

Aulacoseira giraffensis (Bacillariophyceae), a new diatom species forming massive populations in an Eocene lake

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Background and aims – Diatoms began to inhabit freshwater by at least the Late Cretaceous, becoming well established by the early to middle Eocene. *Aulacoseira*, an important diatom in numerous ponds, lakes and rivers today, was one of the earliest known genera to colonize freshwater ecosystems. Members of this genus with characteristics familiar to those found on modern species became increasingly more abundant by the Eocene, and continued to thrive throughout the Miocene to the present. We describe a new species of *Aulacoseira* from an early to middle Eocene site near the Arctic Circle in northern Canada.

Methods – Twelve samples taken from the Giraffe Pipe core were analysed in this study. Light and scanning electron microscopy were used to document morphological characters. Morphometric measurements were made from 200 specimens per sample (n = 1200), and used to investigate changes in valve size over time.

Key results – The new species, *Aulacoseira giraffensis*, has valves with a length:width ratio close to 1, a hyaline valve face, straight mantle striae, a shallow ringleiste, branched linking spines, concave-convex complementarity on adjacent valve faces, and rimoportulae with simple papillae-like structure. The suite of characters, especially the highly branched spines, concave-convex valves and simple rimoportulae, is unique for this species. Large numbers of *A. giraffensis* specimens were found over a ten-metre section of the core, representing thousands of years. These high concentrations are indicative of abundant, bloom-like, growth.

Conclusions – The locality represents one of the earliest known records of *Aulacoseira* dominating a freshwater community. Findings confirm that the morphological body plan for the genus was well established by the Eocene. Although findings indicate evolutionary stasis in morphological structure for *A. giraffensis* over a time scale of thousands of years, oscillations in valve morphometrics could potentially be used to trace changes in the environment of this ancient Arctic waterbody.

Key words – *Aulacoseira*, blooms, Cretaceous, Eocene, freshwater fossil diatoms.

INTRODUCTION

Estimates based on molecular clock studies yield a Mesozoic origin for the diatoms, one of the most successful protistan lineages in recent geologic history (Kooistra & Medlin 1996, Sims et al. 2006, Medlin 2016). Their radiation in the world's oceans commenced in the early Cretaceous (ca. 145

Ma) and has continued throughout the Cenozoic (Harwood & Nikolaev 1995). However, based on fossil evidence, invasion of freshwater habitats by diatoms, presumably from marine environments, did not occur until near the end of the Cretaceous (Chacón-Baca et al. 2002, Ambwani et al. 2003, Singh et al. 2006, Buatois et al. 2016, Siver et al. 2018). Fossil deposits containing abundant freshwater specimens are

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not common before the middle (Krebs 1994, Strelnikova & Lastivka 1999, Siver & Wolfe 2009) to late (Lohman & Andrews 1968, Benson & Kocielek 2012) Eocene. In western North America, freshwater diatomite deposits, many of which represent the remains of large ancient waterbodies, are known from the middle Eocene, and become progressively more abundant by the Miocene (Krebs 1994). *Aulacoseira* Thwaites and araphid pennate genera were common elements of many of the middle Eocene through Oligocene deposits, with other taxa such as *Actinocyclus* Ehrenb. and *Thalassiosira* Cleve becoming more important by the middle Miocene (Krebs 1994). However, details of the *Aulacoseira* taxa present in the earlier (e.g. early to middle Eocene) deposits are few.

The Eocene Giraffe fossil locality is situated within a crater formed during emplacement of a kimberlite pipe near the Arctic Circle in northern Canada (Wolfe et al. 2006, 2017, Siver & Wolfe 2009). The locality contains 65 meters of mudstone from a maar lake situated within the Giraffe crater. The deposit contains abundant fossil remains with extraordinary preservation, including numerous freshwater diatoms, chrysophytes, synurophytes, testate amoebae, heliozoans, phytoliths and sponge spicules (Wolfe & Siver 2009, Siver et al. 2010). The purpose of this contribution is to formally describe a fossil species of *Aulacoseira* that dominated a ten meter section of the Giraffe deposit. Ecological and evolutionary aspects of the new species are also discussed.

MATERIALS AND METHODS

Site and core description

Full and detailed descriptions of the Giraffe Pipe locality are given in Siver et al. (2015) and Wolfe et al. (2017). Briefly, the Giraffe Pipe locality (64°44'N, 109°45'W) is situated within a crater formed during emplacement of an ancient kimberlite diatreme into the Slave Craton, Northwest Territories, Canada, approximately 47.8 million years ago during the early to middle Eocene (Siver & Wolfe 2005, Wolfe et al. 2006). This places the origin of the site at the boundary between the Ypresian (56–47.8 Ma) and Lutetian (47.8–41.2 Ma). Subsequent to emplacement, the diatreme crater harboured an aquatic environment that remained for thousands of years before transitioning to a terrestrial environment. The aquatic and terrestrial sediments were later capped by Neogene glacial deposits (Siver & Wolfe 2005, Wolfe et al. 2006). The Giraffe Pipe is one of many kimberlites emplaced in the Lac de Gras region, most of which were formed between the Late Cretaceous to middle Eocene (Heaman et al. 2004).

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 113.1 m of the core contains well preserved stratified organic sediment, including 68.3 m of lacustrine mudstone, overlain with 44.8 m of peaty and terrestrial remains. The lake sediments were deposited during the earliest phases of the Lutetian and underwent little to no post-deposition alteration, yielding well preserved material containing abundant fossils.

Table 1 – Vertical core depths for the 12 samples examined in this study.

The mean diameter and mean L:W value for valves of each sample (n = 200) is given. The vertical depth is from the land surface.

Sample	Vertical depth (m)	Mean diameter (µm)	Mean L:W
17-2-142	91.46	7.4	0.89
17-1-15	91.63	8.1	0.83
18-3-24	92.79	7.1	0.94
18-1-30	95.03	6.8	1.1
19-3-19	96.05	7.4	0.84
19-3-138	96.92	7.9	0.79
19-2-39	97.29	7.5	0.80
19-2-100	97.74	6.7	0.96
19-1-75	98.65	6.9	0.90
20-3-47	99.54	7.5	0.77
20-3-105	99.97	8.3	0.83
20-2-110	101.10	7.1	0.87

New techniques using U-Pb zircon geochronology are now being applied to date tephra beds found in the Giraffe core near the end of the lacustrine phase. Preliminary findings indicate the lake phase lasted tens to hundreds of thousands of years, suggesting a sedimentation rate of one to a few years per mm. Based on these results the ten-metre core section examined in our study represented a minimum of ten thousand years.

The Giraffe core was stored on site in core boxes. Each core box has three channels that are 1.5 m long. Samples from the core are identified with a three-part number (Siver 2015). The first number represents the core box. The larger the number, the deeper the section is within the core. Seventeen boxes, numbers 27 through 11, contain lacustrine sediments, with box 11 representing the last 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. For example, sample 20-1-40 represents a sample taken from 40 cm down along the core length positioned in channel 1 from box 20.

Field and laboratory methods

Our study includes samples from 12 sections of the core situated between 20-1-40 and 17-2-142 (table 1). Converting distance along the drilled core (taken at 47°) to vertical distance from the surface of the land, these samples are situated between 101.69 and 91.46 m, representing 10.23 m of core. Mudstone fragments (0.5–1.0 g) from each of the 12 sections were oxidized using 30% H₂O₂ under low heat for a minimum of 1-3 hr, rinsed with distilled water, and the slurries stored in glass vials at 4°C. 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 from each slurry was air dried onto a piece of heavy-duty aluminium foil, trimmed, and attached to an aluminium SEM stub with Apiezon®

wax. In addition, fragments of untreated mudstone material were mounted directly onto SEM stubs using double-sided carbon tape, and silver paint used to provide good contact between the rock fragment and the stub to reduce charging. All samples were 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 an Olympus BH-2 or Leica DMR light microscope at 100 x using a Plan Apo lens with a numerical aperture = 1.4, coupled with a Zeiss Axiocam 105 or 503 colour camera. Valve diameter and length were measured using Zeiss camera software. Two hundred valves were measured for each of the 12 samples (n = 2400). SigmaPlot version 12.5 was used for all statistical analyses.

RESULTS

Abundant specimens of a species of *Aulacoseira* were uncovered from mudstones over a ten meter section of the Giraffe core between 91 and 101 m (figs 1–4). Filaments containing four to six frustules were common, and ones with up to nine frustules were observed. Since most filaments lack whole cells on at least one end, even longer ones are likely embedded within the rock matrix but difficult to extract intact. High concentrations of this diatom were consistently found in fractured rocks over this section of the core, with filaments embedded in the rock matrix on top of each other (figs 1A–D). Abundant chrysophyte cysts, synurophyte scales and heliozoan scales were often found in the rock matrix with the *Aulacoseira* specimens. Other diatom taxa, including *Eunotia* spp., *Fragilaria* sp., *Fragilariforma* sp. and *Nupela mutabilis* Siver, Wolfe & Edlund, were also present, but rare. The species of *Aulacoseira* is described as follows:

Aulacoseira giraffensis Siver, A.P.Wolfe & Edlund, **sp. nov.**
Figs 1–4

Type material – CANA # 128319 (Canadian Museum of Nature, Ottawa, Canada). Portion of a single gathering of cells on prepared microscope slide marked “GP 19-1-100 B.” Figs 2A–C are images of a circled representative from the specimen.

Type locality – Section 19-1-100 of the Giraffe Pipe core (64°44'N, 109°45'W), Northwest Territories, Canada.

Etymology – The specific epithet refers to the Giraffe kimberlite fossil locality.

Description – See figs 1–4: valves are cylindrical, range in diameter from 3.6 to 12 µm with a mean of 7.4 µm, and in mantle height from 3 to 11.3 µm with a mean of 6.2 µm (figs 3A–E & 5). The length to width ratio (L:W) ranges from 0.36 to 2 with a mean of 0.87 (fig. 5B). Mantle striae are straight, composed of broadly oval to rectangular areolae, and range from 17 to 20 per 10 µm with a mean of 19 per 10 µm (n = 30) (figs 3D–F, 4A & 4F). On most valves, the mantle areolae do not align neatly between adjacent striae (fig. 2A, F, G, I & K). Areolae are open to the exterior, but covered on the inside of the valve with a velum that is flush with the

inner mantle wall (fig. 4C–E). A series of short volae ribs is attached to the outer velum surface within the areolae chamber (figs 3F & 4D). The valve face is smooth, except for a marginal ring of pores where each pore is situated between two spines (fig. 4A). The valve face is convex or concave, and form complementary fitting pieces on adjacent frustules (figs 2B, C, E, H, J, L & 3C). The collum is distinct, from 1.3 to 1.9 µm wide (n = 15), and consists of short, closely spaced, peralvar parallel ribs each composed of a series of fused papillae (fig. 3E & F). Steps are commonly observed on the mantle just above the collum (fig. 3D & E). Linking spines are short, more or less of even length, expand distally and form a dichotomous branching pattern (fig. 3A–E). The primary branches of the spine branch a second and sometimes a third time, often becoming pressed against adjacent spines forming contorted shapes. Separating spines were not observed. The ringleiste is shallow, U-shaped, and extends only a short distance into the cell cavity (figs 2C L, 4E & F). Rimoportulae are small rounded knobs of silica situated on the mantle just above the ringleiste (fig. 4E–F), with small internal and external openings. Up to three rimoportulae were found on broken specimens. Girdle bands are open, covered with minute pores, narrow at the open end, and becoming approximately 1.2 µm wide where the ligule fits into the adjoining band (fig. 4B). The connecting edge of the girdle bands consists of a series of fimbriae.

Morphometrics – Valve diameter over the ten-metre section of core ranged from 3.6 to 12.1 µm, with a mean of 7.4 µm (fig. 5A). The mean diameters of the smallest (n = 24) and largest (n = 24) valves were 4.3 µm and 11.3 µm, respectively, and the size distribution was slightly skewed towards valves with larger diameter. Valve mantle length ranged from 2.9 to 11.3 µm, with a mean of 6.2 µm. The L:W ratio ranged from 0.4 to 1.9, with a mean of 0.87, and values for the 25th and 75th percentiles were 0.7 and 1.0, respectively (fig. 5B). There was a significant relationship between valve diameter and the L:W ratio (p < 0.001, r² = 0.47, n = 2400), where smaller diameter valves had larger L:W ratios (fig. 5C). The smallest diameter valves tended to be longer, resulting in slightly higher L:W values.

A preliminary analysis of differences in valve morphometrics between the 12 strata examined over the ten-metre section of core was completed by measuring 200 valves for each of 12 strata (table 1, fig. 6). As with the combined data set, there was a significant decline in L:W ratio with an increase in diameter (fig. 6A). The mean valve diameter ranged from 6.7 to 8.3 µm and the L:W ratio from 0.77 to 1.1, over all 12 strata (fig. 6B–C). Although differences in mean valve diameter and L:W ratio were small, values did oscillate over time.

Comments – Frustule characters described above, especially complimentary fitting valves, were consistently observed within populations of specimens from all 12 sections over the ten-metre section containing this organism. Initial valves were observed attached to ends of maternal filaments ranging in diameter from 10 to 11.9 µm. Despite observing thousands of cells with both LM and SEM, a definitive type of separating spines was not found. Some valves did, however, have slightly elongate spines with narrow distal ends (valve

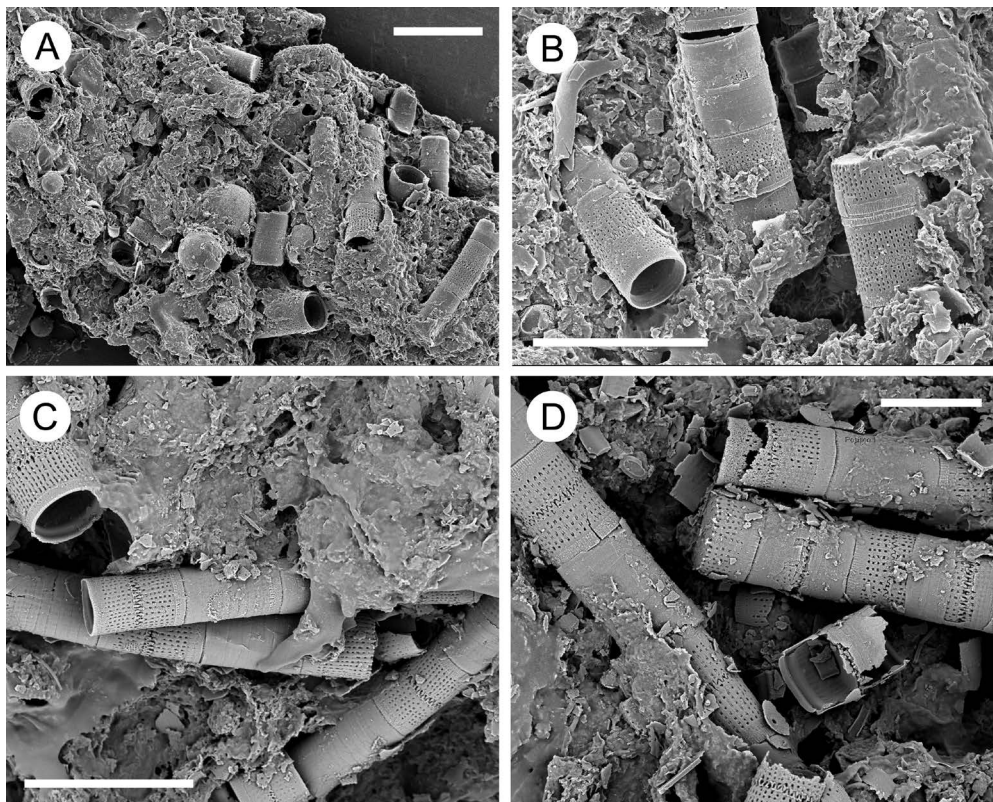


Figure 1 – SEM images of *Aulacoseira giraffensis* specimens found within mudstone fragments representing samples from core boxes 17 (B), 19 (A & C) and 20 (D) of the Giraffe Pipe locality. Scale bars: A–C = 20 µm; D = 10 µm.

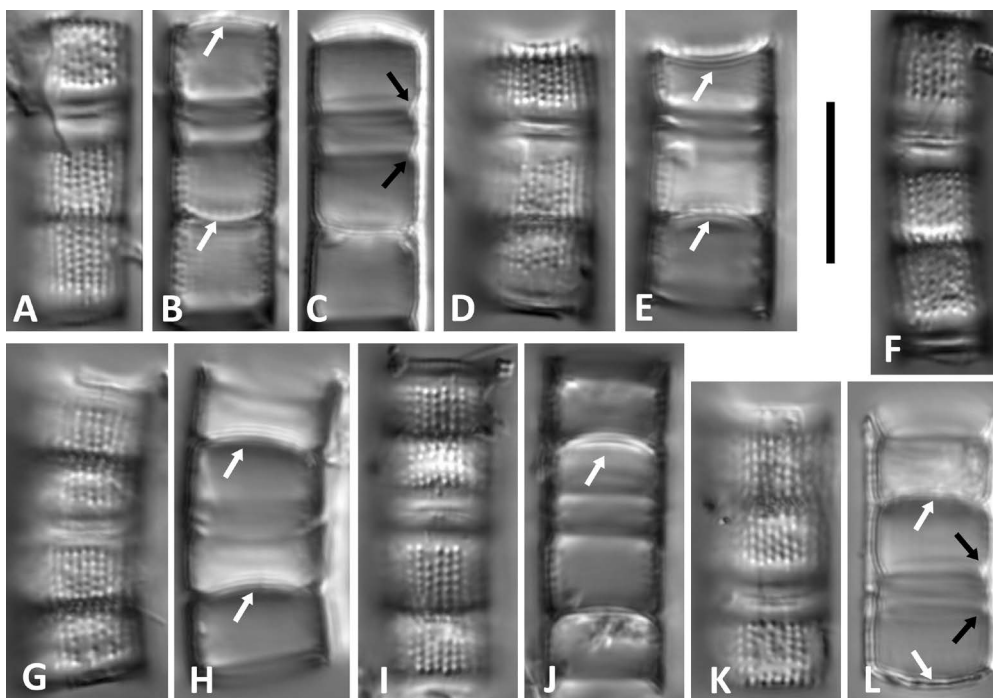


Figure 2 – Light micrograph images of *Aulacoseira giraffensis* specimens from the Giraffe Pipe locality. A–B, D–E, G–H, I–J, and K–L represent images of specimens taken at different focal depths. The specimen illustrated in A–C represents the circled specimen on the Type slide deposited at the Canadian Museum of Nature as CANA# 128319 from section GP 19-1-100. Note the convex-concave nature of the valve face (white arrows on B, E, H, J & L), and the position of the shallow ringleiste (black arrows on C & L). The marginal row of linking spines is visible on the top valve in D. Scale bar = 10 µm.

on right side in fig. 3B) that may serve a role as separating spines.

Numerous specimens of *A. giraffensis* were present in fractured rock surfaces from all 12 sections of the core observed as part of this study, and as illustrated in fig. 1A–D. However, given the variability in the numbers of microfossils representing other groups of organisms (e.g. synurophytes, chrysophytes, testate amoebae, sponges and heliozoans), the relative abundance of *A. giraffensis* specimens varied from 2 to 71% over the ten-metre section of core (fig. 6B). The relative abundance of *A. giraffensis* was especially high (over 60%) from the 96 to 98 m section of the core, and again at 101 m. Between 98 and 101 m high concentrations of *Mallomonas insignis* Penard and *Synura recurvata* Siver &

A.P.Wolfe scales depressed the relative abundance of *A. giraffensis*, while above 96 m heliozoan, testate amoebae and synurophyte scales become more abundant.

DISCUSSION

Specimens of *Aulacoseira* have been recorded from two of the oldest localities known worldwide that bear freshwater diatoms, the Battle Formation in western Canada (Siver et al. 2018) and the Deccan Intertrappean beds in India (Ambwani et al. 2003), both from the latest Cretaceous. In both cases the specimens are not well preserved, but do reveal sufficient information to verify placement in *Aulacoseira*. The Battle Formation stretches across southern Alberta into Saskatch-

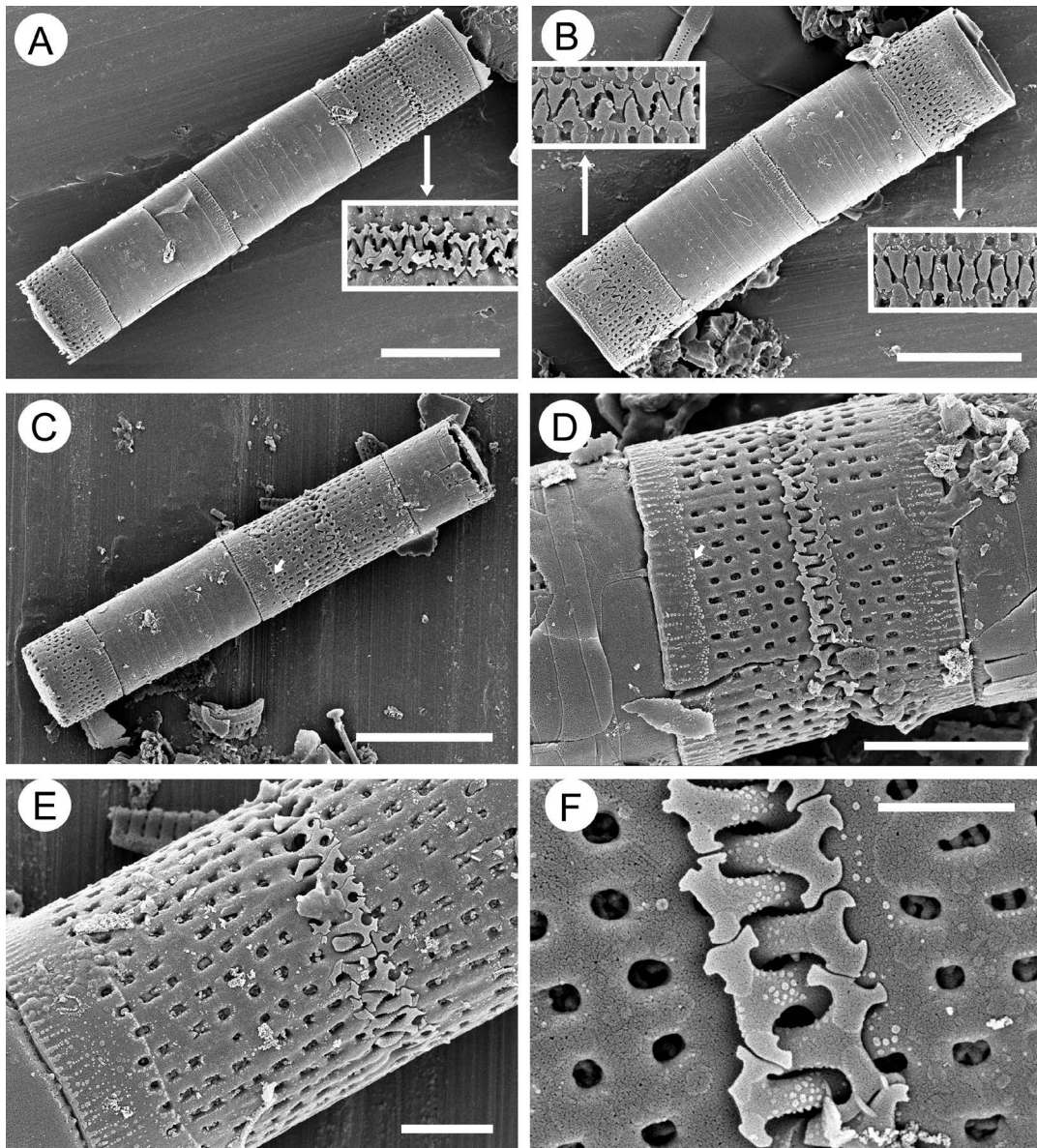


Figure 3 – SEM images of *Aulacoseira giraffensis* specimens from the Giraffe Pipe locality depicting intact short filaments or frustules (A–C), valves (D–E), and close-ups of typical linking spines (inserts on A–B & F). Note the variation in linking spine morphology, even on the same filament (B). The frustule atop the filament in C displays a concave valve (white arrow, right side) and a convex valve (black arrow, left side). White arrows on C–D indicate the location of a mantle step. Scale bars: A–C = 10 μm; D = 5 μm; E = 2 μm; F = 1 μm).

ewan (Canada), and represents either a single large freshwater lake or a series of smaller, interconnected, waterbodies that existed 66.5 million years ago (Binda 1970, Lerbekmo et al. 1987). Specimens of *Aulacoseira* from the Battle Formation formed cylindrical filaments linked together with interdigitating spines (Siver et al. 2018). Although spine morphology on the Battle specimens differs from *A. giraffensis*, both species had valves of similar size and length to width ratios, straight mantle striae, a solid valve face, and a shallow

low ringleiste. The Deccan Intertrappean beds represent remains from a freshwater site that formed approximately 65 million years ago. *Aulacoseira* specimens from those beds also shared features with *A. giraffensis*, including mantle areolae, a shallow ringleiste, and short spines connecting cells into filaments (Ambwani et al. 2003). Unfortunately, since the presence of rimoportulae could not be verified on any the Cretaceous specimens, comparisons of this important character could not be made with those of *A. giraffensis*. Still,

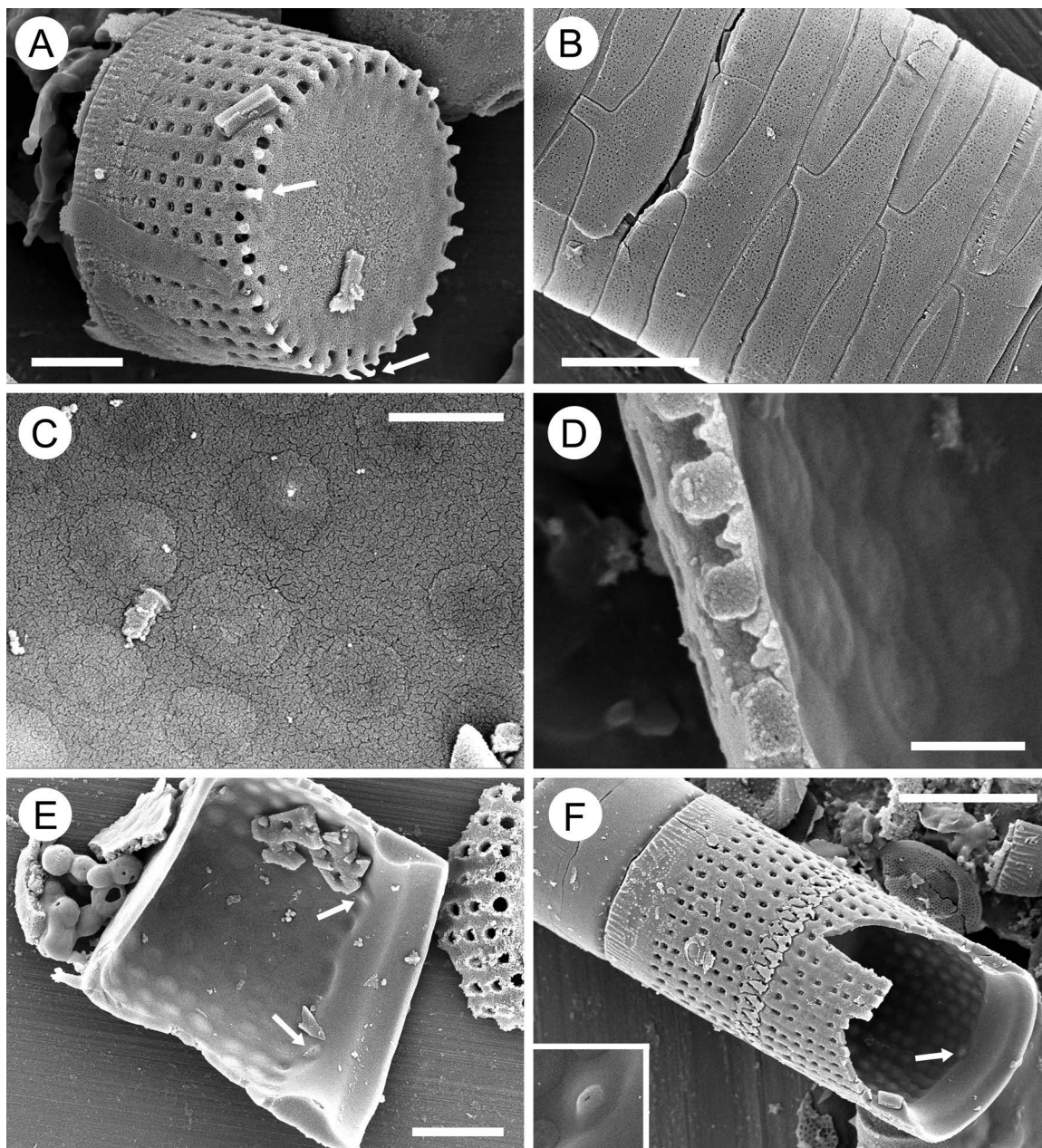


Figure 4 – SEM images of *Aulacoseira giraffensis* specimens from the Giraffe Pipe locality: A, valve with straight rows of mantle striae, and a concave hyaline valve face with a marginal row of pores. A step is present on the lower portion of the mantle. Spines that appear tooth-like are broken. Arrows denote linking spines still intact; B, overlapping open copulae (girdle bands) and associated ligules; C, close-up depicting the intact velum that covers the internal surface of each mantle areolae; D, fractured valve depicting the internal structure of mantle areolae. Note the areolar chamber and internal volae; E & F, internal surfaces of fractured valves depicting the shallow and U-shaped nature of the ringleiste, and the positions rimoportula (arrows) on the mantle just above the ringleiste. The insert in F is a close-up of the rimoportula denoted by the arrow. Scale bars: A, B & E = 2 μm ; C & D = 500 nm; F = 5 μm .

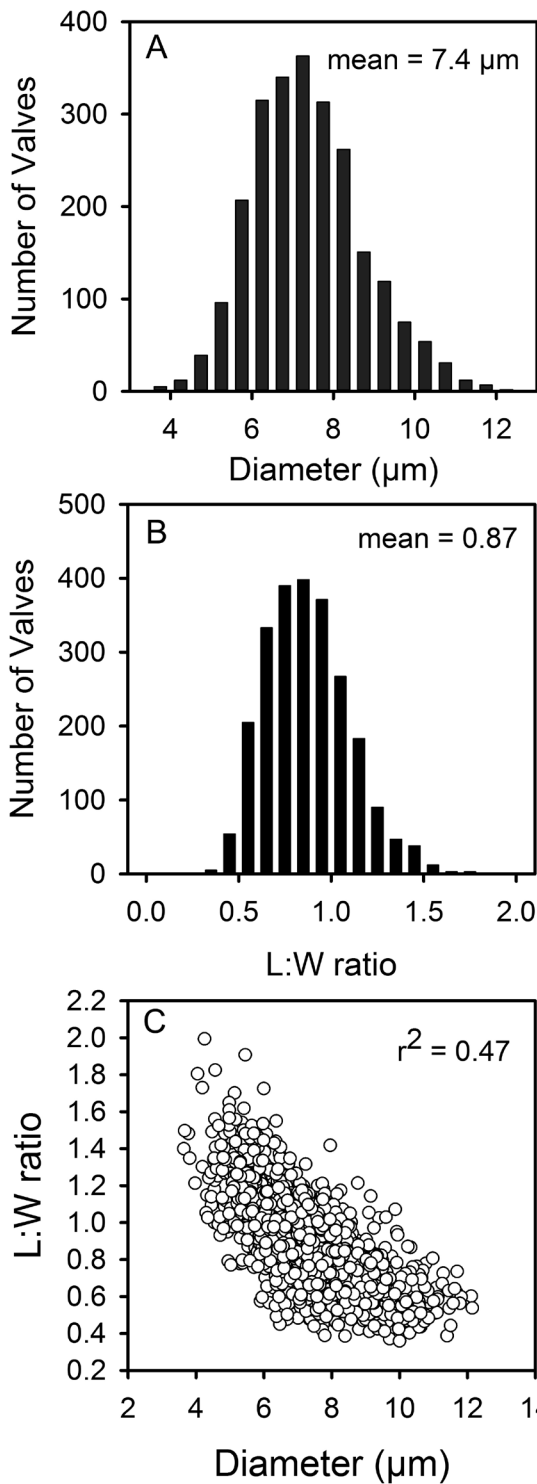


Figure 5 – Morphometric results for valves of *A. giraffensis*: A, distribution of valve diameter; B, distribution of L:W values (length to width ratio) for valves; C, significant relationship ($p < 0.001$, $r^2 = 0.47$) between L:W and valve diameter.

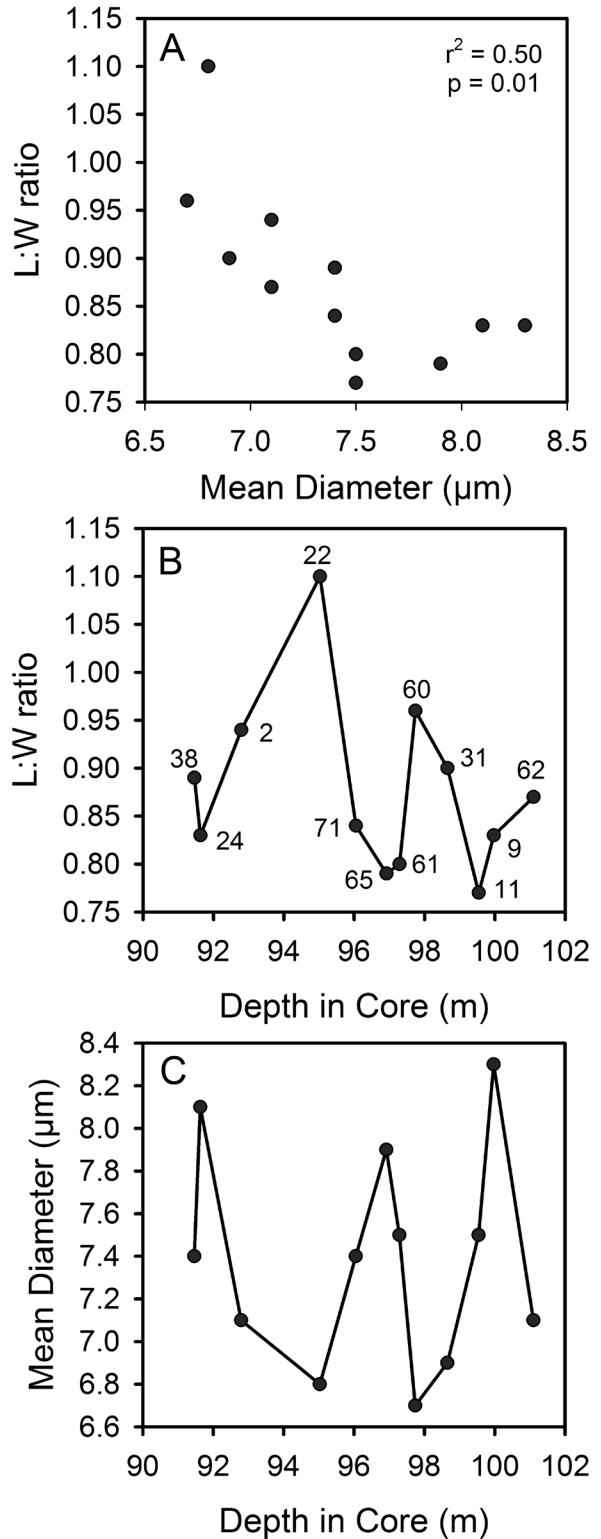


Figure 6 – Morphometric results of *A. giraffensis* valves for 12 strata along a ten metre section of the Giraffe Pipe core: A, the relationship between the L:W value and mean diameter (µm). Each point represents mean values of 200 valves from a given stratum; B, oscillations in the L:W ratio between the 91 and 101 depth interval; C, oscillations in mean diameter (µm) of valves between the 91 and 101 depth interval.

compared with many modern species, the rimoportulae on *A. giraffensis* are of a simple design (Houk 2003, Houk & Klee 2007, Siver & Hamilton 2011).

Specimens of *Aulacoseira* from the latest Cretaceous Battle and Deccan Intertrappean sites were common, but rocks from neither site harbored the massive concentrations revealed in the Giraffe core where *A. giraffensis* filaments were stacked on top of each other and often accounted for over 60% of the microfossil remains. Additional freshwater fossil sites known to harbor *Aulacoseira* that are of similar age to Giraffe, or older, include Wombat (Siver et al. 2016), Horsefly (Wolfe & Edlund 2005) and the Dewey Beds (Leonard & Marvin 1982, Krebs 1994) localities. The Wombat locality, a freshwater Paleocene or older waterbody from northern Canada, contains *Aulacoseira*, but in low numbers (Siver et al. 2016). The Horsefly site, an Eocene fossil freshwater locality approximately 44–52 million years old, also contains specimens of *Aulacoseira*, but rocks from this site do not contain the concentrations observed for *A. giraffensis* in Giraffe (Wolfe & Edlund 2005). The Dewey Beds locality in Idaho is another middle Eocene site (45 million years old: Axelrod 1998) containing *Aulacoseira* (Krebs 1994), however we were not able to compare concentrations at this locality with other sites. Interestingly, the Horsefly locality does harbor high concentrations of *Eoseira wilsonii* A.P. Wolfe & Edlund, a closely related member of Aulacoseiraceae, with concentrations observed in the rock matrix similar to those observed in Giraffe. It is very likely that differences in concentrations of *Aulacoseira* found at these fossil localities reflect differences in growth of the populations, and that the high numbers of *A. giraffensis* and *E. wilsonii* represent bloom-like conditions for these organisms during the early to middle Eocene. In the case of *A. giraffensis*, dense numbers of specimens were observed in the mudstone throughout the ten-meter section of core examined, suggesting that periods of extensive growth occurred in the lake over hundreds to thousands of years.

Many features present on *A. giraffensis* are found on contemporary species suggesting that the overall morphological body plan for the genus was well established by at least the Eocene. In an earlier work regarding *A. giraffensis*, Wolfe et al. (2006) reported the presence of internal cell components, including plastid fragments, pyrenoids and other membrane-bound structures, all evidence of remarkable and unprecedented preservation and suggesting that in addition to siliceous structure, modern cellular organization was also well established by the Eocene. Wolfe et al. (2006) further noted that even though many of the morphological characters of *A. giraffensis* resembled those found on some modern species, the suite of features represented an undescribed taxon. The simple structure of the rimoportulae, coupled with complementary concave-convex adjacent valves and highly dichotomous linking spines, present a suite of characters not known on any previously described species. In fact, the complementary fitting nature of *A. giraffensis* valves is rather unique for the genus. Frustules of the contemporary species *A. crassipunctata* Krammer can form similar convex-concave fitting valves, and this species also has branched linking spines and is known from the fossil record (Houk & Klee 2007). However, the size, structure and distribution of areolae, and de-

tails of the ringleiste, are very different from those found on *A. giraffensis*. Likewise, linking spines of the modern species *A. alpigena* (Grunow in Van Heurck) Krammer, *A. lirata* (Ehrenb.) R. Ross and *A. laevisima* (Grunow in Van Heurck) Krammer are similar to those of *A. giraffensis*, but details of the rimoportulae and areolae differ, and none of the former species have convex-concave fitting valves (Houk & Klee 2007, Wolfe et al. 2006).

We examined the morphological characters of hundreds of *A. giraffensis* specimens per section of the Giraffe core with respect to striae and areolae density and structure, ringleiste shape, rimoportula design and location, valve face and collum structure, and details of spines. We could not discern any notable changes or shifts in any of these morphological characters over the ten-meter section of core, and concluded that this organism represented the same species over a long period of lake history estimated to represent a minimum of ten thousand years. Our findings compare and contrast with those of Theriot et al. (2006) who studied changes in the morphological structure of *Stephanodiscus* Ehrenb. specimens in a core from Yellowstone Lake (Wyoming, U.S.A.) over thousands of years. In that study, Theriot et al. (2006) concluded that rapid fine-scale changes observed over 3.7 thousand years recorded the evolution of a new species, *S. yellowstonensis* E.C. Ther. & Stoermer, presumably the result of directional selection processes and possibly reflecting impacts of regional warming. However, over the ensuing ten thousand years, *S. yellowstonensis* remained morphologically stable. Similarly, our findings represent evolutionary stasis in morphological structure for *A. giraffensis* over a time scale of thousands of years, which may reflect relatively stable conditions for this time period. It is not surprising that evolution of a new species and stasis of another can occur over similar time scales, but driven by different processes.

Many modern species of *Aulacoseira* form two different types of spines referred to as linking and separating spines (Houk 2003, Houk & Klee 2007). As the names imply, linking spines hold frustules together such that they cannot be separated unless broken, while separating spines allow cells to slide apart from each other. Only linking spines could be confirmed for *A. giraffensis*. Some of the *A. giraffensis* specimens did have slightly elongated spines that were less branched. Although still overlapping, but to a much lesser degree, perhaps this spine morphology can allow cells to separate. A number of valves found on the ends of filaments (e.g. fig. 4A) appeared to have short tooth-like separating spines. However, upon closer examination the spines on these specimens were almost always broken, and evidence of linking spines could still be observed on most specimens (e.g. arrows on fig. 4A). It is also possible that true separating spines were rare and we simply did not observe them. However, this seems less likely given the large number of cells studied.

Although the size distributions of *A. giraffensis* specimens oscillated over time, the differences were within the range for species previously studied in this genus, and most likely represent slight shifts in growth patterns. In an extensive study of *Aulacoseira subarctica* (O. Müller) E.Y. Haw. in Lough Neagh, Northern Ireland, Jewson (1992) reported a range in valve diameter from 3 to 14 μm , but further noted

that the majority of the population had a smaller range of between 4 and 7 μm . Comparable findings for *A. subarctica* were reported by Lepskaya et al. (2010) based on a study of this organism in Lake Kurilskoye, Russia. Similar and even larger ratios in the ranges of valve diameter (e.g. max size/min size) have been reported for other *Aulacoseira* species (Babanazarova et al. 1996, Siver & Hamilton 2011). Findings for *A. giraffensis* derived from an extensive section of core yielded similar morphometric distributions, and support the morphological findings that the same taxon grew in the Giraffe waterbody over an extended time period. Further, populations with a greater percentage of small-diameter valves are likely the result of additional cell divisions prior to auxospore formation (Jewson 1992). This idea needs to be explored further for fossil populations.

Although there can be a fair degree of variation in valve length for a given diameter within species of *Aulacoseira*, in general, there is an increase in length as the diameter decreases (Jewson 1992, Lepskaya et al. 2010). Typically, the increase in length is not enough to compensate for the loss in volume due to the decreased diameter, resulting in cells with smaller volume as growth of the population continues. A similar result was found for *A. giraffensis*. In the case of *A. giraffensis*, the majority of valves were wider than long, resulting in L:W values less than 1. A fair number of the larger diameter valves were two or more times as wide, yielding L:W values below 0.5. On the other hand, about 1/3 of the valves had an L:W value above 1, and none were measured with a ratio above 2. Although a more thorough study is needed, species that grow primarily in the plankton tend to have high L:W values, often above two, relative to those species found in littoral zones that tend to have valves with an L:W ratio below 1. Perhaps *A. giraffensis* was a tytoplanktonic organism able to grow in the littoral zone and also able to maintain a planktonic existence if cells were blown into the open water. Perhaps the oscillations observed in valve diameter and L:W ratio over time reflect differences in lake depth or other shifts in habitat availability. Regardless, the ability of *Aulacoseira* to sustain planktonic populations is the result of a complex set of variables, including the degree of mixing, lake depth, depth of the photic zone, filament length, grazing, resuspension characteristics, nutrient concentration and temperature, among other factors (Jewson 1992, Jewson et al. 2008, Lepskaya et al. 2010). Additional investigation is needed to determine if the oscillations in valve size observed for *A. giraffensis* are indeed linked to specific changes in the lake.

In summary, *Aulacoseira* is an ancient genus and an important component of many of the earliest known freshwater diatom sites. This genus was capable of establishing large populations by at least the early to middle Eocene, and remains a dominant element of numerous freshwater ponds, lakes and rivers today. Lastly, many morphological and morphometric characters found on early species of *Aulacoseira* resemble those present on modern species, indicating evolutionary stasis with respect to body design for the genus.

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REFERENCES

- Ambwani K., Sahni A., Kar R.K., Dutta D. (2003) Oldest known non-marine diatoms (*Aulacoseira*) from the uppermost Cretaceous Deccan Intertrappean beds and Lameta Formation of India. *Revue de Micropaléontologie* 46: 67–71. [https://doi.org/10.1016/S0035-1598\(03\)00011-4](https://doi.org/10.1016/S0035-1598(03)00011-4)
- Axelrod D. (1998) The Eocene Thunder Mountain Flora of Central Idaho. University of California Publications, Geological Sciences, vol 142.
- Babanazarova O.V., Likhoshway YE.V., Sherbakov D.Yu. (1996) On the morphological variability of *Aulacoseira baicalensis* and *Aulacoseira islandica* (Bacillariophyta) of Lake Baikal, Russia. *Phycologia* 35: 113–123.
- Benson M.E., Kocielek J.P. (2012) Freshwater diatom floristics of the late Eocene Florissant Formation, Clare's Quarry site, central Colorado, USA. *Bibliotheca Diatomologica* 58: 1–136.
- Binda P. (1970) Sedimentology and vegetal micropaleontology of the rocks associated with the Cretaceous Kneehills Tuff of Alberta: PhD Thesis, University of Alberta, Edmonton, Canada.
- Bradbury J.P., Krebs W.N. (1995) The diatom genus *Actinocyclus* in the Western United States. U. S. Geological Survey Professional Paper 1543 A-B., Washington, DC, U.S. Government Printing Office.
- Buatois L.A., Labandeira C.C., Mángano M.G., Cohen A., Voigt S. (2016) The Mesozoic lacustrine revolution. In: Mángano C.C., Buatois L.A. (eds) The trace-fossil record of major evolutionary events. *Topics in Geobiology* 40: 179–263. https://doi.org/10.1007/978-94-017-9597-5_4
- Chacón-Baca E., Beraldi-Campesi H., Cevallos-Ferriz S.R.S., Knoll A.H., Golubic S. (2002) 70 Ma nonmarine diatoms from northern Mexico. *Geology* 30: 279–281. [https://doi.org/10.1130/0091-7613\(2002\)030%3C0279:MNDFFNM%3E2.0.CO;2](https://doi.org/10.1130/0091-7613(2002)030%3C0279:MNDFFNM%3E2.0.CO;2)
- Harwood D.M., Nikolaev V.A. (1995) Cretaceous diatoms: morphology, taxonomy, biostratigraphy. In: Blome C.D., Whalen P.M., Reed K.M. (eds) *Siliceous Microfossils: Short Courses in Paleontology* 8: 81–106. <https://doi.org/10.1017/S247526300001434>
- Heaman L.M., Kjarsgaard B.A., Creaser R.A. (2004) The temporal evolution of North American kimberlites. *Lithos* 76: 377–397. <https://doi.org/10.1016/j.lithos.2004.03.047>
- Houk V. (2003) Atlas of freshwater centric diatoms with a brief key and descriptions. Part I. Melosiraceae, Orthosiraceae, Paraliaceae and Aulacoseiraceae. *Fottea, Olomouc* 7: 85–255.
- Houk V., Klee R. (2007) Atlas of freshwater centric diatoms with a brief key and descriptions. Part II. Melosiraceae and Aulacoseiraceae (Supplement to Part I). *Czech Phycology Supplement* 1: 1–112.
- Jewson D.H. (1992) Size reduction, reproductive strategy and the life cycle of a centric diatom. *Philosophical Transactions of the Royal Society, London, B* 336: 191–213. <https://doi.org/10.1098/rstb.1992.0056>
- Jewson D.H., Granin N.G., Zhdanov A.A., Gorbunova L.A., Bondarenko N.A., Gnatovsky R.YU. (2008) Resting stages and ecology of the planktonic diatom *Aulacoseira skvortzowii*

- in Lake Baikal. *Limnology and Oceanography* 53: 1125–1136. <https://doi.org/10.4319/lo.2008.53.3.1125>
- Kooistra W.H.C.F., Medlin L.K. (1996) Evolution of the diatoms (Bacillariophyta). IV. A reconstruction of their age from small subunit rRNA coding regions and fossil record. *Molecular Phylogenetics and Evolution* 6: 391–407.
- Krebs W.N. (1994) The biochronology of freshwater planktonic diatom communities in western North America. In: Proceedings of the 11th International Diatom Symposium, San Francisco, California, 12–17 August 1990: 458–499. *Memoirs of the California Academy of Science*.
- Leonard B.F., Marvin R.F. (1982) Temporal evolution of the Thunder Mountain Caldera and related features, central Idaho. In: Bonnicksen W., Breckenridge R.M. (eds) *Cenozoic Geology of Idaho*. Idaho Bureau of Mines Geology Bulletin 26: 23–42.
- Lepskaya E.V., Jewson D.H., Usoltseva M.V. (2010) Aulacoseira subarctica in Kurilskoye Lake, Kamchatka: A deep, oligotrophic lake and important Pacific salmon nursery. *Diatom Research* 25: 323–335. <https://doi.org/10.1080/0269249X.2010.9705853>
- Lerbekmo J.F., Sweet A.R., Louis R.M.St. (1987) The relationship between the iridium anomaly and palynological floral events at three Cretaceous-Tertiary boundary localities in western Canada. *Geological Society of America Bulletin* 99: 325–330. [https://doi.org/10.1130/0016-7606\(1987\)99%3C325:TRBTIA%3E2.0.CO;2](https://doi.org/10.1130/0016-7606(1987)99%3C325:TRBTIA%3E2.0.CO;2)
- Lohman K.E., Andrews G.W. (1968) Late Eocene nonmarine diatoms from the Beaver Divide Area, Fremont County, Wyoming. U. S. Geological Survey Professional Paper, v. 593-E. Washington, D.C., U.S. Government Printing Office. <https://doi.org/10.3133/pp593E>
- Medlin L.K. (2016) Evolution of the diatoms: major steps in their evolution and a review of the supporting molecular and morphological evidence. *Phycologia* 55: 79–103.
- Sims P.A., Mann D.G., Medlin L.K. (2006) Evolution of the diatoms: insights from fossil, biological and molecular data. *Phycologia* 45: 361–402.
- Singh R.S., Stoermer E.F., Kar R. (2006) Earliest freshwater diatoms from the Deccan Intertrappean sediments of India. *Micropaleontology* 52: 545–551. <https://doi.org/10.2113/gsmicro-pal.52.6.545>
- Siver P.A. (2015) *Mallomonas schumachii* sp. nov., a fossil Synurophyte bearing large scales described from an Eocene maar lake in northern Canada. *Nova Hedwigia* 101: 285–298. https://doi.org/10.1127/nova_hedwigia/2015/0270
- Siver P.A., Wolfe A.P. (2005) Eocene scaled chrysophytes with pronounced modern affinities. *International Journal of Plant Science* 166: 533–536. <https://doi.org/10.1086/428702>
- Siver P.A., Wolfe A.P. (2009) Tropical ochrophyte algae from the Eocene of northern Canada: A biogeographic response to past global warming. *Palaios* 24: 192–198. <https://doi.org/10.2110/palo.2007-p07-077r>
- Siver P.A., Hamilton P.B. (2011) Diatoms of North America: The Freshwater Flora of the Atlantic Coastal Plain. *Iconographia Diatomologica* 22: 1–920.
- Siver P.A., Wolfe A.P., Edlund M.B. (2010) Taxonomic descriptions and evolutionary implications of Middle Eocene pinnate diatoms representing the extant genera *Oxyneis*, *Actinella* and *Nupela* (Bacillariophyceae). *Plant Ecology and Evolution* 143: 340–351. <https://doi.org/10.5091/plecevo.2010.419>
- Siver P.A., Jo B.Y., Kim J.I., Shin W., Lott A.M., Wolfe A.P. (2015) Assessing the evolutionary history of the class Synurophyceae (Heterokonta) using molecular, morphometric, and paleobiological approaches. *American Journal of Botany* 102: 921–941. <https://doi.org/10.3732/ajb.1500004>
- Siver P.A., Wolfe A.P., Edlund M.B. (2016) *Fideliacyclus wombatiensis* gen. et sp. nov. – a Paleocene non-marine centric diatom from northern Canada with complex frustule architecture. *Diatom Research* 31: 397–408. <https://doi.org/10.1080/0269249X.2016.1256351>
- Siver P.A., Velez M., Cliveti M., Binda P. (2018) Early Freshwater Diatoms From the Upper Cretaceous Battle Formation in Western Canada. *Palaios* 33(12): 525–534. <https://doi.org/10.2110/palo.2018.045>
- Strelnikova N.I., Lastivka T.V. (1999) The problem of the origin of marine and freshwater diatoms. In: Mayama S., Kozumi I. (eds) Proceedings of the 14th Diatom Symposium, 1998: 113–123. Koenigstein, Koeltz Scientific Books.
- Wolfe A.P., Edlund M.B. (2006) Taxonomy, phylogeny, and paleoecology of *Eoseira wilsonii* gen. et sp. nov., a Middle Eocene diatom (Bacillariophyceae: Aulacoseiraceae) from lake sediments at Horsefly, British Columbia, Canada. *Canadian Journal Earth Science* 42: 243–257. <https://doi.org/10.1139/e04-051>
- Wolfe A.P., Edlund M.B., Sweet A.R., Creighton S. (2006) A first account of organelle preservation in Eocene nonmarine diatoms: observations and paleobiological implications. *Palaios* 21: 298–304. <https://doi.org/10.2110/palo.2005.p05-14e>
- Wolfe A.P., Reyes A.V., Royer D.L., Greenwood D.R., Doria G., Gagen M., Siver P.A., Westgate J.A. (2017) Middle Eocene CO₂ and climate reconstructed from the sediment fill of a subarctic kimberlite maar. *Geology* 45: 619–622. <https://doi.org/10.1130/G39002.1>

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