Aulacoseira chockii sp. nov., an early freshwater centric diatom from the Eocene bearing a unique morphology

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ABSTRACT

Aulacoseira is a freshwater diatom genus found today in numerous lakes, ponds and rivers worldwide, and inhabiting a wide range of environmental conditions. The genus is one of the oldest diatom lineages known to colonize freshwater environments, dating to the late Cretaceous and radiating over much of the Cenozoic. The purpose of this paper is to describe a new species of *Aulacoseira*, *A*. *chockii*, from an early Eocene locality situated near the Arctic Circle in northern Canada. The exquisitely preserved specimens have allowed for a detailed examination of frustule morphology of this early Cenozoic taxon. Three characteristics clearly separate *A*. *chockii* from all other known fossil and modern species in the genus. First, the spines of *A*. *chockii* are formed by coalescence of extensions from three to five mantle costae and multiple ribs that originate on the valve face. This type of spine design has never been reported and represents a potentially ancient trait in the Aulacoseiraceae lineage. Second, the valve has multiple sessile rimoportulae that are each connected to the end of a tube or canal that runs parallel to, and inside of, the mantle wall. Rimoportulae with this structure are rare, and found primarily on extinct species of *Aulacoseira*. Third, the mantle striae are sinistrorse, and represent another rarely observed character within the genus. Because frustules of *A chockii* possessed only separating spines, existed largely as single cells and not in long filaments, and was found in associated with remains of numerous heliozoans as well as testate euglyphids and sponges, it is believed this species grew in the littoral zone of a shallow waterbody.

Keywords: *Aulacoseira*, Eocene, *Eoseira*, freshwater fossil diatoms, Giraffe Pipe locality, rimoportulae, sinistrorse

Introduction

Most evidence suggests that diatoms evolved in a marine setting during the Mesozoic (Kooistra & Medlin, 1996; Sims *et al.*, 2006; Medlin, 2016), and radiated throughout the world's oceans by the early Cretaceous (Harwood & Nikolaev, 1995). Based on fossil evidence, diatoms began to invade, most likely from the marine environment, and successfully inhabit freshwater ecosystems much later in the Cretaceous (Chacón-Baca et al., 2002; Ambwani et al., 2003; Singh et al., 2006; Buatois et al., 2016; Siver et al., 2018; Siver et al., 2019). *Aulacoseira* was an early freshwater colonizing diatom having been uncovered from late Cretaceous deposits in North America (Siver et al., 2018) and India (Ambwani et al., 2003), and along with several araphid pennate genera became well established by the Eocene (Siver et al., 2018). The genus continued to radiate throughout the Cenozoic and remains an important component of numerous freshwaters worldwide today.

Aulacoseira Thwaites is in the family Aulacoseiraceae Moisseeva 1990 consisting of freshwater centric genera that possess spines on the margin of the valve face, an areolated mantle, and rimoportulae (Crawford, 1981; Round et al., 1990; Likhoshway and Crawford, 2001; Wolfe and Edlund, 2006). Currently, the family consists of five genera, *Aulacoseira*, *Eoseira* Wolfe & Edlund, *Miosira* Krammer, Lange-Bertalot & Schiller, *Pseudoaulacoseira* (Lupikina) Lupikina & Khursevich and *Alveolophora* Moisseeva & Nevretdinova, and except for *Aulacoseira*, the remaining genera are only known from the fossil record and presumed extinct (Wolfe and Edlund, 2006).

Common to all genera in the family Aulacoseiraceae, many, but not all, species of *Aulacoseira* can form two morphologically different types of spines, linking spines that permanently hold cells together, and separating spines that allow cells to slip apart from each other (Davey and Crawford, 1986; Siver and Kling, 1997; Houk, 2003). Except for *Eoseira*, the spines for all members of the family form in association with mantle costae, either as extensions of a single costae, or coalescence of two adjacent costae (Wolfe and Edlund, 2006; Siver and Hamilton, 2011). Spines on *Eoseira* are large, referred to as megaspines, and are not directly associated with mantle costae, a feature also found on the marine genus *Archepyrgus* Gersonde & Harwood described from the Lower Cretaceous (Gersonde and Harwood, 1990). In addition to the large spines linking frustules into filaments, *Archepyrgus* valves also have mantle striae and a ringleiste, prompting some authors (Gersonde and Harwood, 1990; Wolfe and Edlund, 2006; Sims et al., 2006; Farooqui et al., 2015) to suggest that this genus may represent an ancient link with family Aulacoseiraceae.

Rimoportulae vary across the genera in family Aulacoseiraceae with respect to where they are located on the mantle, the number per valve, and their morphology. One rare type of structure consists of a simple rimoportulae connected at one end of a straight or curved tube that runs along the inner mantle wall and most often terminates near the ringleiste or close to the top of the mantle at the valve face. Except for a few modern species, this rimoportulae design is only known from fossil taxa.

The objective of this study is to describe a new species of *Aulacoseira* from the early Eocene Giraffe Pipe locality. The species possesses a unique combination of characters, including a new type of spine structure associated with both mantle costae and the valve face, rimoportulae connected to long tubular structures, and sinistrorse mantle striae. The unique morphological features are discussed relative to other fossil and modern species.

Materials and methods

Study Locality: Detailed descriptions of the Giraffe Pipe locality are given elsewhere in Siver et al. (2015) and Wolfe et al. (2017). Briefly, the Giraffe fossil locality (64°44' N, 109°45' W), located near the Arctic Circle in northern Canada, is situated within a crater formed during emplacement of a kimberlite pipe 48 Ma years ago in the early Eocene (Wolfe et al., 2006; Siver & Wolfe, 2009; Wolfe et al., 2017). The locality contains 45 meters of rich peaty and organic terrestrial remains on top of 68 meters of mudstone rock formed in an ancient freshwater maar lake that existed within the Giraffe crater. A thick layer of post-glacial till overlays the entire terrestrial and aquatic sequence, essentially entombing the deposit within the crater walls (Wolfe et al., 2017). The mudstones represent a continuous history of the Eocene maar lake that spanned hundreds of thousands of years (Siver et al., 2019). The ancient mudstone deposit contains a rich and diverse assemblage of extraordinarily preserved fossils, including numerous freshwater diatoms, chrysophytes, synurophytes, testate amoebae, heliozoans, phytoliths, sponge spicules and pollen (e.g. Wolfe & Siver, 2009; Siver et al., 2010; Siver et al., 2019).

The Core: A 163 m long core, drilled at a 47° angle, was recovered from the Giraffe maar in 1999 by BHP Billiton Inc. (Siver & Wolfe, 2009). The lower 113 m of the core contains the peaty/ terrestrial remains overtop of the aquatic mudstones. The core was stored on site in preconstructed core boxes. Each core box contains 4.5 meters of core, divided into three 1.5 meter-long sections and in three channels. Samples from the core are identified with a three part number (Siver, 2015). The first number represents the core box, numbered sequentially from the surface down to the bottom of the core. Eighteen boxes, numbers 11 through 27, contain the lacustrine mudstones, with box 11 representing the last (most recent) phase of the aquatic environment. The second number represents the channel within the box. The third number is the measurement in cm from the top of a core length. The primary sample containing the new *Aulacoseira* species described in this paper was 17-3-26, taken from 26 cm down along the core length positioned in channel 3 from box 17.

Sample Preparation: A 1 g mudstone sample from 17-3-26 was oxidized using 30 % H_2O_2 under low heat for a minimum of 1-3 hr, rinsed with distilled water, and the slurry stored at 4 ºC. This mild oxidation procedure results in separation of numerous siliceous microfossils from the mudstone matrix, and fragments containing numerous microfossils, still in-situ. An aliquot of the final slurry was air dried onto a piece of heavy duty aluminum foil, trimmed, and attached to an aluminum SEM stub with Apiezon® wax. Samples were then coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and examined with a Leo (Zeiss) 982 FESEM (Jena, Germany) or a FEI Nova NanoSEM 450 FESEM.

Aliquots of each slurry were also dried onto coverslips, mounted onto glass slides using Naphrax, and examined with a Leica DMR light microscope at 100 x coupled with a Zeiss Axiocam 503 color camera. Valve diameter and length were measured directly from SEM micrographs, or from the permanent glass slide mounts using Zeiss camera software.

Results

Taxonomic diagnosis

Aulacoseira chockii **Siver sp. nov.** (Figs 1-40)

Species diagnosis. Valves range in diameter from 5.5-12.6µm (mean = 9.0µm), height from 5.0-11.5µm (men = 7.7µm), have a mean height to width ratio of 0.95µm, and have an areolated valve face, widely spaced spines, and rimoportulae that are associated with both the ringleiste and the abfallzone or juncture between the mantle and valve face (Figs 1-24, 25-30, 40). The valve face is flat and covered with numerous small areolae (Figs 25, 31). The spines are thick, pointed, widely spaced, and of relatively even lengths. The base of a fully developed spine spans three to five mantle costae, and it is formed by the coalescence of multiple siliceous extensions, or ribs, originating from both the mantle costae and valve face (Figs 28, 30, 31). Up to seven siliceous extensions can take part in forming the spine (Fig. 32). No other spine type was observed. The mantle striae, consisting of small and circular areolae, are sinistrorse, curving to the left when traced from the collum to the valve face margin (Figs 27, 30, 40). Each areola opens externally, forms a chamber with straight sides within the valve wall, and is occluded internally with a velum consisting of a series of small finger-like projections (Figs 34, 38). The velum is often, in turn, covered by a thin, solid, and circular covering that is flush with the inside mantle wall (Figs 34, 37). Internally, the juncture between the mantle and the valve face is curved, not angled, the mantle areolae continuous with those on the valve face (Fig. 34), and the costae in this region often become thickened (Fig. 35). The collum is well defined and mostly smooth. The ringleiste is solid, shallow, and positioned near the top of the collum (Figs 27, 29, 36). There are multiple sessile rimoportulae per valve, each of which is connected to one end of a tube or canal situated within, and running parallel to, the mantle wall (Figs 26, 27, 29, 33-36). The tubular canals range in shape from straight (Figs 33, 39) to highly curved (Figs 34, 37, 39), and the end of the canal opposite of the rimoportulae usually terminates either at the valve face/mantle junction (Figs 33-35, 37, 39), or on the advalvar side of the ringleiste (Figs 33, 36, 39-40).

Holotype specimen: The circled specimen on LM slide marked “GP 17-3-26” “M” and deposited at the Canadian Museum of Nature as CANA 129147. The holotype is shown in Figs 1-4.

Isotype specimen: The circled specimen on LM slide marked “GP 17-3-26” “A”and illustrated in Figs 7-11. This slide is currently part of Siver’s personal slide collection.

Type material: Material is from section 17-3-26 of the BHP Billiton exploration core from the Giraffe Pipe kimberlite (64.73°N, 110.59°W).

Etymology: The specific epithet is in honor of Dr. Jan Chock, a phycologist, teacher, long-time colleague and dear friend.

Additional Information: Mudstone chips containing specimens of *A. chockii* were examined with LM and SEM. Numerous valves and whole frustules were common in the rock remains. A few filaments consisting of only two frustules were observed (Figs 23-24), but longer filaments were not uncovered.

Co-occurring organisms: Remains of multiple heliozoan taxa, including both plate and spine-bearing scales, were abundant and dominated this section of the Giraffe core. Multiple types of chrysophyte cysts were common, along with scales of *Chrysosphaerella* sp. In addition to *A. chockii*, other diatoms included several *Fragilaria* spp. and *Nupela mutabilis* Siver, Wolfe &

Edlund. Plates of testate euglyphids, scattered sponge spicules, and numerous phytoliths were also observed.

Discussion

The presence of a deep and striated mantle, a series of spines on the valve face/mantle junction, a solid and largely structureless collum at the base of the mantle, and presence of both a ringleiste and mantle rimoportulae, place *A. chockii* in the genus *Aulacoseira* (Round et al., 1990; Likhoshway and Crawford, 2001; Houk, 2003; Tuji and Houki, 2004). Unique characteristics of the spines and rimoportulae, coupled with a suite of additional features, serve to distinguish *A. chockii* from all other known species in the genus, both modern and fossil. Many modern species of *Aulacoseira* have two types of spines, linking spines that hold adjoining cells together in a filament, and separation spines that allow for frustules to separate from each other (Round et al., 1990; Likhoshway and Crawford, 2001; Houk, 2003). In addition, the bases of spines found on almost all known modern and fossil species of *Aulacoseira* are associated with either one or two adjacent mantle costae. In the former case, the costa extends past the valve face to form the spine. In the latter case, two adjacent mantle costae fuse to form the base of the spine, with the mantle stria between the two costae terminating along the center of the spine (Crawford, 1981; Siver and Kling, 1997; Houk, 2003). For species with two costae forming each spine, there is at least one mantle striae between adjoining spine bases, depending on the spacing of the spines. Given the close association between spines and mantle costae, spines of *Aulacoseira* species are said to have a specific geometric relationship with respect to the mantle costae (Wolfe and Edlund, 2006). An exception to this rule is the modern species, *A. herzogii* (Lemmermann) Simonsen, which possesses one to a few long and thick spines that are not associated with mantle costae, but instead are situated directly on the valve face near the margin (Hickel and Håkansson, 1991; Siver and Hamilton, 2011). A second exception, are the spines found on *A. brasiliensis* Tremarin, Torgen & Ludwig. Although most spines of *A. brasiliensis* are anchored by two mantle costae, some span three costae and have a thickened base (Tremarin et al., 2012). The spines of *A. chockii* are unique and different from all known modern and fossil species of *Aulacoseira* in that the base is formed by coalescence of three to five mantle costae, and further supported by multiple ribs that originate from, and are anchored to, the valve face. This type of spine design has never been reported and may represent an ancient trait in the Aulacoseiraceae lineage.

The large triangular-shaped spines on valves of the marine genus *Archepyrgus* described from the Lower Cretaceous (Gersonde and Harwood, 1990) span numerous (n=15) mantle striae, and as is the case for *Eoseira*, are not associated with mantle costae. This prompted Wolfe and Edlund (2006) to suggest that *Archepyrgus* may share a common ancestor with the freshwater Aulacoseiraceae, and more specifically with *Eoseira*. In a similar fashion, the spine morphology of *A. chockii*, being both associated with more than two mantle costae and ribs connected to the valve face, may be ancestral to taxa in the genus *Aulacoseira*.

The fact that many mantle costae are associated with each spine on the *A. chockii* valve means that the spines are widely spaced, and there are fewer of them available for adjoining frustules into filaments. Indeed, based on observations of numerous in-tact mudstone fragments, only specimens consisting of at most two frustules were observed for *A. chockii*, suggesting this species did not produce filaments, which would not be surprising given the low number of spines per valve, coupled with the fact that they are not linking spines. Many species of *Aulacoseira* that form long filaments consisting of numerous cells held together with linking spines, such as

A. ambigua (Grunow) Simonsen, *A. subarctica* (O. Müller) Haworth, *A. granulata* (Ehrenberg) Simonsen, *A. islandica* (O. Müller) Simonsen, *A. skvortzowii* Edlund, Stoermer & Taylor and *A. nyassensis* (O. Müller) Simonsen, typically inhabit, and often bloom, in the planktic environment (Stoermer et al., 1981; Jewson, 1992; Edlund et al., 1996; Siver and Kling, 1997; Houk and Klee, 2007; Jewson et al., 2008). These species typically have frustules with length to width ratios over two, and filament lengths that may be controlled through production of separating spines (Davy and Crawford, 1986). In contrast, many *Aulacoseira* species that lack linking spines and have small length to width ratios, such as *A. distans* (Ehrenberg) Simonsen, *A perglabra* (Østrup) Haworth, *A. tenella* (Nygaard) Simonsen, *A. brasiliensis*, and *A. subborealis* (Nygaard) Denys, Muylaert & Krammer, often form short filaments consisting of at most a few cells, or exist as single cells, and are more likely observed in littoral habitats (Florin, 1980; Haworth, 1988; Siver and Kling, 1997; Denys et al., 2003; Tremarin et al., 2012). *Aulacoseira giraffensis* Siver, Wolfe & Edlund is a fossil species with long filaments of cells held together with linking spines (Siver et al., 2019). This species formed extensive populations in the planktic community of the Giraffe waterbody spanning hundreds of years at a time when the lake level was inferred to have been deepest. In contract, *A. chockii* was found in a different section of the extensive Giraffe core and associated with organisms more commonly found in littoral zones and/or shallow waterbodies, including heliozoans, testate euglyphids and sponges. This association suggests that *A. chockii* was likely a littoral species existing primarily as single cells.

Sessile rimoportulae associated with internal canals that range from straight to highly curved are rare, but not unique to *A. chockii*. Interestingly, all but one species, *A. herzogii*, known to possess rimoportulae with a similar structure as found on *A. chockii* specimens are fossil organisms. In the case of *A. herzogii*, as is true of *A. chockii*, the rimoportulae are found primarily close to the valve/mantle margin, or close to the ringleist on the advalvar side of the mantle (Houk and Klee, 2007; Siver and Hamilton, 2011). The rimoportulae of the fossil species *A. jonensis* (Grunow in Van Heurck) Houk & Klee and *A. reichelti* Houk & Klee, both known from the Oligocene, are similar in form to ones found on *A. chockii*, but the position on the mantle differs. The rimoportulae can be found in different locations on the mantle of *A. jonensis*, while they are found just above or on the ringleiste on *A. reichelti* valves. Based on a review of images given in Houk and Klee (Fig. 8 on Tab LXXlX, 2007), an additional fossil taxon, *A. mocsarensis* (Pantocsek) Houk & Klee, also possesses rimoportulae associated with similar curved tubes. Given that this intriguing rimoportulae design has been found on fossil species of *Aulacoseira* from the early Eocene, Oligocene and Miocene, and lacking on all but one extant taxon, indicates that this structure is ancient. This fact further hints that, coupled with its unique spine structure, *A. herzogii* may represent an ancient lineage within the genus. At the present time, rimoportulae as found on *A. chockii* have not been observed on the oldest known specimens of *Aulacoseira* uncovered from the Battle Formation in Canada (Siver et al., 2018) or from the slightly younger Deccan Intertrappean beds in India (Ambwani et al. 2003), both dating to the latter part of the Cretaceous. However, given the poor preservation of the specimens, details of the rimoportulae were not uncovered in these studies.

Although not unique to *A. chockii*, three additional characteristics in combination with spine and rimoportulae structure serve to further separate this species from all others. First, the two-part covering of the areolae, consisting of the velum with finger-like projections near the base of the areolae, and a second solid covering flush with the inner surface of the mantle wall. Second, the left curved or sinistrorse mantle striae found on *A. chockii* specimens are also rare among taxa in this genus. The majority of *Aulacoseira* species, both modern and fossil, have straight mantle striae that are parallel with the longitudinal axis of the cell. Examples of fossil species with straight mantle striae include *A. solida* (Eulenst. in Van Heurck) Krammer, *A. zautigensis* Houk & Klee, *A. mocsarensis* and *A. spiralis* (Ehrenberg) Houk & Klee. Most species that lack straight mantle striae have ones that are dextrorse, curving to the right. Fossil taxa with dextrorse mantle striae include *A. procera* (Ehrenberg) Houk & Klee, *A. scalaris* (Grunow in Van Heurck) Houk, Klee & Passauer and *A. jonensis*. Based on examination of Type material from the Ehrenberg collection, Crawford et al. (2003) concluded that the mantle striae on specimens of *A. italic* (Ehrenberg) Simonsen, a contemporary species also commonly reported from fossil localities, are also sinistrorse. Other than *A. italica* and maybe some varieties of *A. distans*, *A. chockii* is the only fossil *Aulacoseira* species known to possess sinistrorse mantle striae. A third characteristic of *A. chockii* specimens uncommon among *Aulacoseira* species is the nature of the valve face/mantle juncture. On most species the mantle forms a right angle with the valve face. On *A. chockii* valves this juncture is more continuous and curved along the internal surface. Internally, the costae at the abfallzone on *A. chockii* specimens are often thickened, presumably adding strength to the valve. Although a different organism, it is worth noting that species belonging to the extinct fossil Aulacoseiraceae genus *Miosira* possessed internal siliceous supports making for a more robust valve (Krammer et al., 1997; Wolfe and Edlund, 2006; Houk and Klee, 2007).

Although the overall morphological structure of *A. chockii* is distinctive and unique, there are some similarities with *A. brasiliensis*, a modern tropical species reported from Brazil (Tremarin et al., 2012). First, both species have only separation valves with similar length to width ratios, and exist as single cells or in filaments consisting of only a few cells. Second, both species possess spines that are widely spaced and pointed. Spines of *A. brasiliensis* can sometimes span more than two mantle costae and have additional supports associated with the base that place this spine type in between other modern species and those found on *A. chockii*. Third, both species have rimoportulae that are associated with the ringleiste and the juncture of the valve face and mantle. However, *A. brasiliensis* valves possess many more rimoportulae per valve and these structures are not associated with long tubes as they are on *A. chockii* valves. Lastly, the valve face is areolated and the ringleiste is shallow on both species. Valves of *A. brasiliensis* also differ from those of *A. chockii* in having straight mantle striae. Despite the differences, *A. brasiliensis* may represent the closest living modern congener of *A. chockii* with respect to overall morphology.

In summary, *A. chockii* is one of the oldest known species of *Aulacoseira* dating to at least the early Eocene, and provides further support for the importance of the genus in early freshwater habitats containing diatoms. The structure of the spines is unique, being both associated with mantle costae and ribs originating from the valve face, and coupled with features of the rimoportulae and striae, offer insights into the early evolution of this important freshwater diatom genus.

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FIGURE LEGENDS

Figures 1-24. Light micrographs of *Aulacoseira chockii*. Specimens of frustules (Figs 1-11, 18-19), single valves (Figs 14-17, 21-22), three connected valves (Figs 12-13), and a close up of a rimoportula (Fig. 20) are illustrated. Images of the same specimen taken at different focal planes are depicted in Figs 1-4, 5-6, 7-11, 14-16, 18-19 and 21-22. Rimoportula are indicated by arrows on the specimens shown in Figs 2-3, 8 and 15. Note the curved sinistrorse striae, and position of the shallow ringleiste. Figures 23-23 depict mudstone fragments with microfossils still held in place within the rock matrix, including specimens of *A. chockii* (arrows). The specimen denoted by the double arrow in Fig. 24 shows two frustules potentially held together in a short filament. The specimen illustrated in Figs 1-4 represents the Type deposited at the Canadian Museum of Nature, and the specimen represented in Figs 7-11 an Isotype in Siver's collection held at Connecticut College. Scale bar = 10 µm.

Figures 25-30. SEM micrographs of *Aulacoseira chockii* specimens. Figs 25-26. External and internal views of the areolated valve face. Note the wide spacing of spines (Fig. 25), and the two rimoportulae (arrows), shallow ringleiste, and thickened costae at the juncture of the valve face/mantle (Fig. 26). Fig. 27. Specimen depicting the sinistrorse mantle striae, narrow column and associated shallow ringleiste, and two rimoportulae. Fig 28. Frustule partially covered with girdle bands, and with widely spaced spines spanning three to five (arrow) mantle costae. Fig. 29. Internal view of the shallow ringleiste associated with a rimoportula (arrow). Fig. 30. Valve depicting the sinistrorse mantle striae, column, and an incomplete spine spanning five costae. Scale bars = 2 (Fig. 26), 3 (Fig. 29), 4 (Fig. 30) and 5 (Figs 25, 27-28) µm.

Figures 31-36. SEM micrographs of *Aulacoseira chockii* specimens. Close-up micrographs depicting the multiple ribs supporting the base of the spines (Figs 31-32), rimoportulae associated with the juncture of the valve face/mantle (Figs 33-35) and advalvar side of the ringleist (Figs 33-36), the solid nature of the ringleiste (arrow on Fig. 36), and the thickened internal costae associated with the juncture of the valve face/mantle (Fig. 35). Note the long and curved tube associated with the rimoportula of Fig. 34. The internal chamber and coverings associated with the areolae on Fig 34 (arrow). Scale bars = 1 (Figs 32, 34), 2 (Figs 31, 35-36) and 5 (Fig. 33) µm.

Figures 37-40. SEM micrographs of *Aulacoseira chockii* specimens. Fig. 37. Internal view showing the shallow ringleiste, a rimoportula connected to a long and curved tube (single arrow), and internal coverings on some of the areolae (double arrow). Fig. 38. Internal view depicting the vela, each consisting of small finger-like projections. The inner-most coverings are lacking on this specimen. Fig. 39. Rimoportula with curved tubes associated with the juncture of the mantle/valve face (black arrow), and the advalvar side of the ringleiste (white arrow). Fig. 40. Valve depicting spines, the sinistrorse mantle striae, and a rimoportulae associated with the ringleiste. Scale bars = 1 (Fig. 38), 2 (Fig. 37), 4 (Fig. 39) and 5 (Fig. 40) µm.