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Fideliacyclus wombatiensis gen. et sp. nov. – a Paleocene non-marine centric diatom from northern Canada with complex frustule architecture

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Marine diatoms began colonizing freshwater habitats in the early Cenozoic, or possibly earlier, becoming well established by the Eocene. However, because of a sparse fossil record, little is known about the earliest diatom representatives that signalled this important ecological and evolutionary event. We describe a new centric diatom genus, *Fideliacyclus*, from lake sediments deposited during the Paleocene in the Canadian Arctic. This organism, one of the oldest known freshwater diatoms reported to date, has a unique, highly complex wall structure composed of areolae with large, bulbous, spherical shaped chambers that are open to the external environment but rest on a solid siliceous surface referred to as the solum, and are surrounded by an open space, or hypocaust. The solum is only perforated by marginal labiate processes, which largely isolates the protoplast from ambient conditions hence limiting exchange; this may have represented an adaptive response to living in freshwater. Given the complement of microfossils found in the fossil locality, the lake was an unambiguously softwater, slightly acidic, limnic system of moderate nutrient content. Although the exact taxonomic position of *Fideliacyclus* remains uncertain, it appears to be most closely allied to *Actinocyclus* (Class: Coscinodiscophyceae) or possibly *Spumorbis* given the range of synapomorphies.

Keywords: *non-marine fossil diatoms, Paleocene, solum, hypocaust,* Fideliacyclus, Actinocyclus, Spumorbis

Introduction

Little is known concerning the early colonization of freshwater habitats by diatoms, under evolutionary models that assume a marine origin for the group as a whole (Sims et al. 2006, Alverson et al. 2007). Despite the apparently rapid proliferation of marine diatoms during the Cretaceous (Harwood & Nikolaev 1995, Harwood et al. 2007), the fossil record suggests that invasion of freshwater habitats began near the end of the Cretaceous (Chacón-Baca et al. 2002, Ambwani et al. 2003, Singh et al. 2006) and extended well into the early Cenozoic. However, diatoms do not appear to become prominent in freshwater environments until the middle (Strelnikova & Lastivka 1999, Wolfe & Edlund 2005; Siver et al. 2010) to late (Lohman & Andrews 1968, Benson & Kociolek 2012) Eocene. In North America, numerous and mostly large freshwater lakes in the western United States became dominated by diatoms by the Miocene (Bradbury & Krebs 1995), but far less is known about other regions of the continent, earlier time periods, and other types of habitats (Krebs 1994, Wolfe & Edlund 2005). A fuller appreciation of early Cenozoic non-marine diatoms therefore enhances our understanding of the colonization of freshwaters by marine

ancestors, and informs the character of radiations over the last 65 million years (Ma).

Chacón-Baca et al. (2002) interpreted diatom fossils from the 70-million-year-old Huepac chert deposit in Mexico as representing a freshwater habitat. Further work at this locality documented additional non-marine pennate diatoms (Beraldi-Campesi et al. 2015). If correct, these fossils would represent the oldest known freshwater diatoms. However, this has been challenged by Sims et al. (2006), and the Huepac chert has been attributed to a brackish ecotype (Singh et al. 2006). Compelling representatives of *Aulacoseira* Thwaites (Ambwani et al. 2003), *Nitzschia* Hassall and *Planothidium* Round & Bukhtiyarova (Singh et al. 2006) have been recovered from latest Cretaceous (Maastrichtian) non-marine sediments intercalated by Deccan flow basalts, provisionally representing the oldest known freshwater diatoms. *Aulacoseira* and other members of the family Aulacoseiraceae, along with araphid taxa from the family Fragilariaceae, are dominant elements of floras described from early freshwater fossil localities worldwide, mainly of Eocene age (Lohman & Andrews 1968, Krebs 1994, Wolfe & Edlund 2005, Benson & Kociolek 2012). *Eoseira* Wolfe & Edlund, another

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aulacoseiroid genus distinguished in part by its extraordinarily, large linking and separation spines, was described from middle Eocene shales in western Canada and is regarded as one of the oldest genera of freshwater diatoms (Wolfe & Edlund 2005). Unlike most freshwater genera from the Eocene that retain modern congeners, *Eoseira* appears to be extinct.

The centric genus *Actinocyclus* Ehrenberg was a dominant component of the plankton in freshwater lakes during the Miocene, often co-occurring with *Aulacoseira*, *Melosira* C.A. Agardh and *Ellerbeckia* R.M. Crawford in Europe (Ognjanova-Rumenova & Krstič 2007), Eurasia (Khursevich & Rubina 1991, Usoltseva et al. 2010) and the western United States (Krebs 1994, Bradbury & Krebs 1995). Except for *A. normanii* f. *subsalsa* (Juhlin-Dannfelt) Hustedt, which can survive in brackish and eutrophic fresh waters, all modern species of *Actinocyclus* are obligately marine. However, numerous extinct species of *Actinocyclus* are found in lacustrine sediments of late Oligocene to early Pliocene age, reaching maximum diversity in the Miocene (Usoltseva et al. 2010). These authors have documented the oldest known freshwater *Actinocyclus* from the Oligocene of west Siberia. In what is now present day Serbia, *Actinocyclus* colonized freshwater habitats soon after the marine regression in the early Miocene (Ognjanova-Rumenova & Krstič 2007). Thus, even though many once prominent species of *Actinocyclus* eventually went extinct during the later part of the Cenozoic, this genus had successfully invaded freshwater environments multiple times since the Oligocene.

Spumorbis S. Kumora is a rare diatom thought to be closely allied with *Actinocyclus* and known only from Miocene marine sediments (Komura 1998). Like *Actinocyclus*, valves of *Spumorbis* are bullulate with a marginal ring of rimoportulae, but they differ from the former genus in lacking a pseudonodule. In addition, all three described species of *Spumorbis* can form a unique type of heterovalvar frustule that possibly represents a resting stage (Komura 1998).

This paper describes a new genus of centric diatom from the Wombat fossil locality, an early Cenozoic maar lake sequence in subarctic Canada. The new genus, representing one of the oldest known freshwater forms, is characterized by a unique, highly complex wall structure that largely isolated the protoplast from the external environment and may have represented an adaptive response to life in freshwater environments. Potential affinities to other centric diatoms, including *Actinocyclus*, *Spumorbis*, *Pseudoaulacosira* and *Melosira*, are discussed.

Materials and methods

The Wombat locality (64.73°N, 110.59°W) is a diatreme formed by phreatomagmatic volcanism in the Lac de Gras kimberlite field of the Northwest Territories, Canada (Heaman et al. 2004). The kimberlite intrudes Proterozoic country rocks (largely granodiorites) of the Slave Province. The crater was post-eruptively infilled with a long sequence of frequently laminated lacustrine sediments, and subsequently entombed under Quaternary glacial deposits. A precise age for intrusion of the Wombat kimberlite is not available, given that phlogopite ^{87}Rb/^{87}Sr ratios are contaminated by local bedrock, yielding model ages between 1.8 and 2.5 Ga (R.A. Creaser, pers. comm.). However, five distinct age clusters for the emplacement of Lac de Gras kimberlites have been defined, centering on 72, 66, 61, 54, and 48 Ma (Sarkar et al. 2015). We therefore use stratigraphic palynology to establish a provisional age for the lake sediments in the Wombat crater (Hu et al. 2011). Angiosperm pollen is abundant in Wombat sediments, including *Alnipollenites* Potonié, *Betulaceoipollenites* Potonié, *Caryapollenites imparalis* Nichols & Ott, *C. veripites* Wilson & Webster, *Ericaceiopollenites* Potonié, *Fraxinoipollenites variabilis* Stanley, *Momipites coryloides* Wodehouse, *M. tenuipolus* Anderson, *Plicatopollis triradiatus* (Nichols) Frederiksen & Christopher, and *Triporopollenites bituitus* (Potonié) Elsik. The abundance of angiosperm taxa relative to gymnosperms and spores, coupled with the conspicuous absence of Late Cretaceous index taxa *Aquilapollenites* Rouse and *Wodehouseia* Stanley, effectively eliminate a Maastrichtian or older age for the Wombat post-eruptive sediments. On the other hand, the abundance of *Ericaceiopollenites* and *Alnipollenites*, coupled with the absence of *Platycarya swasticoides* (Elsik) Frederiksen & Christopher and *Pistillipollenites macgregorii* (Rouse), implies that the deposit is older than Eocene. We therefore surmise that a Paleocene age is most probable for the Wombat post-eruptive sequence. This suggests that emplacement of the Wombat kimberlite most likely occurred during the regionally recorded 61 Ma pulse (Sarkar et al. 2015), while not eliminating the possibility of a Late Cretaceous emplacement with crater sedimentation beginning at some later point after the K-Pg transition.

A 386.7 m drill core was recovered from the Wombat locality by BHP Billiton Diamonds Inc. in 1993. The 227.6–386.7 m section of the core represents laminated aquatic sediments contained in core boxes 43 (youngest) through 67 (oldest). The majority of sediments, down to approximately box 62, contain significant mineral content, while boxes 62–65 are more organic and have significantly lower density. Each box contains four 1.5 m core lengths, identified as channels 1, 2, 3, and 4. Each sample from the core is identified with a three number code: the first represents the core box number (43–67), the second the channel within the box (1–4), and the third the depth in the channel in question (0–150 cm). For example, sample 65-1-130 represents a sample taken from 130 cm down the core length positioned in channel 1 from box 65. This study focuses on samples taken from 7 m of core contained in boxes 64 and 65.

Rock chips (0.1–0.5 g) from the Wombat core were oxidized using 30% H_2O_2 under low heat for a minimum

of an hour, rinsed with distilled water, and the resulting slurries stored in glass vials. This mild oxidation procedure yields separation of small fragments each containing many embedded microfossils, as well as isolated specimens. Other chips were subjected to a strong acid treatment involving a mixture of potassium dichromate and sulphuric acid. Aliquots of each slurry were air dried onto pieces of heavy duty aluminium foil. The aluminum foil samples were trimmed, attached to aluminum stubs with Apiezon® wax, coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and examined with a Leo 982 field emission scanning electron microscope (SEM) or an FEI Nova SEM. Measurements reported were made directly from SEM observations or from digital images.

Results

Taxonomic diagnoses

Fideliacyclus P.A. Siver, A.P. Wolfe and M.B. Edlund gen. nov. (Figs 1–18)

Frustules and valves circular in valve view, rectangular in girdle view, not joined to form filaments. Valve face flat, forming a right angle with the mantle, and with a thick, complex wall structure. Rimoportulae widely and unevenly spaced in a ring on valve margin. Internally, rimoportulae open onto valve face margin or upper part of mantle. Rimoportulae thickened nodules of silica, lacking stalks, and each with a thin slit aligned perpendicular to a tangent to valve margin. Externally, each rimoportula forms a circular opening on the upper mantle, flush with the valve surface. Pseudonodules are absent. Transverse section of the valve wall is divided into three components, the external surface, middle compartment, and internal solid surface. Areola large, each with a bulbous, spherical shaped chamber within the middle wall, not occluded externally, attached to solid internal basal siliceous layer herein referred to as the solum. Upper part of areolar chamber of similar diameter to external opening, lower part constricted where attached to solum. Areolae widely spaced, separated by hypocaust forming a continuous enclosed space within the cell wall. Mantle areolae with cylindrical chambers. Solum solid, smooth, lacking internal openings except for rimoportulae.

Fideliacyclus wombatiensis P.A. Siver, A.P. Wolfe and M.B. Edlund sp. nov. (Figs 1–19)

Valves are circular, flat, 9.5–17.0 μm in diameter (mean = 13.3 μm, *n* = 25), with a thick, complex wall structure (Figs 1–18). The shallow mantle forms a right angle with the valve face (Figs 1–2, 4), and ranges in height from 2.7 to 4.0 μm. Rimoportulae are widely and unevenly spaced, usually at least 5 μm apart, in a ring along the valve margin (Figs 3–6). Internally, the rimoportulae open

near the valve face margin, but on smaller valves they may be positioned on the upper part of the mantle. The rimoportulae are thickened nodules of silica that lack stalks, opening internally by a radially aligned thin slit (Figs 5–6). Externally, the rimoportula is a circular opening on the upper portion of the mantle, flush with the valve surface (Fig. 14, arrowheads). Each rimoportula opens to the inner valve wall through a cylindrical tube (Figs 17–18, arrows), but a direct connection with the exterior of the valve was not observed.

The valve wall is divided into three distinct components, the external surface, middle compartment, and internal solid surface (Figs 17, 19). The external surface of the valve face is smooth and covered with relatively evenly spaced foramina 110–245 nm in diameter (mean diameter 150 nm) (Figs 1–2, 7–9). Each foramen connects to a large, bulbous, spherical shaped chamber within the middle region of the wall (Figs 10–12, 19). The upper portion of the chamber is similar in diameter to the external opening, whereas the inner spherical section of the chamber expands to approximately 400–450 nm (Figs 10–13, 19). Each chamber is secured to the internal solid surface, referred to herein as the solum or floor. The base of the chamber becomes slightly constricted where it attaches to the solum. The middle portion of the wall surrounding the spherical chambers forms a continuous space, referred to as a hypocaust. In intact valves the hypocaust would form an enclosed space, sealed from the external environment (Figs 11, 19). Mantle wall structure is like that on the valve face, except that the areolar chambers are more cylindrical rather than spherical (Figs 10, 13). The transition from spherical to cylindrical chambers is abrupt and occurs over a short distance near the margin of the valve face (Figs 10, 13). Areolae are usually aligned into striae on the mantle. The base of the mantle is thickened (Figs 3–5, 7).

The solum, upon which the areolar chambers rest, is solid, smooth, and except for the rimoportulae, lacks any opening to either the internal portion of the wall or the external surface (Figs 5–6, 11). The solum ranges in thickness from 110 to 150 nm over the valve face and mantle, and is slightly thicker at the junction between the valve face and mantle.

Holotype specimen: The specimen on SEM stub CANA 123970 deposited at the Canadian Museum of Nature and illustrated in Fig. 1. Material from section 65-3-30 of the BHP Billiton exploration core, Wombat kimberlite (64.73°N, 110.59°W), collected by P.A. Siver and A.P. Wolfe.

Etymology: The genus name is derived from the Latin words *Fidelia* meaning earthen vessel or vase, depicting the morphology of the inner portion of the areola, and *cyclus* for the circular outline of the valve face. The specific epithet is named after the Wombat kimberlite fossil locality.
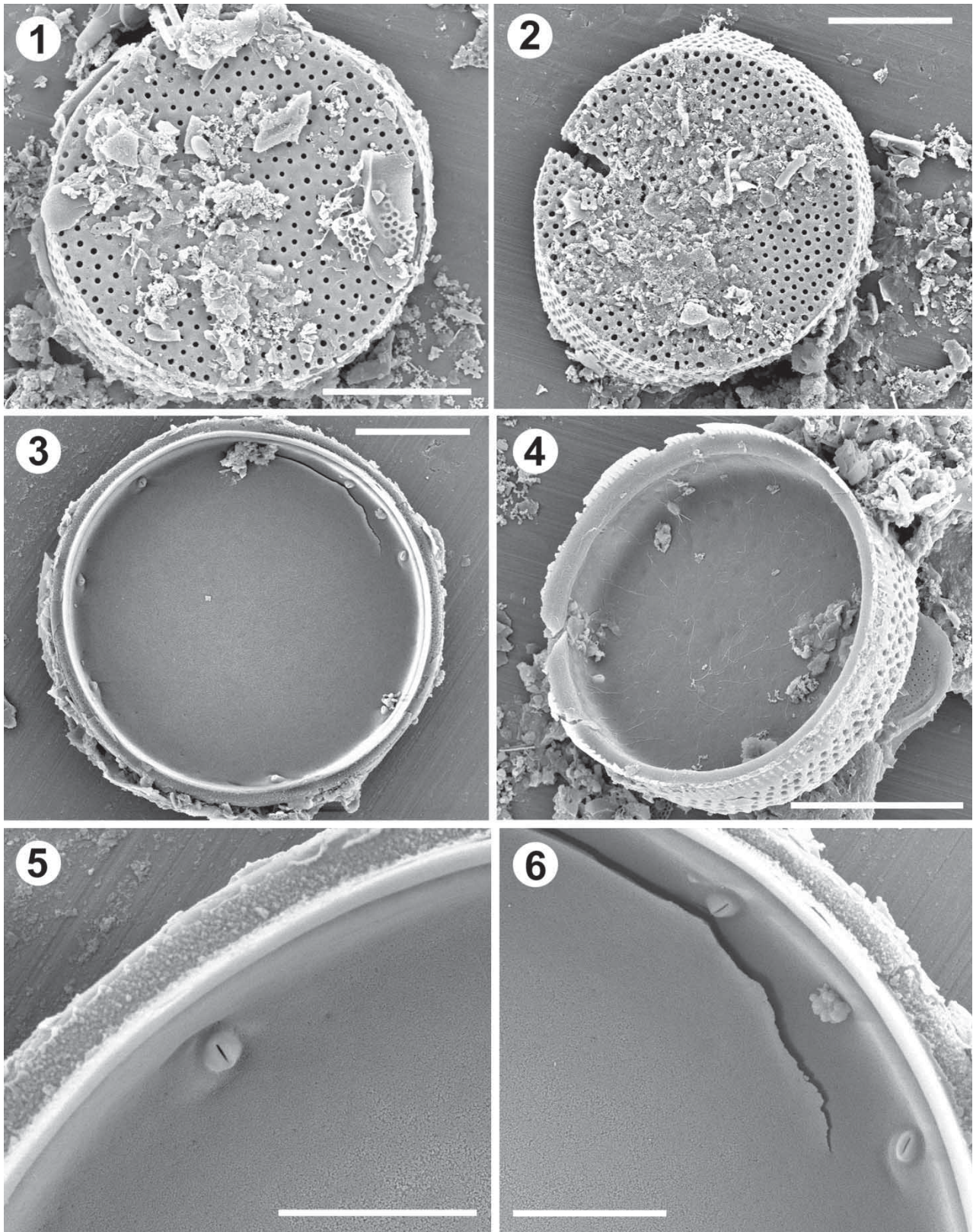
Figs 1–6. Scanning electron micrographs of *Fideliacyclus wombatiensis*. Figs 1–2. External views of whole valves depicting the arrangement of areolae on the valve face. Note the open foramina and right angle formed between the valve face and mantle. Fig. 1 is the holotype specimen. Figs 3–4. Internal views of whole valves showing the solid internal surface (solum), the uneven arrangement of the rimoportulae in a marginal ring, and the thickened base of the mantle. Figs 5–6. Details of the rimoportulae and solid nature of the solum. The rimoportulae are simple swollen siliceous nodules that lack a stalk and with the slit aligned perpendicular with the valve face margin. Scale bars = 5 μm (Figs 1–4) and 2 μm (Figs 5–6).
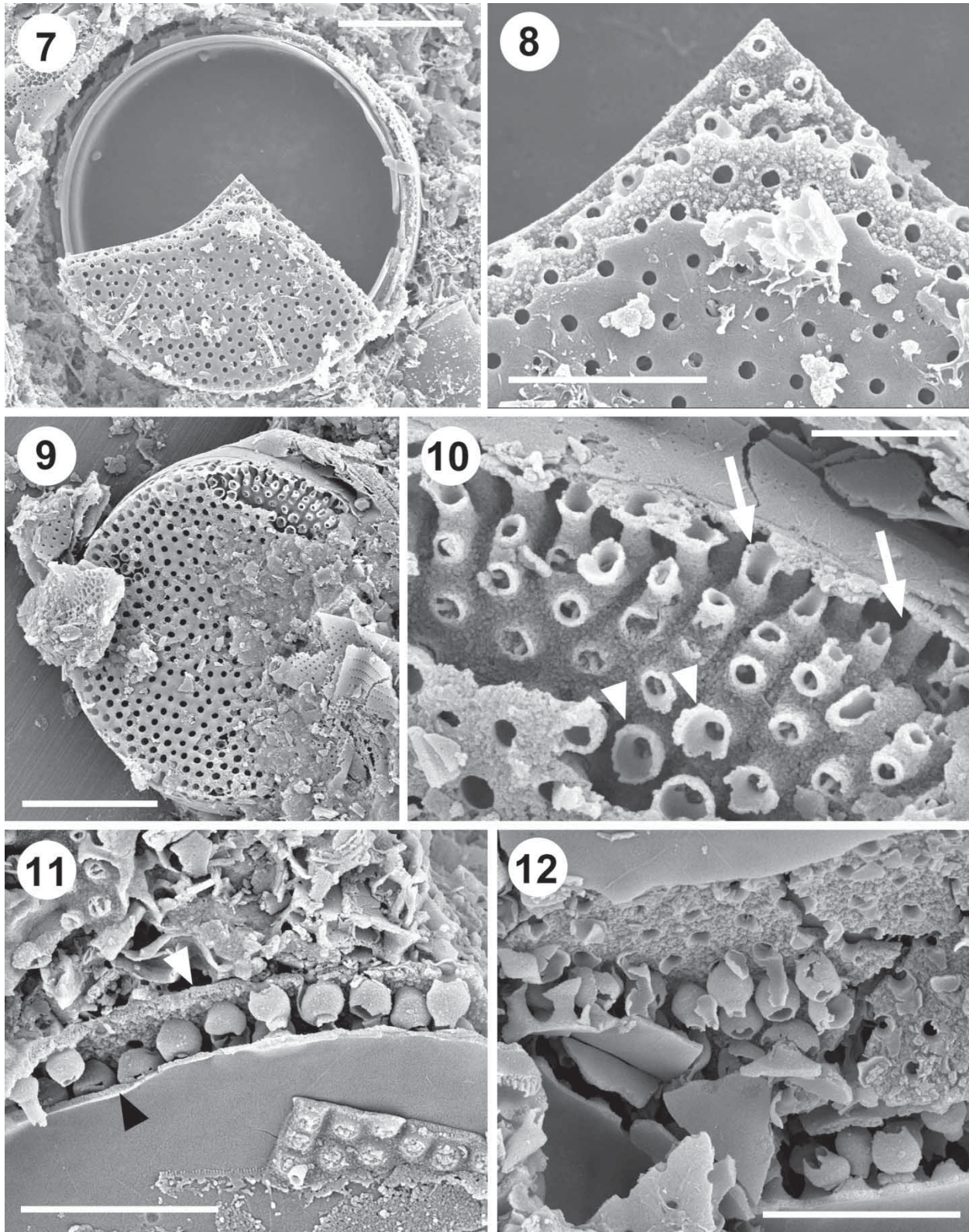
Figs 7–12. Scanning electron micrographs of *Fideliacyclus wombatiensis*. Fig. 7. Fractured frustules depicting the areolate valve face on one valve, and the solum and marginal rimoportulae on the sibling valve. Fig. 8. Close-up of Fig. 7 showing the layered nature of the valve wall including the smooth outer surface, the chambered areolae and the solum. Fig. 9. Whole frustule with part of the outer valve wall missing along the margin. Note the arrangement of the areolae and the smooth outer surface of the valve face. Fig. 10. Close-up of the broken wall on the frustule in (Fig. 9) showing the spherical shaped chambers on the valve face (arrowheads) and cylindrical chambers on the mantle (arrows). Note the remains of a girdle band. Figs 11–12. Fractured valve walls depicting the spherical chambers surrounded by a hypocaust, and attached to a solid solum. White arrow in Fig. 11 denotes the outer surface and the black arrow the solum. Scale bars = 5 μm (Figs 7, 9), 2 μm (Figs 8, 11, 12), and 1 μm (Fig. 10).
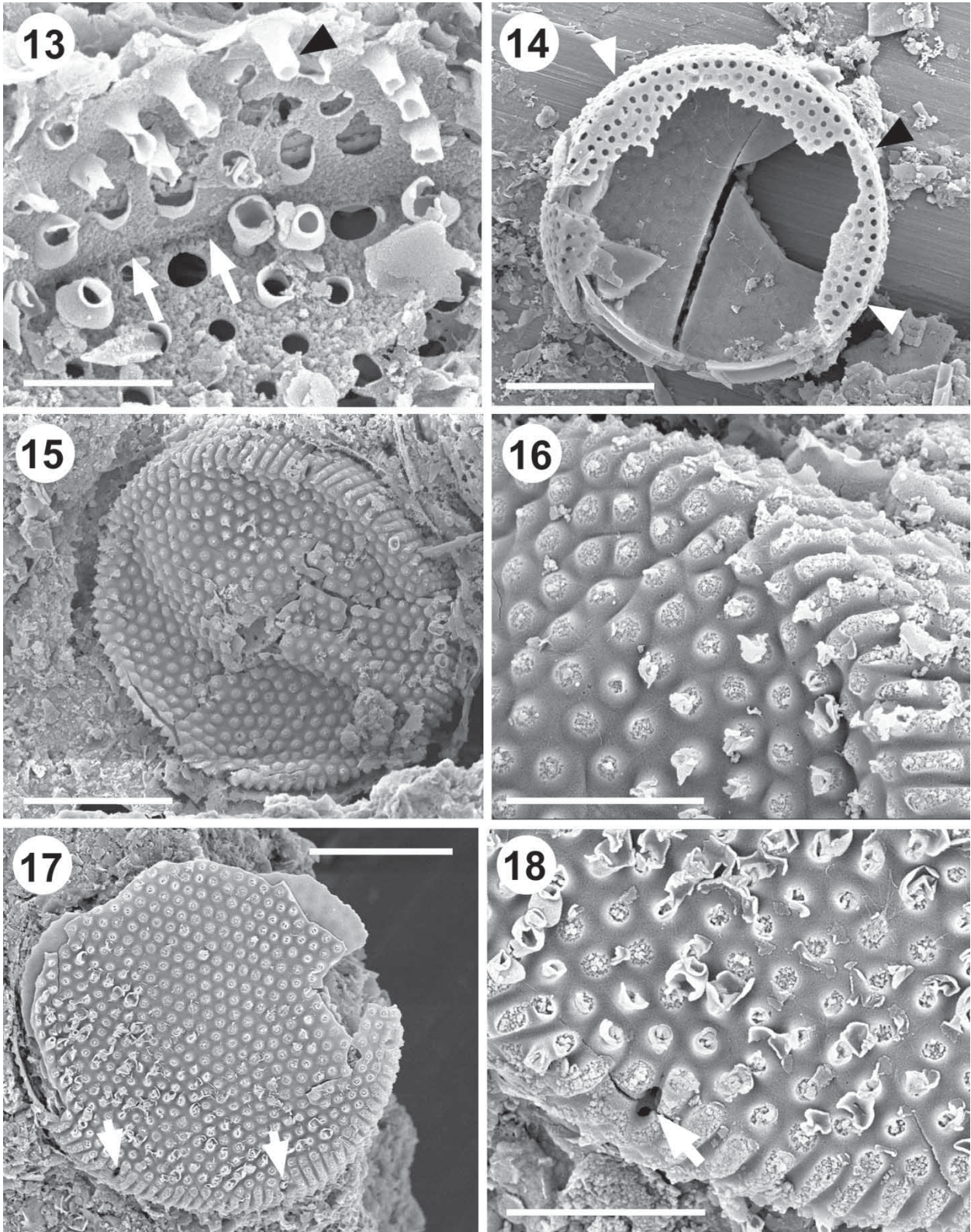
Figs 13–18. Scanning electron micrographs of *Fideliacyclus wombatiensis*. Fig. 13. Internal view of a fractured wall showing the transition (white arrows) between the valve face and the mantle. Note the spherical chambers of the areolae on the valve face, and the cylindrical shaped chambers along the mantle (black arrowhead). Fig. 14. Fractured frustule denoting the alignment of areolae, solum, thick base of the mantle, and the external positions of three rimoportulae (arrowheads). Figs 15, 17. Frustules partially embedded along a fractured rock surface, missing the outer layers of the wall exposing the outer surface of the solum where the areolae chambers attach. The arrangements of the areolae, including the striae along the mantle, and positions of two rimoportulae (arrows) are observed. Fig. 16. Close-up of a frustule missing the outer parts of the wall. Fig. 18. Close-up of the specimen in Fig. 17 showing a rimoportulae. Note the remains of the thin-walled areolae chambers. Scale bars = 5 μm (Figs 14, 15, 17), 2 μm (Figs 16, 18), and 1 μm (Fig. 13).
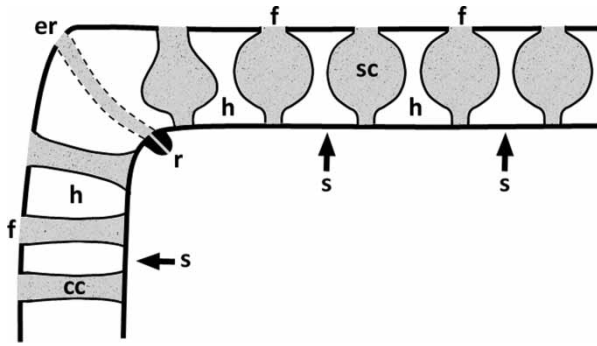
Figs 19.   Line diagram depicting the internal structure of the valve wall of *Fideliacyclus wombatiensis*. The areolae chambers and rimoportula tube (dashed line) are stippled grey. Key: **s** with arrows = location of the internal floor, or solum; **h** = hypocaust space; **f** = foramen; **sc** = spherical chamber of areola on the valve face; **cc** = cylindrical chamber of areola on mantle; **r** = rimoportula; **er** = external opening of rimoportula.

Co-occurring organisms

Fideliacyclus wombatiensis has been observed in six sections of the Wombat core spanning seven meters, 64-2-88, 64-3-65, 65-2-137, 65-3-30, 65-3-120, and 65-4-55. Numerous remains of chrysophyte cysts, synurophyte and chrysophyte scales, heliozoans, and other diatoms co-occur with *F. wombatiensis*. Scales representing at least five species of *Mallomonas* Perty, two species of *Synura* Ehrenberg, and two species of *Paraphysomonas* De Saedeleer are commonly observed within these strata, including exceptionally large numbers of *Mallomonas porifera* Siver & Wolfe and *Synura cronbergiae* Siver. Other diatoms include representatives of the genera *Eunotia* Ehrenberg, *Fragilaria* Lyngbye, *Eoseira* and *Aulacoseira*, along with specimens possibly representing extinct taxa allied to the modern genera *Asterionella* Hassall and *Pinnularia* Ehrenberg.

Discussion

Based on morphological structure, *F. wombatiensis* is most likely aligned with taxa within the Hemidiscaceae, a family that includes the genera *Actinocyclus*, *Hemidiscus* Wallich, *Roperia* A. Grunow ex. J. Pelletan, and, according to some authors, *Azpeitia* M. Peragallo in J. Tempère & H. Peragallo (Fryxell et al. 1986, Round et al. 1990). All Hemidiscaceae have chambered areolae, marginal rimoportulae and, with the exception of a few *Actinocyclus* species, are predominantly marine (Table 1). Some authors argue that inclusion in the Hemidiscaceae also demands the presence of a single pseudonodule per valve, generally situated near the valve margin, and easily distinguished from the rimoportulae (Simonsen 1975). However, species of *Azpeitia* lack a pseudonodule and differ from other genera in this family by the presence of a centrally positioned labiate process. Nevertheless, Fryxell

Table 1.   Morphological and inferred ecological characteristics of *Fideliacyclus wombatiensis* in relation to genera within, or closely related to, the family Hemidiscaceae.

Taxon	Presence of solum	Presence of pseudonodule	Presence of central process	Spacing of marginal rimoportulae	Orientation of rimoportula slit[a]	Wall structure	External areola covering	Internal areola covering	Habitat
Fideliacyclus wombatiensis	Yes	No	No	Uneven	Perpendicular	Hypocaust	Foramen	Sits on solum	Freshwater
Actinocyclus	No	Yes, some highly reduced	No	Even except on two fossil taxa[b]	Perpendicular or tilted to one side	Bullulate or hypocaust[c]	Channel[b]	Basket[b]	Marine and fresh water[d]
Hemidiscus[e]	No	Yes	No	Uneven	Parallel	Loculate	Cribrum	Foramen	Marine
Roperia	No	Yes	No	Uneven	Parallel	Loculate	Cribrum	Foramen	Marine
Azpeitia	No	No[f]	Yes	Uneven	Parallel	Loculate	Cribrum	Foramen	Marine
Spumorbis[g]	No	No	No	Even	Parallel	Bullulate	Cribrum	Raised foramen	Marine

[a] Orientation is relative to a tangent to the valve margin.
[b] According to Andersen et al. (1986). Basket is an organic matrix supported by a series of siliceous ribs.
[c] One species, *A. octonarius* has hypocaust wall structure.
[d] One modern species, *A. normanii* f. *subsalsa* and numerous fossil species are freshwater.
[e] Cuneiform valve shape.
[f] Several fossil species with a pseudonodule (Fryxell et al. 1986).
[g] Three Miocene species with either cylindrical or bulb-shaped areola chambers.

et al. (1986) argued that *Azpeitia* belonged in the Hemidiscaceae because certain fossil taxa possess a pseudonodule. Although the pseudonodule is usually easily recognized, it can be highly reduced, difficult to identify, and perhaps lacking, as in some Miocene *Actinocyclus* species (Bradbury & Krebs 1995). *F. wombatiensis* specimens lack a pseudonodule. All taxa within the Hemidiscaceae also have either a cribrum or complex sieve structure (e.g., *Actinocyclus*, Andersen et al. 1986) covering the external areola openings. Apomorphies, including the lack of both a pseudonodule and an external covering on the areolae, coupled with the presence of the thick solum, clearly establish *Fideliacyclus* as a separate genus, distinct from all other genera in the Hemidiscaceae. Placement of *Fideliacyclus* into the Hemidiscaceae remains tentative, awaiting more detailed morphological and molecular characterization of the family.

Among genera within the Hemidiscaceae, the wall structure of *Fideliacyclus* is most closely aligned with *Actinocyclus*. Both these genera have chambered areolae that are clearly separated from one another, as opposed to the more loculate condition found in other Hemidiscaceae, where the margins of adjacent areolae firmly abut. All but one species of *Actinocyclus* have bullulate cell walls (Ross et al. 1979), in which a sponge-like siliceous matrix fills the space between areolae (Andersen et al. 1986). Exceptionally, *Actinocyclus octonarius* Ehrenberg has a hypocaust wall in which a continuous space devoid of silica surrounds and encloses the widely spaced areolae (Ross & Sims 1972), a condition closely reminiscent to *F. wombatiensis*. The areolar chambers of *A. octonarius* are cylindrical and similar to those found on the mantle of *F. wombatiensis* valves, but quite different from the spherical chambers composing the valve face in the newly described genus.

There are other differences that serve to distinguish *Fideliacyclus* from *Actinocyclus*. First, the external openings are unoccluded in *Fideliacyclus*, forming foramina, as opposed to the elaborate cribra that cover the areolae of *Actinocyclus* (Andersen et al. 1986). We find no evidence for such occluded areolae in any specimens of *Fideliacyclus*. Further, given that intact nanostructural detail is observed on other diatoms and numerous synurophyte scales in the same samples, we do not believe lack of preservation is an issue. Secondly, the simple structure and uneven spacing of marginal rimoportulae in *Fideliacyclus* serve to distinguish it easily from species of *Actinocyclus* (Round et al. 1990, Bradbury & Krebs 1995, Usoltseva et al. 2010). Even if differences in the wall, areola coverings, and rimoportulae are considered species-level characters, which remain debatable (Hasle 1977, Andersen et al. 1986, Fryxell et al. 1986), the presence of the inner solum clearly separates *Fideliacyclus* from *Actinocyclus* on morphological grounds.

Fideliacyclus also shares features with the Miocene fossil diatom *Spumorbis*, another genus closely aligned with *Actinocyclus* (Table 1), but lacking a pseudonodule (Komura 1998). As with *Actinocyclus* and *Fideliacyclus*, valves of *Spumorbis* also have a marginal ring of rimoportulae. The chambered areolae of *Spumorbis* are either cylindrical or bulb-shaped, morphologically similar to those on the mantle and valve face of *Fideliacyclus*, respectively. However, unlike *Fideliacyclus*, the valve wall in *Spumorbis* is distinctly bullulate, and the areolae are covered externally by a cribrum (Komura 1998). In addition, some frustules of *Spumorbis* are heterovalvar, girdleless, with limited space between the adjoining valves and occluded areolae on the hypovalve.

Another possibility is that *Fideliacyclus* represents a taxon related to *Actinocyclus* or *Spumorbis*, but has an internal resting stage preserved within it (Edlund & Stoermer 1997). In this model, the thick solum structure represents the formation of a resting spore. Indeed, Komura (1998) hypothesized that the heterovalvar frustules of *Spumorbis*, which he termed "cavernous" frustules, were a response to dormancy. Internal resting spores are produced by some diatoms in response to environmental stresses, such as temperature, light levels, nutrient conditions, and desiccation (Hargraves & French 1983, Round et al. 1990, Edlund & Stoermer 1997), particularly among planktonic and neritic centric forms (Hargraves 1976, Round et al. 1990). However, several observations do not support this interpretation of *Fideliacyclus* valves. First, the inner wall is clearly fused with, and part of, the valve wall. All known resting spores are separated from the parent valves by regular, thickened, or vestigial valves (Kaczmarska et al. 2013), at different times in the life cycle, and are not physically fused. Second, of the hundreds of specimens observed, both whole and fragmented, all possess the thick interior wall. Resting spores are usually morphologically distinct from vegetative cells, from which they can be differentiated unambiguously (Edlund & Stoermer 1997). For example, isovalvar frustules of *Spumorbis* occur with frequency alongside heterovalvar specimens, respectively attributed to vegetative cells and resting spores (Komura 1998). Thus, if the solum was merely a component of a resting spore, specimens lacking this structure should also be present, which is not the case in the Wombat material.

Fortification of the frustule through the formation of the solum could have been a response to increased osmotic stress associated with invading a freshwater habitat from a marine environment. It is well known that freshwater diatoms are up to tenfold more heavily silicified than marine diatoms (Conley et al. 1989). Species of *Actinocyclus* are known from both marine and freshwater environments, but the genus is thought to have originated in the marine environment and later colonized freshwater habitats, sometimes as an actively invasive species (Bradbury & Krebs 1995, Spaulding et al. 2010). Under this hypothesis, fortifying a thin fragile wall along its inner surface could offer a mechanism to avoid potential breakage

from increased osmotic stress. Without the thick siliceous solum, the valve wall of *Fideliacyclus* would be quite fragile compared to other diatoms with chambered areolae. The spaces between the spherical thin-walled areolae are devoid of silica, providing virtually no structural support. In contrast, areola chambers in *Actinocyclus* and *Spumorbis* are reinforced by a network of siliceous ribs, producing the bullulate nature of the valve (Andersen et al. 1986, Round et al. 1990, Komura 1998). Perhaps *Fideliacyclus* represents an early colonizer of freshwater habitats enabled by morphological apomorphies that were temporally and evolutionarily constrained to the early Paleocene.

Several other centric diatom genera with robust valve walls are worth mention, including *Pseudoaulacosira* Lupikina et Khursevich, *Ellerbeckia* Crawford (a member of the family Paraliaceae), and *Melosira* C.A. Agardh. Although none of these genera have a wall structure resembling that found in *Fideliacyclus*, they each have features that reflect a structurally robust *Bauplan* that may also represent, partially or wholly, adaption to living in waters of low ionic content relative to the marine habitats of ancestral taxa. *Pseudoaulacosira,* a fossil genus with two described species, possesses a heavily silicified wall with its own unique, complex design (Lupikina & Khursevich 1991, Usoltseva & Houk 2016). Of these species, one is reported from a brackish locality and the other from a freshwater Miocene deposit (Usoltseva & Houk 2016). Valves of most *Ellerbeckia* species are robust with a solid hyaline central zone lacking areolae, and a ring of closely spaced and radially aligned ridges and grooves along the valve face margin (Crawford 1988; Kociolek & Spaulding 2002). Like *Actinocyclus*, there are fossil, recent, marine and freshwater members of *Ellerbeckia*, and these two genera co-occur in many Miocene sediments from western North America (Bradbury & Krebs 1995). Large-celled *Melosira*, including *Melosira undulata* (Ehrenberg) Kützing and its allies, also have a thick, almost solid, basal siliceous layer lining the interior of the valve. *Melosira undulata* forms are found in a wide range of Cenozoic fossil deposits (Hustedt 1930) and are occasionally encountered in modern habitats, such as aerophilic, arctic ponds, and deepwater oligotrophic lakes. Perhaps a more robust valve structure was a common apomorphy for diatoms beginning to colonize freshwater habitats.

The thickened siliceous valves of another freshwater centric diatom, *Eoseira*, which co-occurs with *Fideliacyclus*, are noteworthy with respect to the solum. Valves of *Eoseira* are thick and often the areolae provide little to no direct connection between the inside of the frustule and the external environment (Wolfe & Edlund 2005). This condition was viewed as either a potential deterrent to predation, or more likely providing a mechanism for the organism to migrate to more nutrient-rich waters during quiescent periods by increasing the sinking velocity, perhaps similar

to modern *Aulacoseira baicalensis* (K. Meyer) Simonsen (Jewson et al. 2010). The quiescent periods would have to be coupled with periods of wind-induced turbulence to assure adequate exposure to sunlight for growth.

It is difficult to image how nutrients and other substances were exchanged between the protoplast and the external environment in *Fideliacyclus* given its valve morphology. The thick, solid solum covers the entire valve face and mantle, and would appear to serve as an effective barrier blocking flow with the external environment. The only exceptions are the rimoportulae that presumably provide an open connection to the external environment, and possibly the girdle region. Although the locations of the rimoportulae on the internal and external surfaces are clear, we were not able to confirm if both ends were connected or if they opened to the hypocaust space. If the rimoportulae connect directly to the external surface, then the hypocaust space is completely sealed. In this scenario, materials would presumably have been exchanged between the cell and external environment through rimoportulae alone. However, if rimoportulae open into the hypocaust, then the latter space would fill with ambient water, including possibly symbionts, and serve a unique role in the diatom's physiology. We do not know of another diatom that limits the flow of materials solely through the rimoportulae with the possible exception of some species of Aulacoseiraceae. Siver & Hamilton (2011) described a thick and uniform siliceous layer in *Aulacoseira lancea* Siver & Hamilton that completely covers the inside of the valve with the exception of the rimoportulae. Crawford & Likhoshway (2002) reported that other species of *Aulacoseira* have a thin film covering the inner cribra, possibly composed of a mix of silica and organic material that is acid soluble. The solum in *Fideliacyclus*, on the other hand, survives strong acid treatment and is therefore a much more robust structure and accordingly a highly effective barrier. Lastly, we cannot rule out the possibility of microchannels in the solum (undetected with SEM) beneath the bases of the areolae through which solutes are exchanged.

Given that *Fideliacyclus* coexisted with a host of synurophyte species and other freshwater diatoms, including *Eoseira*, *Aulacoseira*, *Eunotia*, and *Fragilaria*, the maar lake was unambiguously a freshwater ecosystem. Other than its presence in the Wombat locality, *Eoseira* has only been reported from an Eocene lake in British Columbia, Canada, known as Horsefly (Wolfe & Edlund 2005). Based on features of the *Eoseira* specimens, coupled with the remains of other aquatic organisms and chemical characteristics of the rocks, Wolfe & Edlund (2005) proposed that the Horsefly locality represented a relatively deep, well mixed, warm monomictic, softwater lake with possible episodes of high nutrient input. Synurophytes are planktonic organisms that thrive in softwater habitats with slight to moderate acidic conditions (Siver

1995, 2015). Likewise, the remains of *Eunotia* specimens are also indicative of acidic conditions low in dissolved salts (Camburn & Charles 2000, Siver & Hamilton 2011), and the Wombat deposit also contains heliozoans typical of acidic habitats. Although as a genus *Aulacoseira* can be found over a wide pH gradient, some species are important components of acidic and softwater waterbodies (Camburn & Charles 2000, Gaiser & Johansen 2000, Siver et al. 2005, Siver & Hamilton 2011). Thus, we envision the Wombat maar lake to have been an acidic, softwater lake. Further, assuming that both *Fideliacyclus* and *Eoseira* were planktonic or tychoplanktonic, and given the high density of their valves, the lake was likely well mixed at least during part of the year. Given the warm greenhouse conditions that existed during the Paleogene, coupled with the lack of winter ice (Zachos et al. 2008, Eberle & Greenwood 2012), we suspect that the lake was warm, monomictic, with enhanced mixing during the fall, winter, and spring months.

In summary, *Fideliacyclus wombatiensis* represents one of the oldest known genera of freshwater diatoms, reported herein from a maar lake in northern Canada during the Paleocene. This centric diatom is characterized by a highly complex valve structure comprising areolae with large, bulbous, spherical shaped chambers that rest on a solid siliceous floor and are surrounded by a hypocaust. The thick floor, or solum, undoubtedly provided structural support, but at the same time reduced the ability of the organism to exchange materials between the protoplast and the external environment. The unique structure of the valve may represent the evolutionary response of a species invading a freshwater environment from the marine realm. *Fideliacyclus* shares characteristics with, and is possibly related to, *Actinocyclus* or *Spumorbis*. Features of these and other early freshwater inhabitants, coupled with physical and chemical characteristics of the environments, ultimately add to our understanding of diatom evolutionary events.

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