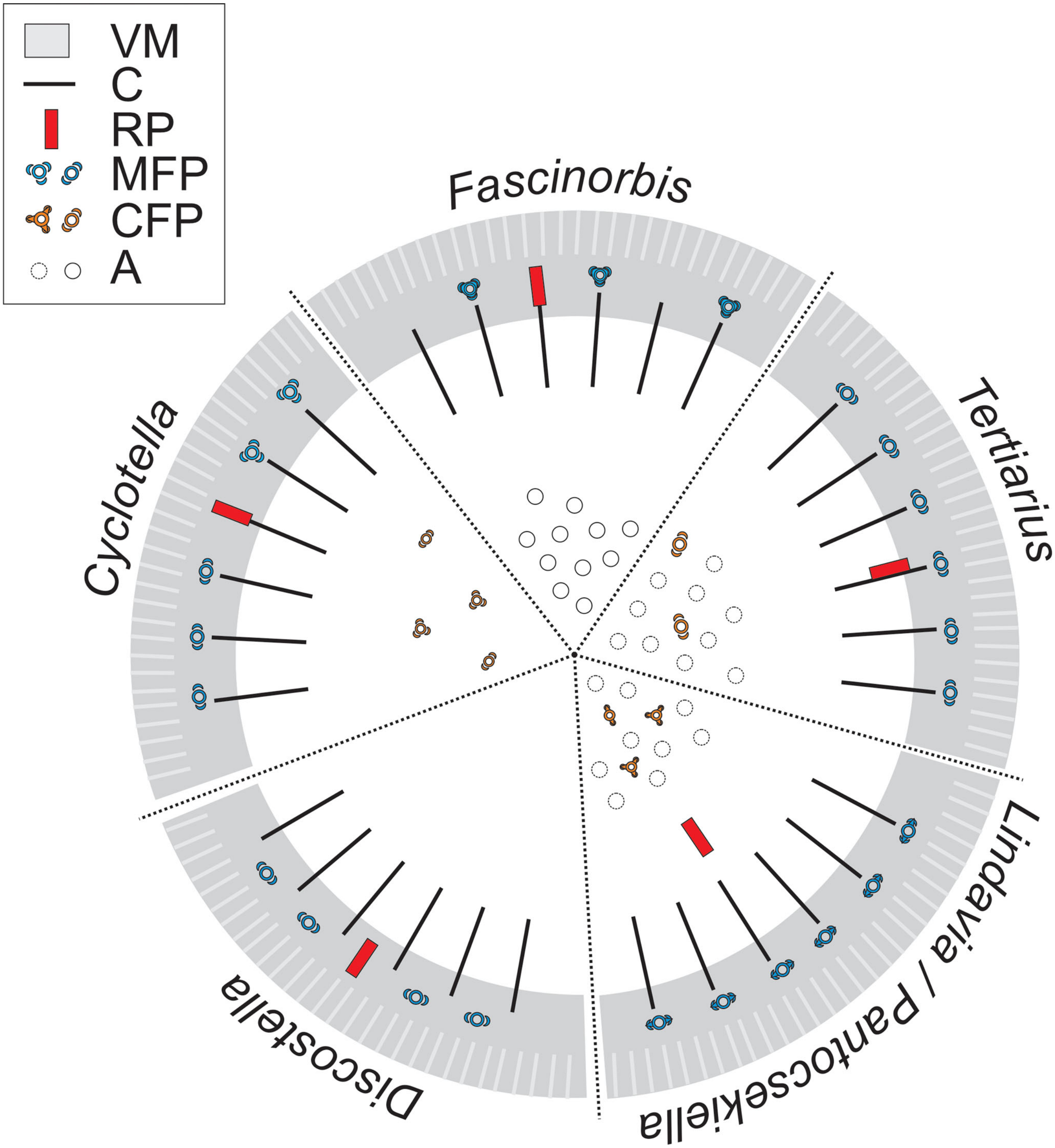


Fig. 40. Diagram highlighting distinguishing features of the genus *Fascinorbis* in comparison with four other cyclotelloid genera. Valve mantle (VM) in grey, position of rimoportula (R) shown relative to internal costae (C), position of areolae (A) on the valve face illustrated *with dashed outlines* may be *present or absent* within genera, and presence/absence and structure of central fultoportulae (CFP) and mantle fultoportulae (MFP) illustrated for comparison. Diagram concept is based on Nakov et al. (2015).

located on the valve face. Many *Lindavia* have a derived fultoportula ultrastructure as well, with satellite pore covers that have a broad attachment point to the central tube and attenuate distally, creating a distinct triangular-shaped structure that is also unique to this group (fig. 3G in Theriot & Serieyssol 1994). This ultrastructure is found in both the mantle-area (two radially oriented satellite pores) and central area (often three satellite pores) fultoportulae of *Lindavia* taxa (Fig. 40).

With domed cribra on the valve face and unequal striae, *Fascinorbis* resembles, in many respects, a typical bodanicoid species of *Lindavia*, but its rimoportula is located within the ring of mantle fultoportulae (the ancestral location), placing it outside the *Lindavia* s.l. clade. The marginal fultoportulae of *Fascinorbis* also differ markedly from *Lindavia* in that they have three, rather than two, satellite pores (Figs 26 and 27) and lack the characteristic triangular-shaped satellite pore covers (Fig. 27); instead, the satellite pore covers in *Fascinorbis* are broad and flat, resembling those in *Edtheriotia* (Kociolek et al, 2016) and many other cyclostephanoids. This combination of features suggests a phylogenetic position sister to *Lindavia* s.l and, if this hypothesis is upheld, provides insight into the sequence of character evolution in this clade. That is, many of the diagnostic features of *Lindavia*, including complex alveolae and a well-defined areolate central area with domed cribra, were present prior to relocation of the rimoportula off the valve mantle and evolution of the triangular-shaped satellite pore covers.

The hypothesized phylogenetic position of *Fascinorbis* compelled us to either broaden the definition of *Lindavia* s.l. or erect a new genus. However, the rimoportula position so clearly and accurately diagnoses *Lindavia* s.l. that obscuring this definition to include a mix of ancestral and derived rimoportula positions would devalue this character and encourage follow-up classification schemes not based on phylogenies or on phylogenetic reasoning. In short, the new species described here was not placed in a new genus simply because it surpassed some arbitrarily applied threshold of morphological differentiation from existing genera (Williams 2009), a practice that leads to ambiguous or non-natural classification schemes (Williams 2013). Based on our phylogenetic interpretation, *Fascinorbis* does not render any of the remaining cyclostephanoid genera non-monophyletic, a consideration that should, but rarely does, accompany the establishment of new genera (Kociolek & Williams 2015).

As far as we are aware, *Fascinorbis* is an extinct genus. It should be noted that the combination of characters that define *Fascinorbis* are shared with several Miocene to Pliocene fossil taxa currently assigned to *Cyclotella* (e.g., *C. kansasensis*, *C. pseudokansasica*, *C. stoermeri*) from sediments of ancient lake systems that are arrayed in a narrow biogeographic range in the western US (McLaughlin 1992, Kociolek & Khursevich 2013). Like *F. illustris*, the location of the rimoportula on the mantle, combined with the presence of domed cribra on the valve face, indicates that these taxa do not belong to any existing genus, but instead also represent transitional forms in the evolution of the *Lindavia* s.l. lineage. However, in the absence of an obvious synapomorphy supporting monophyly of these four species, they might be considered, under further analysis, to belong to *Fascinorbis*. Like many fossil diatoms, these species present a special challenge in creating natural classification systems.

In general, ancient lake sediments represent only a fraction of the lakes that once existed on Earth. Because geological processes are constantly at work to gradually erase terrestrial archives on the continents, ancient lake sediments extending beyond even the last one million years are uncommon. Lacustrine diatomite deposits still hold a wealth of information to be discovered, including new diatom species that are likely to reshape our understanding of the relationships among extant genera (Wolfe et al. 2006, Siver et al. 2016). As we continue to explore the remnants of these ancient systems, they will continue to shape our understanding of diatom diversity and character evolution through time.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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