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Miocene *Aulacoseira* species from the Virgin Valley Formation, Nevada, U.S.A.

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Abstract: *Aulacoseira* Thwaites is one of the oldest known diatom genera to inhabit freshwater ecosystems, having been recorded from multiple localities from the late Cretaceous. The genus continued to evolve throughout the Cenozoic and today continues to thrive in aquatic environments globally, often forming an important contributor to phytoplankton communities. Morphological characters that define *Aulacoseira* had largely evolved by the Eocene, and many additional species have been uncovered since that time, especially in the Miocene. The Virgin Valley Formation, located in the northwestern portion of Nevada, USA, represents an extensive deposit that dates to middle Miocene (~14.4 Ma) and spans a period of time that covers the end of the Middle Miocene Climatic Optimum (MMCO) and onset of the Middle Miocene Climatic Transition (MMCT). The formation contains strata consisting of organic lignite, mudstones and diatomite, ranging in thickness from a few cm to tens of meters. During an investigation of the biological remains, *Aulacoseira* was found to dominate many of the strata, indicating the importance of this diatom in these ancient aquatic ecosystems. The objective of this communication is to provide a detailed accounting of the most common *Aulacoseira* species found at the Virgin Valley locality, including the descriptions of six new species. Collectively, the new taxa represent a wide range of morphological characters, and their remains are used to infer aspects of the paleoecology of the ancient habitats.

Keywords: *Aulacoseira*, diatoms, fossil, Miocene, Nevada, new species, Virgin Valley

Introduction

Aulacoseira Thwaites is a freshwater centric diatom genus that is globally distributed, commonly found in lakes, ponds, rivers and other aquatic environments, and is often reported as an important component of planktic environments (Jewson 1992; Siver & Kling 1997; Edgar & Theriot 2004). *Aulacoseira* is in the family Aulacoseiraceae Moisseeva, and although all genera in the family are known from the fossil record, *Aulacoseira* is the only one represented in modern floras and not presumed to be extinct (Wolfe & Edlund 2005). In fact, *Aulacoseira* is one of the oldest known freshwater diatoms, having been found in multiple deposits from the late Cretaceous, including ones in India (65 Ma, Ambwani et al. 2003) and North America (67 Ma, Siver et al. 2018; 83 Ma, Siver et al. 2016). The genus became more common during the Paleogene and throughout the latter part of the Cenozoic, and remains widespread and abundant today (Bradbury & Krebs 1995; Wolfe & Edlund 2005; Siver et al. 2016). Van Landingham (1971, 1979) recognized 116 species and subspecific taxa of *Aulacoseira*, although at that time they were mostly placed under the genus *Melosira* Agardh, and later transferred to *Aulacoseira*. Today, 225 species and subspecific taxa are recognized under *Aulacoseira* (Guiry & Guiry 2022).

Frustules of *Aulacoseira* can be solitary, but are most often linked together into either short or long filaments. Valves have moderate to deep mantles that usually form a right angle with the valve face on the exterior surface, and possess areolae on the mantle that are most often aligned as striae (Crawford 1981; Round et al. 1990; Siver & Kling 1997; Likhoshway & Crawford 2001). Spines are arranged in a ring on the margin of the valve face, and are most often aligned with one to a few mantle (pervalvar) costae. Two types of spines can be found and are present on most species. Linking spines hold adjacent frustules together in a filament and often form a zipper–like arrangement that secures the attachment of valves from adjacent frustules. Separating spines differ in morphology from linking spines, such that the frustules can slide apart. Areolae or smaller pores can cover the valve face, be randomly scattered, restricted to the margin, or lacking altogether. Mantle areolae are usually open to the exterior, but can have a covering or volate occlusion within the chamber and/or on the interior surface. Three additional characteristics, the presence of a ringleiste, rimoportulae, and a collum, help to further define the genus, and distinguish among species. The collum is the portion of the mantle at its base that lacks areolae. That is, the mantle striae terminate at the top of the collum. On the inside of the mantle, close to the top of the collum is a thickening, the ringleiste, that protrudes inward and encircles the mantle forming a ring. The depth that the ringleiste protrudes into the interior of the frustule, and its cross–sectional shape, vary among species. A rimoportula is a longitudinal slit found along the inner wall, typically on the mantle for *Aulacoseira* species, connected to a tube that penetrates the wall and opens to the exterior (Houk & Klee 2007). The number, position, arrangement and shape of the rimoportulae vary widely among taxa. These structures can be found close to or associated with the ringleiste, along the mantle wall, close to the mantle/valve face juncture, and less often on the valve face (Siver 2021). Variations in all of these characters are used to define the numerous species.

Kenneth E. Lohman was a diatomist employed for many years with the United States Geological Service (USGS). Lohman published numerous articles and reports on diatoms during his tenure with the USGS, primarily based on fossil localities in the western United States. Interestingly, Lohman earned a Ph.D. from the California Institute of Technology with a focus on diatoms from the Great Basin many years after he first reported on this group of organisms with the USGS (Lohman 1957). His thesis examined collections made from five formations in the Great Basin covering the Middle Miocene to the late Pleistocene, including samples from the Virgin Valley that he collected in 1938. Lohman (1957) reported a total of 353 diatom species and subspecific taxa from all five formations, including 85 as new. Of the 353 taxa, 20 were reported from the Virgin Valley under the genus *Melosira*, all of which today would be recognized within the genus *Aulacoseira*. Of the 20 taxa, eleven were described as new, six as species and five as varieties. Unfortunately, because the results from Lohman's thesis were never officially published, his proposed new descriptions are invalid, and not recognized (Guiry & Guiry 2022).

In 2018, I had the opportunity to make collections from a remote section of the Virgin Valley Formation with the goal of examining the remains of all microscopic siliceous freshwater organisms, including diatoms, from the ancient freshwater environments represented within this extensive deposit. The samples were especially rich in *Aulacoseira*. I was also able to examine original samples collected by Lohman in 1938 from a nearby, but different, suite of outcrops of the Virgin Valley Formation that he used in his thesis, and later archived subsamples at the California Academy of Sciences (CAS). These samples included both prepared slides and raw rock material. The objective of this work was to examine and describe the *Aulacoseira* flora in the collections made by Lohman in 1938 and myself in 2018, with a primary focus on undescribed taxa.

Description of the Virgin Valley Formation. The Virgin Valley Formation (Fig. 1), situated in the Great Basin, is located in Humboldt County, Nevada, in the northwestern–most part of the state (Wendell 1970; Davis & Pyenson 2007). The formation spans approximately 457 m and comprises three members (Lohman 1957; Fyock 1963). The middle member of the Virgin Valley formation consists of tuffaceous sandstones and siltstones, diatomite, mudstone and vitric tuffs (Fig. 2) largely deposited in lacustrine environments at the end of the Middle Miocene Climatic Optimum (MMCO) and into the subsequent Middle Miocene Climatic Transition (MMCT) (Fyock 1963). This portion of the expansive formation ranges in age between 16.3 Ma and 13.6 Ma based on remains of land mammals (Davis & Pyenson 2007), and has a mean age of 14.4 Ma using fission tracking age dating (Zielinski 1982). Organic lignite strata ranging in thickness from 0.5 to 40 cm (Fig. 2b, e) are interspersed between sandstone, siltstone and diatomaceous mudstone strata in seven of 24 units as detailed by Wendell (1970). All of the rocks examined in the current study (Fig. 2) originated in the Wendell's middle member unit. A detailed stratigraphy of the Virgin Valley Formation is given in Wendell (1970).

Multiple investigations of the vertebrate fauna from the Virgin Valley Formation have been completed, including early and extensive studies made by Merriam (1910, 1911), and are reviewed by Davis & Pyenson (2007). Using vertebrate fossil remains, Merriam (1911) proposed three distinct units, which were also identified and used by Lohman (1957) in his thesis on diatoms of localities in the Great Basin. However, Lohman (1957) referred to Merriam's upper unit as the "Upper Virgin Valley," and combined Merriam's middle and lower units as the "Lower Virgin Valley." According to Lohman (1957), the lower unit of Merriam (1911) consisted largely of hard tuffs and clays of various colors, and was devoid of diatoms. The middle unit contained distinct strata of shale, lignite layers, and white to brown–colored diatomaceous beds, each ranging in thickness from between 2–3 cm to ~14 m (Lohman 1957). The Lower Virgin Valley (LVV) is separated from the Upper Virgin Valley (UVV) by a layer of rhyolitic rock remains. The Upper Virgin Valley (UVV) extends close to 100 m, consists of ash beds and diatomaceous beds, and is capped by an extensive horizontal basalt deposit that forms a flat highland butte, or mesa, known as Gooch Table (Fig. 1). Outcrops of the UVV are bright white and stand in stark contrast with the dark brown to black colored volcanic basalt rocks that cap Gooch Table. The rocks collected by Lohman in 1938, and used in his thesis (Lohman 1957), align with the middle member described in Wendell's (1970) stratigraphy.

Although global climate during the Miocene (23 to 5.3 Ma) was moderately warm compared with that of the late Oligocene, Pliocene and today (Frigola et al. 2018), major shifts are particularly noteworthy during the Middle Miocene (16–11.6 Ma). The warm MMCO period that peaked near 15 Ma, was followed by a 2 Ma–long cooling trend, the MMCT (Bouchal et al. 2018; Frigola et al. 2018). The causes for the MMCT cooling are debated, but are likely coupled with declining atmospheric CO_2, changes in oceanic circulation patterns, and increased volcanism (Dillhoff et al. 2009; Frigola et al. 2018). As noted, the age estimates for the Virgin Valley Formation reflect a time period that corresponds to the end of the MMCO and beginning of the MMCT. During this time frame, the climate in the Great Basin was initially warm and with moderate precipitation, then began to transition to a cooler and more arid environment (Wallace 2003). Despite the cooling trend, the climate was still significantly warmer than today.

Materials and Methods

Samples examined. Rock samples from 14 locations in the Virgin Valley, including eight collected as part of this study and six originally collected by Lohman and archived at CAS, were examined (Table 1). In addition, 12 prepared slides originally made by Lohman and archived at CAS were closely studied (Table 1). As noted below, type specimens and material for new taxa will be deposited at the Canadian Museum of Nature (CMN). Isotype specimens and associated rock material will also

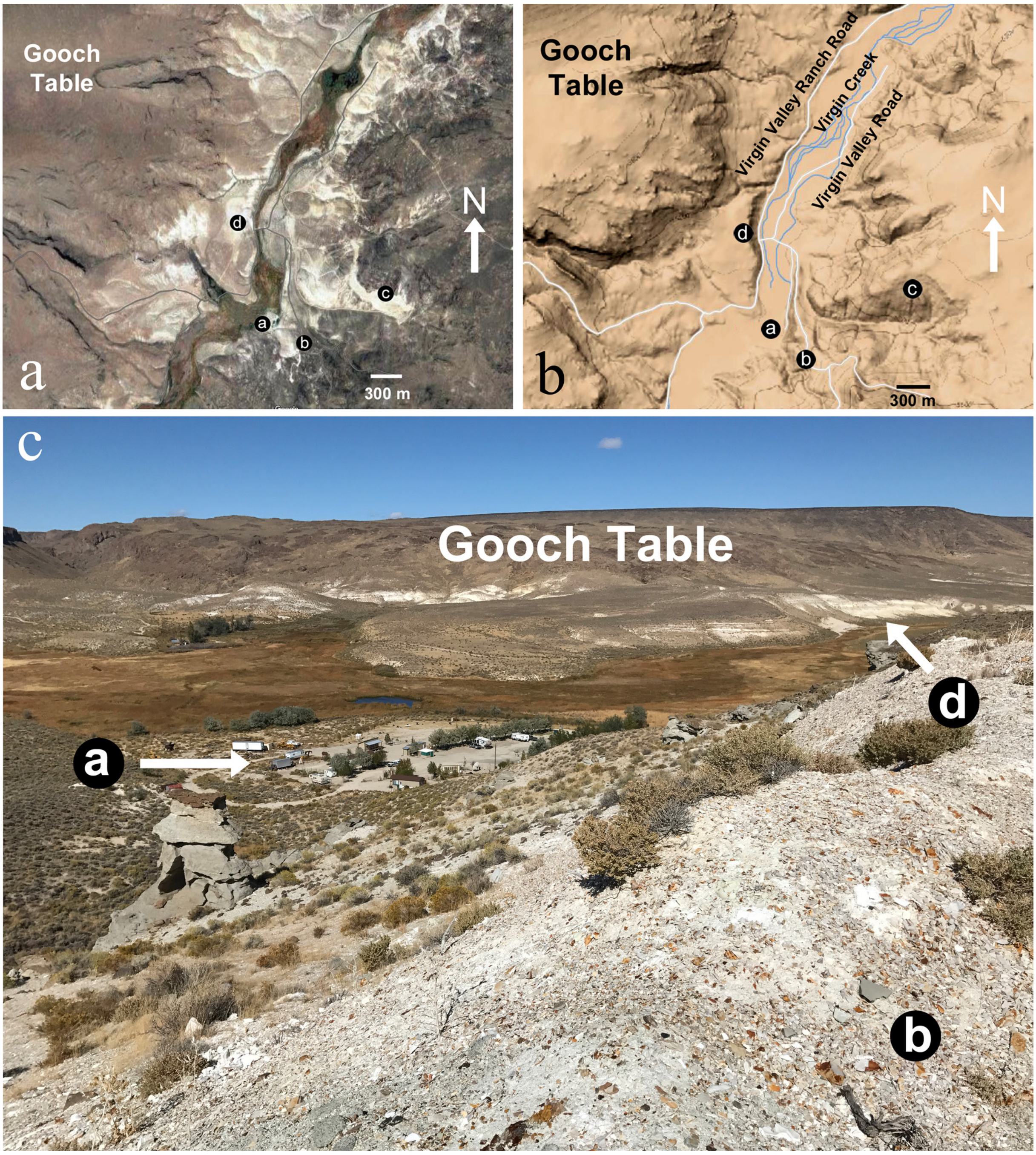

Fig. 1. Aerial views of the Virgin Creek section of the Virgin Valley Formation taken from Google Earth (a–b) and by P.A. Siver (c), indicating the locations of collection sites for samples taken by Siver in 2018 as listed in Table 1; the letters within black circles indicate: (a) the location of the Royal Peacock mining camp and buildings; (b) the location shown in Fig. 2c on the Royal Peacock property for collections #18, #20, #21 and #25; (c) the location of the Royal Peacock open mine for collections #37, #38 and #40 and (d) the location along the Virgin Valley Ranch Road for collection #2; latitude and longitude coordinates for all sites are given in Table 1.

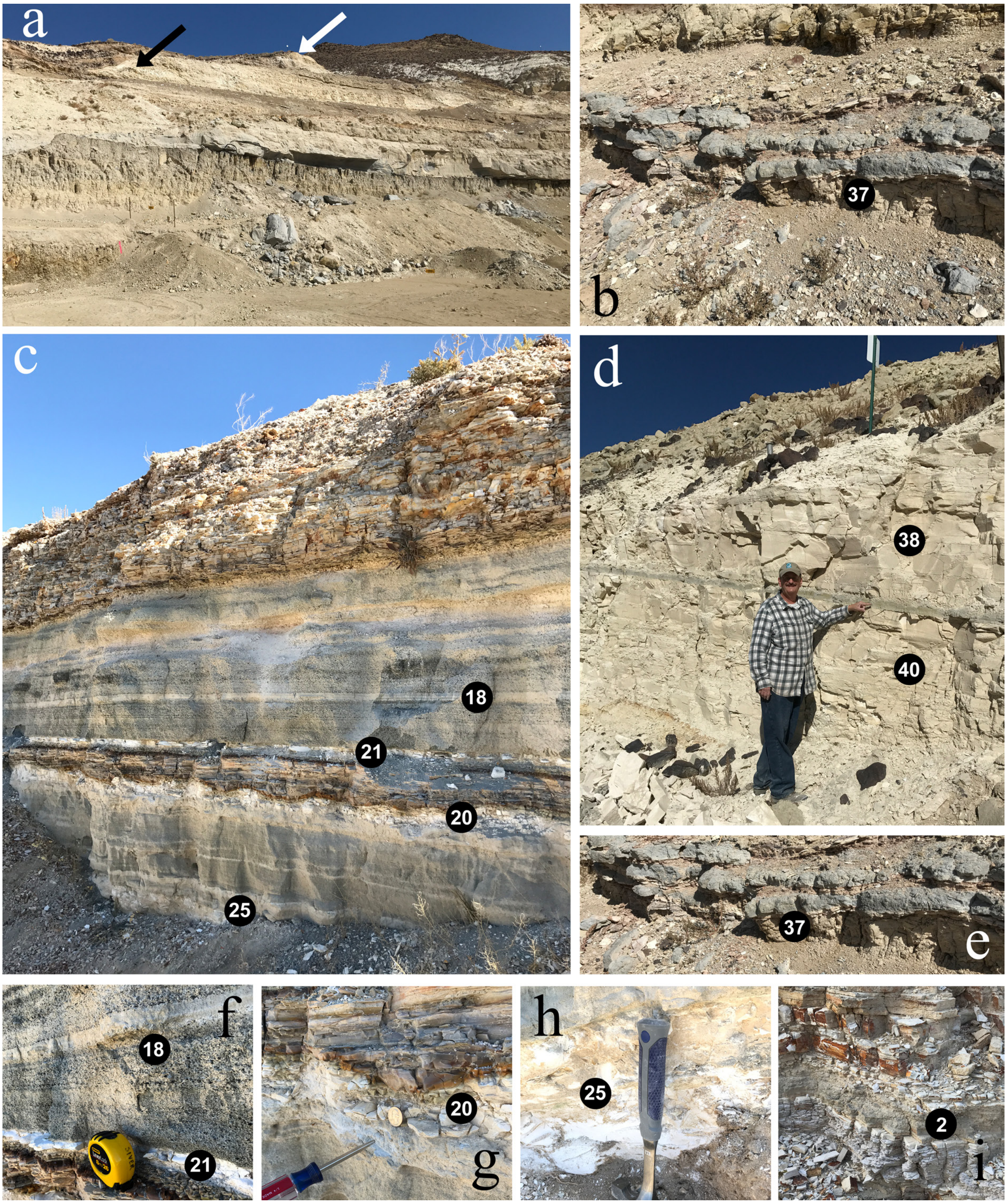

Fig. 2. Field images of the collection sites for samples taken by Siver in 2018 as listed in Table 1: (a, b, d, e) photos taken at the Royal Peacock open mine location; (a) overall view of the Royal Peacock open mine; the white arrow indicates the top of the Upper Virgin Valley exposed at this site; the black arrow shows a small layer of brown lignite/diatomite; (b, e) light brown diatomite where collection #37 was taken at the open mine location; this is one of several thin strata of brown diatomite shown in this image, each separated by a grey igneous layer; (c) exposed section of the Lower Virgin Valley situated at location b (black circle) in Fig. 1b; the outcrop is directly behind the spot where the image in Fig. 1c was taken; locations where samples #18, #20, #21 and #25 were taken are indicated; (d) close–up of where collections #38 and #40 were taken at the open mine site; Siver is pointing to a thin stratum of grey diatomite located between these two collection locations; (f–h) close–ups of strata #18, #20, #21 and #25; (i) close–up of the stratum representing collection #2 taken along the Virgin Valley Ranch Road.

be archived at CAS to complement the Lohman collections.

Sample preparation. Rock chips (0.5–1.0 g) from each sample were oxidized using 30 % H_2O_2 under low heat for a 1–3 hr, rinsed multiple times with distilled water, diluted to 10 ml with DW, and stored at 4 °C in glass vials. This oxidation procedure was sufficient to separate microfossils from the rock matrix for most samples. Some of the rocks that contained

Table 1. Summary of the samples investigated in the current study that were collected either by P.A. Siver in 2018, or by K.E. Lohman in 1938. Rock samples and prepared slides of Lohman material are archived at the California Academy of Sciences (CAS). Subsamples of rocks collected by Lohman were given to Siver, and Lohman's prepared slides were examined while on loan from CAS. Locations, including latitude/longitude coordinates, for the Siver collections are given, and correspond with site images in Figs 1–2. Virgin Valley zone refers to Lohman's (1957) classification as either Lower Virgin Valley, or Upper Virgin Valley. Descriptions of CAS samples were taken from Lohman's notes archived at CAS. RPP = Royal Peacock Property located in the Virgin Creek section of the Virgin Valley (Fig. 1).

Siver (VV#)/Lohman (USGS) collection #	CAS accession #	CAS slide #s	VirginValley zone	Notes
VV#2	n.a.	n.a.	Lower	Virgin Creek section, light brown diatomite/lignite; 41.7991° N, –119.1003° W
VV#18	n.a.	n.a.	Lower	RPP, light grey, crumbly, laminations, 4 cm thick layer; 41.7939° N, –119.0977° W
VV#20	n.a.	n.a.	Lower	RPP, white diatomite, chalky, 6 cm thick layer; 41.7939° N, –119.0977° W
VV#21	n.a.	n.a.	Lower	RPP, white diatomite, 3 cm thick layer; 41.7939° N, –119.0977° W
VV#25	n.a.	n.a.	Lower	RPP, white diatomite, top of layer exposed at base of the outcrop; 41.7939° N, –119.0977° W
VV#37	n.a.	n.a.	Lower	RPP, brown diatomite, lignite, below grey volcanic (?) rock; 41.7939° N, –119.0977° W
VV#38	n.a.	n.a.	Upper	RPP, thick, white, massive diatomite layer; 41.7992° N, –119.0874° W
VV#40	n.a.	n.a.	Upper	RPP, thick, white, massive diatomite layer; 41.7992° N, –119.0874° W
USGS 3525	601505	367095, 367096	Lower	Opal Creek section, chocolate brown lignite
USGS 3527	601507	367099, 367100	Lower	Opal Creek section, chocolate brown lignite diatomite
USGS 3530	601510	368005, 368006	Lower	Opal Creek section, white punky diatomite
USGS 3534	601512	368009, 368010	Lower	Opal Creek section, pale brown organic diatomite
USGS 3536	601514	368013, 368014	Lower	Opal Creek section, brown lignitic diatomite
USGS 3540	601516	368017, 368018	Upper	Virgin Creek section, white punky diatomite

high concentrations of organic remains required further treatment with H_2O_2, or additional oxidation with a sulfuric acid–potassium dichromate solution (Marsicano & Siver 1993). Known aliquots of each resulting slurry were diluted with DW and air dried onto both a piece of heavy–duty aluminum foil, and onto multiple circular glass coverslips. The aluminum foil samples were trimmed, attached to aluminum SEM stubs with Apiezon® wax, coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and observed with a FEI Nova Nano SEM 450 field emission scanning electron microscope. The coverslips were mounted onto glass slides using Naphrax, examined with a Leica DMR light microscope, and images of specimens taken with a Zeiss Axiocam 506 color camera. The prepared slides made by Lohman and on loan from CAS were also studied with the Leica DMR.

Other information. Multiple attempts were made to secure and examine material from Virgin Valley collected by Lohman and deposited as part of the USGS protocol at the Smithsonian museum. However, curators at the Smithsonian were unable to locate Lohman's slides and rock samples. Luckily, rock and prepared slides were also archived by Lohman at CAS, and these materials were studied in the current investigation. Holotype and isotype specimens of the six new species were archived at the CMN and the CAS, respectively. Type material was also deposited at CMN.

Throughout this communication, the use of a) mantle striae is equivalent to "pervalvar rows of areolae"; b) mantle costae, pervalvar costae and interstriae regions refer to the same structure and c) mantle height to mantle diameter ratio is equivalent to the length to diameter (L:D) ratio.

Results

Overview: All 14 samples examined from the Virgin Valley Formation contained more than one species of *Aulacoseira*. Of the taxa uncovered, eight contributed more than 90% of the total number of *Aulacoseira* specimens examined and will be described in detail below. Six of the species are described as new, and two were assigned to known taxa.

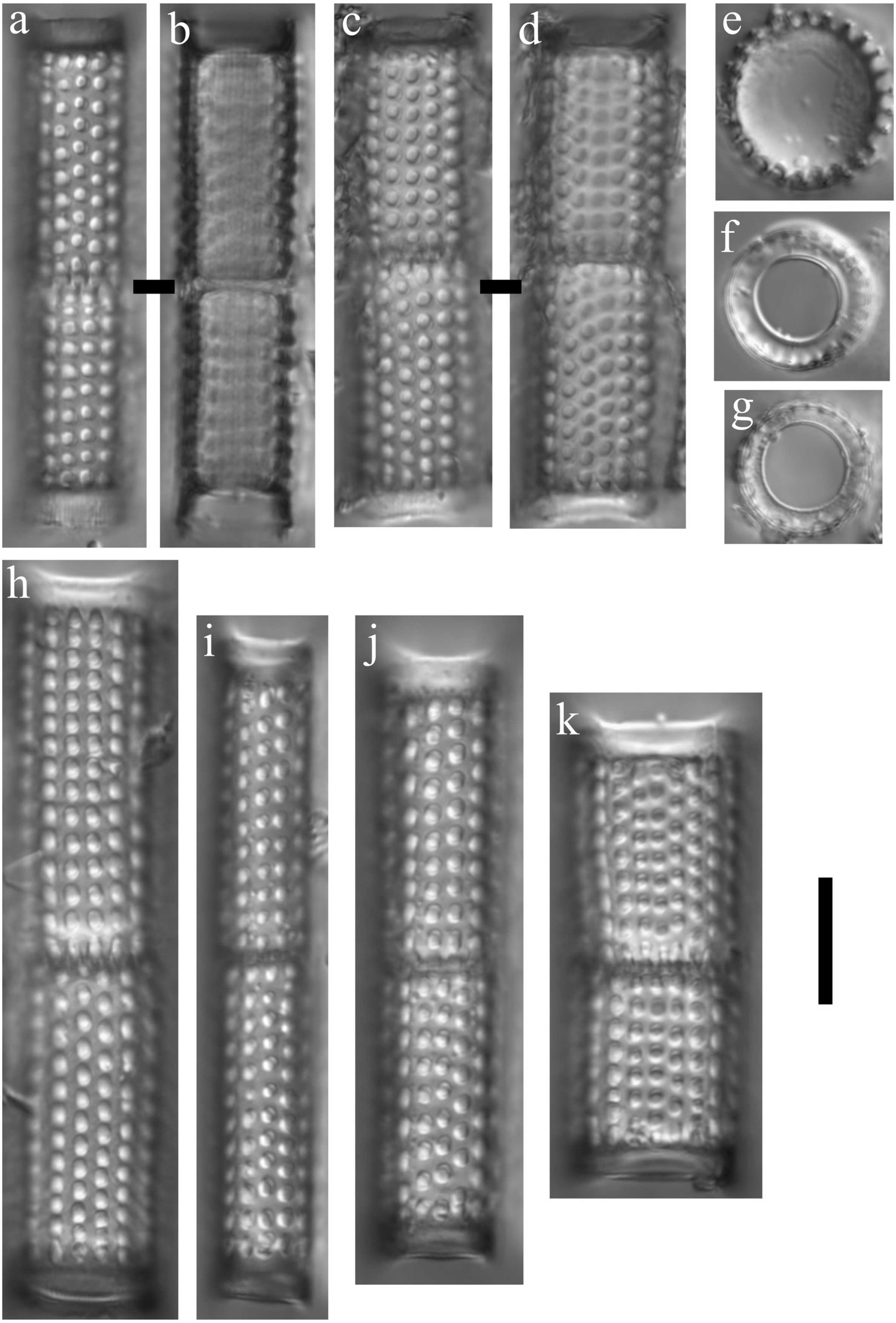

Fig. 3. Light micrographs of *Aulacoseira ponderosa* from the Miocene Virgin Valley Formation denoting girdle (a–d and h–k) and valve (e–g) views; note the straight mantle striae consisting of large areolae, smooth and distinct collum (e.g. h–k), smooth and non–areolated valve face (e), ringleiste (f–g) and small linking spines (e.g. a and h); specimens connected with a black bar (a–b and c–d) represent the same specimen at different focal planes; the holotype and isotype specimens are illustrated in a–b and c–d, respectively. Scale bar 10 μm.

Descriptions of new species:

***Aulacoseira ponderosa* sp. nov. Siver (Figs 3–5)**

Description: Valves long, with a mantle height ranging from 7.5–35µm, a diameter from 7–18 µm, and a mean height to diameter ratio of 3 (Table 2; Figs 3a–d, h–k; 4a, c, e). Striae straight (Fig. 3), 7–8 per 10 µm, evenly–spaced between the spines, and consisting of large, oval to slightly square–shaped areolae with a mean diameter along the long axis of 1.3 µm (Table 2; Fig. 4a–d). Areolae are occluded with complex volae that are slightly recessed from the external surface and connected to the sides of the areola with typically 5–10 short rotae (Figs 4b, d). Internally, each areola is covered with a thin layer of silica, or hymen, that is flush with the inner valve surface (Fig. 5e). The row of mantle areolae adjacent to the valve face form a ring of openings that can be seen between the spines on the margin of the valve face (Fig. 5a–b). On some valves, there may be a few additional occluded pores near the periphery of the valve face. Otherwise, the surface of the valve face is smooth and flat (Fig. 5a–b). Slightly elevated, flat, circular nodules are scattered on the mantle costae (Fig. 4d). Both linking and separating spines are present. Linking spines are short, with a mean length of 2 µm, of even lengths, spatula–shaped, and with several short and uneven teeth on the distal margin (Fig. 4a–e). Linking spines extend from each costa, and form a tight zig–zag or zipper–like arrangement to adjoin frustules. Separating spines are short, of even length, with a mean length of 1.8 µm, and terminate with a sharp point (Fig. 4f). The ringleiste is wide, extends inward approximately 2–3 µm, and has a thickened inner marginal rim (Figs 4f; 5c). There are multiple rimoportulae positioned in a ring on the valve mantle above the ringleiste, and mostly spaced every 3–4 µm (Figs arrows on Fig. 5d–f). The rimoportulae are on the mantle wall, are slightly twisted or curved, stalked, and terminate with a small slit surrounded by a pair of lips. The external openings of the rimoportulae appear to be within terminal areolae aligning the top of the collum (arrows on Fig. 4e). The collum is well defined, with a mean height of 2.3 µm, and a row of short and closely–spaced ribs along the base (Figs 4a, c, e). A step is often observed midway along the mantle.

Holotype: Circled specimen on prepared slide labeled "VV 40 Calgon, A" deposited at the Canadian Museum of Nature, CANA 131184. The holotype specimen is illustrated in Fig. 3a–b.

Isotype: Circled specimen on prepared slide labeled "Virgin Valley 40, Siver 1" and deposited at the California Academy of Sciences, CAS (slide number 223048). The isotype specimen is illustrated in Fig. 3c–d.

Type material: Diatomite material taken from the Upper Virgin Valley outcrop at the Royal Peacock Opal mine and deposited at the Canadian Museum of Nature, CANA 131184. The material was collected by P.A. Siver, and represents sample #40 in his collection.

Type locality: Royal Peacock Property located in the

Table 2. Morphometric statistics of eight valve characters for eight species of *Aulacoseira* from the Miocene Virgin Valley Formation. The range and mean (values separated by a "/") for each character are given except for the diameter of the ringleiste where only a mean valve is presented. The mantle height includes the collum, the diameter of the ringleiste is the distance from the inner mantle wall to the inner margin of the structure, and the areola diameter was taken along the longest axis. Measurements for *A. moralesii* do not include the dome cap. Measurements were primarily taken from high resolution scanning electron micrographs.

Name	Mantle height range/mean (µ)	Mantle diameter range/mean (µ)	Height: Diameter range/mean (µ)	Collum width range/mean (µ)	Ringleiste diameter mean (µ)	Linking spine range/mean (µ)	Areola diameter range/mean (µ)	Striae density (# / 10 µ)
A. ponderosa	7.5–35/20	7–18/13	0.9–4.5/3	2–2.6/2.3	2.8	1.7–2.45/2.0	1.12–1.53/1.3	7–8/7.5
A. lohmanii	9.4–24.8/14.2	3.9–17/11.2	0.63–6.36/1.7	1.4–2.2/1.9	2.3	0.9–1.8/1.4	0.9–1.3/1.16	7–8/7.6
A. vanlandinghamii	3.6–6.4/4.7	11.6–17.2/14.6	0.25–0.45/0.32	0.6–1.5/1.0	3.9	1.2–1.6/1.4	0.12–0.29/0.2	15–20/17.7
A. virginvalleyana	2.3–5.8/3.45	8.8–16.5/12.4	0.17–0.54/0.29	0.5–0.94/0.74	Not detected	1.3–2/1.6	0.29–0.51/0.38	11–14/12.3
A. royalpeacockii	2.9–5.2/4.3	4.9–7.6/6.4	0.4–0.9/0.69	0.8–2/1.36	0.72	0.74–1.91/1.07	0.25–0.45/0.33	11.5–14/12.7
A. moralesii	8.5–24.3/11.6	8–21.5/12.7	0.62–1.3/0.97	2.5–4.7/3.5	1.8	1–1.8/1.5	0.07–0.42/0.17	27–32.5/29
A. laevissima	4.8–8.5/6.5	6.1–12.1/9.1	0.6–1.1/0.74	0.8–1.9/1.4	1.04	0.6–1/0.81	0.09–0.19/0.13	18–24/21.1
A. italica	7–12/9.3	7–10.4/9.2	0.73–1.5/1.04	1.7–2.2/1.9	Not measured	2.6–3.4/3	0.41–0.5/0.4	18–22/20

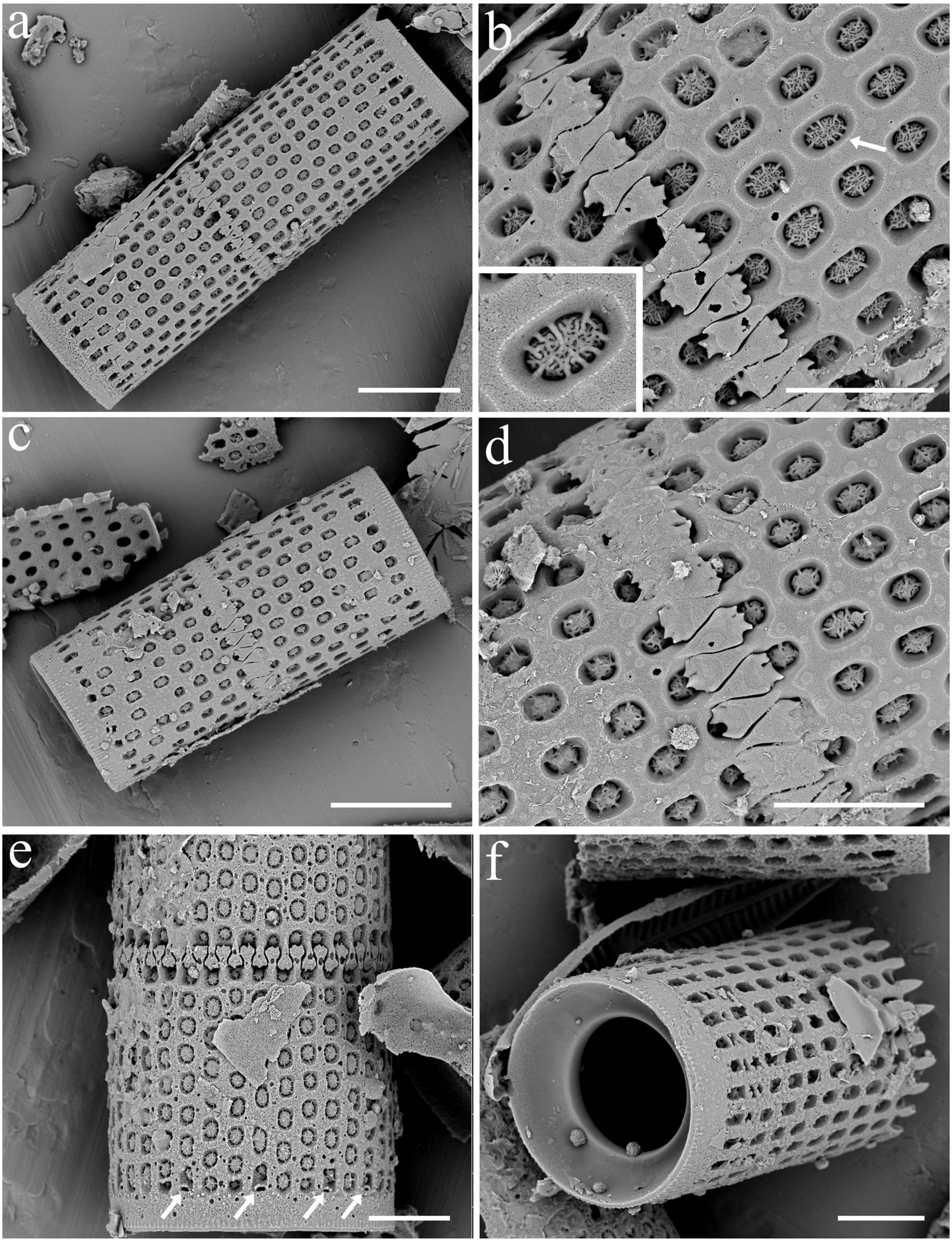

Fig. 4. Scanning electron micrographs of *Aulacoseira ponderosa* from the Miocene Virgin Valley Formation: (a, c) two valves adjoined with linking spines; note the straight striae composed of large oval areolae, flat and circular nodules on the costae, and well–defined collum; note the step midway along the mantle on the upper valve in (a); (b, d) close–ups of the specimens in (a) and (c), respectively, showing details of the spatula–shaped linking spines and details of the areolae; each areola is occluded with a complex vola attached to the sides with 5–10 rotae; the insert in (b) depicts a close–up of an areola; (e) valve showing the external openings of the mantle rimoportulae (white arrows); (f) a valve with separating spines and yielding a view of the ringleiste positioned near the top of the collum. Scale bars 4 µm (b, d), 5 µm (e–f) and 10 µm (a, c).

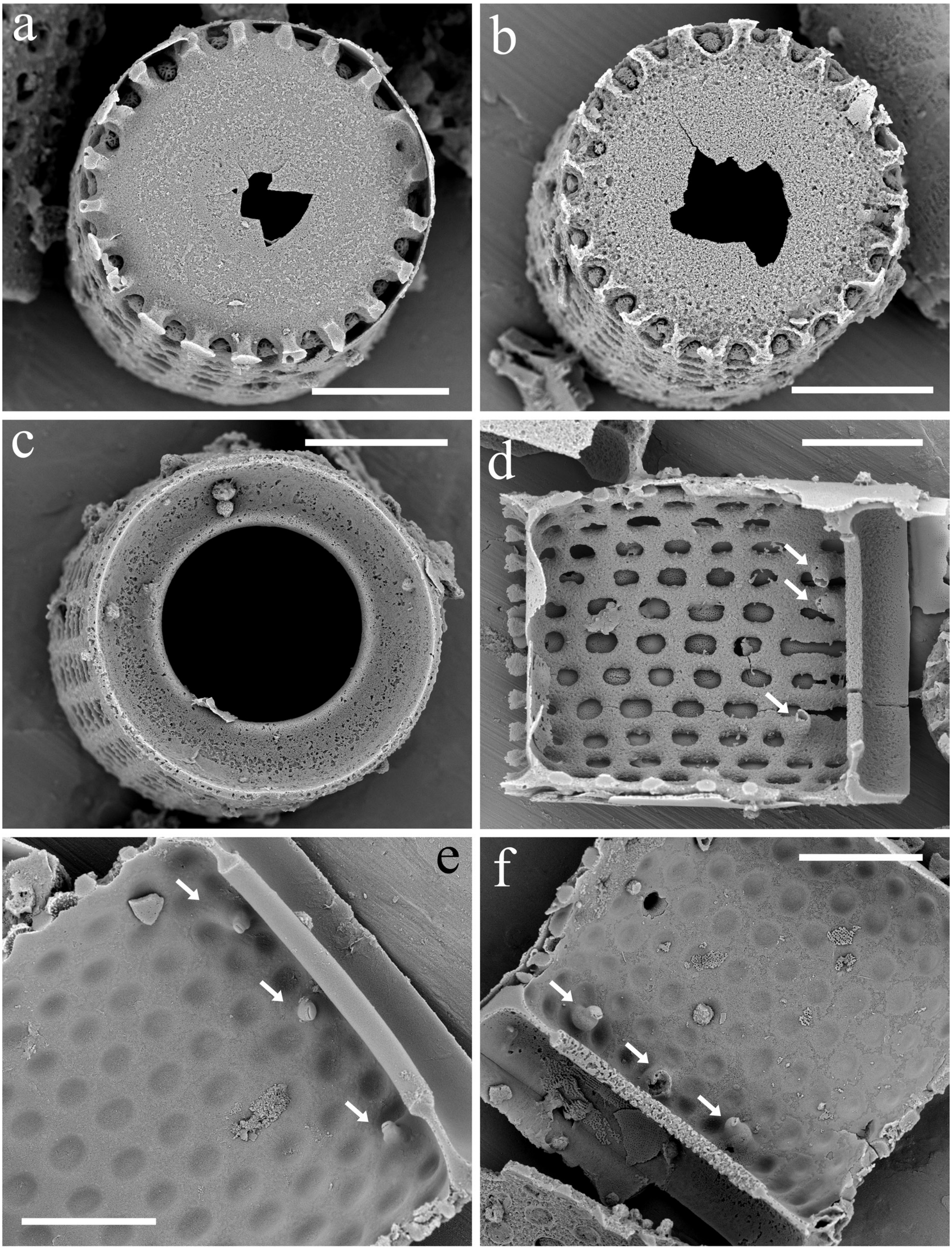

Fig 5. Scanning electron micrographs of *Aulacoseira ponderosa* from the Miocene Virgin Valley Formation: (a–b) valve face depicting the flat, smooth surface, and marginal ring of pores formed by the top row of areolae on the mantle; (c) inside view showing the relatively wide ringleiste; (d–f) internal views showing the multiple rimoportulae (white arrows) more or less in a ring on the valve mantle above the top of the ringleiste; note the curved nature of the rimoportula tube and the terminal pair of closely oppressed lips. Scale bars 4 µm (a, e) and 5 µm (b–d, f).

Virgin Creek section of the Virgin Valley, 41.7992° N, –119.0874° W.

Epithet: The species name refers to a combination of uses of "ponderosa," including the ponderosa pine, a region in Nevada, and reference made by Ken Lohman.

Distribution: *Aulacoseira ponderosa* was found in four samples (Table 3). This species formed massive and dominant numbers in the three collections made from the Upper Virgin Valley, all of which represented extensive deposits of white diatomite.

Comments: *Aulacoseira ponderosa* is closely related to *A. canadensis* (Hustedt) Simonsen, a species originally described by Hustedt (1952) as *Melosira canadensis* from a Miocene deposit in British Columbia, Canada. More recently, Bahls et al. (2009) reported specimens of *A. canadensis* from numerous sites in the western United States, mostly in Montana and Idaho, and concluded this species to be an extinct taxon widely distributed during the Miocene in the western United States. The valve shape, linear rows of large areolae, and types of spines are similar between the two species. Thus, based on this suite of similar characteristics, coupled with the fact that *A. ponderosa* was also found in a Miocene deposit from the western United States, it is tempting to conclude that *A. canadensis* and *A. ponderosa* are the same species. However, because the species differ in two important respects, the Virgin Valley specimens are described as a new species. First, according to Bahls et al. (2009), the majority of *A. canadensis* specimens have an areolated valve face (see fig. 3, Plate 577 in Simonsen 1987; fig. 6 in Bahls et al. 2009), and in fact it was originally described by Hustedt (1952) with an areolated valve face. Bahls et al. (2009) did report that some of the specimens they studied and reported as *A. canadensis* had several circular rows of areolae on the valve face perimeter (e.g. fig. 20 in Bahls et al. 2009), and Houk et al. (2017) stated that the areolae could be restricted to the perimeter, found across the entire valve face, or less commonly lacking altogether. Although the terminal–most areolae of the striae are visible between each pair of spines on the valve face of *A. ponderosa* valves, it is otherwise smooth and not areolated. Second, the shape and position of the rimoportulae differ significantly in the two taxa. *Aulacoseira canadensis* specimens have multiple rimoportulae associated with the ringleiste, where the tubes merge with, and extend out onto, the ringleist. Houk et al. (2017) show multiple images from the lectotype slide (figs 10, 13, 21 and 22 on Plate 232), and from the isolectotype slide (figs 18–19, 22 on Plate 233) illustrating the long rimoportula tubes on the ringleiste. *Aulacoseira ponderosa* valves also have a ring of rimoportulae positioned on the mantle wall close to the ringleiste. However, in this case the rimoportulae tubes are curved or twisted and integrated with the mantle wall, and do not form canals within the ringleiste. In addition, the rimoportulae of *A. ponderosa* specimens are stalked and terminate with a small slit, unlike those of *A. canadensis*. For these reasons, the Virgin Valley specimens are described as a new species. Further, given these findings, it is possible that some of the previous reports of *A. canadensis* could indeed represent *A. ponderosa*.

It is also worth noting the similarities between *A. canadensis* and two other organisms known from Miocene deposits, *Melosira temperei* Pant. and an undescribed organism reported by Houk & Klee (2007) as *Aulacoseira* sp. 5. Both of the latter taxa appear to be very similar to *A. canadensis*, especially with respect to overall valve shape, and possessing straight mantle striae composed of large areolae, similar linking and separating spines, and rimoportulae associated with a deep ringleiste. According to Houk & Klee (2007), who examined type material, the velum differs between *M. temperei* and *A. canadensis*, and the valve face of *M. temperei* valves is mostly smooth and not completely areolated as on *A. canadensis* specimens. Houk & Klee (2007) also commented on the similarity between *A. canadensis* and *A.* sp. 5, based on images they took of *A.* sp. 5 from slide 2202 "Virginia City Nevada Cleve No. 48" in the Grunow Collection in Vienna. However,

Table 3. Distribution of eight species of *Aulacoseira* in 14 strata from the Miocene Virgin Valley Formation, Nevada, USA, as described in Table 1. The stratum numbers correspond to those in Table 1. Estimates of the abundance of each species is based on a range of four categories: R = rare; C = common; A = abundant; D = dominant.

	Siver collection Number								**Lohman USGS Number**					
Taxon	**2**	**18**	**20**	**21**	**25**	**37**	**38**	**40**	**3525**	**3527**	**3530**	**3534**	**3536**	**3540**
A. ponderosa							D	D		R				A
A. lohmanii							R							A
A. royalpeacockii			A	C	A									
A. vanlandinghamii			C	C	A									
A. moralesii										R	C		C	
A. virginvalleyana			C	C	C							C		
A. italica	R		R	C	R	R			R	C	C		R	
A. laevissima	R	R	R	C	C	R			R		C	C	R	

because there was no material that could be examined with SEM, Houk & Klee (2007) could not conclude if indeed *A.* sp. 5 was the same species as *A. canadensis*. In summary, available evidence supports the idea that all of these taxa were closely related species during the Miocene.

***Aulacoseira vanlandinghamii* sp. nov. Siver (Figs 6–8)**

Description: Valves have a shallow mantle height ranging from 3.6–6.4 µm, and a diameter ranging from 11.6–17.2 µm, yielding a mean height to diameter ratio of 0.32 (Table 2; Figs 6e–h; 7a–d). Striae are straight, 15–20 per 10 µm, evenly–spaced, and consist of an average of seven small and circular–shaped areolae (Fig. 7a–d). Areolae are simple pores, with a mean diameter of 0.2 µm, and are not occluded on either the external or internal surface. The areolae at the ends of the striae at the top of the collum are larger, more elongated, and some of them contain the rimoportula openings (Fig. 7b–c). The mantle costae are lined with slightly raised and flat nodules that are circular to elongate in shape (Fig. 7c–d). The valve face is flat and covered with small, closely–spaced pores (Figs 6a, c, j, k; 8c–d) that are open to the interior of the valve (Fig. 8f). The collum is short, with a mean height of 1 µm, and lined with closely–spaced and parallel ribs (Figs 7b–c). Both linking and separating spines are present. Linking spines are short, with a mean length of 1.4 µm, flat, of similar length, triangular to spatula–shaped with a broader distal end, and positioned on approximately every other costa (Figs 7a–b). The base of a linking spine does not span more than one mantle costa. Separating spines are of two types. The most common type of separating spine is short, with a mean length of 1.1 µm, of equal diameter (Fig. 7c) or slightly broader at the base, with rounded and blunt distal ends, and positioned on every other costa. The outer surface of this type of separating spine is flush with the mantle, but the inner surface is expanded slightly onto the valve face. A second and rarer type of separating spine is short with a broadly rounded distal end and a base spanning two pervalvar costae (Fig. 7d). The ringleiste is wide, thick, and extends inward ¼ to ⅓ of the valve diameter, leaving an opening of only ½ to ⅓ of the valve diameter (Figs 6b, d, i, l; 7e–f; 8b, e–f). There are numerous rimoportulae aligned in a ring on top of the ringleiste (Figs arrows 6i, l; 8a–c). Each rimoportula consists of a simple straight tube with one end opening on top of the ringleiste close to the mantle wall, and the other end opening on the external surface within a terminal areola of a stria. A step is sometimes observed midway along the mantle on the epivalve of a complete frustule. Frustules can be linked into relatively long filaments (Fig. 7a). Remains of valvocopulae are commonly observed on specimens (e.g. Figs 7b–d; 8e–f).

Holotype: Circled specimen on prepared slide labeled "Virgin Valley 25, Siver 3" deposited at the Canadian Museum of Nature, CANA 131187. The holotype specimen is illustrated in Fig. 6k–l.

Isotype: Circled specimen on prepared slide labeled "Virgin Valley 25, Siver 1" deposited at the California Academy of Sciences, CAS (slide number 223051). The isotype specimen is illustrated in Fig. 6i–j.

Type material: Diatomite material taken from the Lower Virgin Valley outcrop at the Royal Peacock Opal mine and deposited at the Canadian Museum of Nature, CANA 131187. The material was collected by P.A. Siver, and represents sample #25 in his collection.

Type locality: Royal Peacock Property located in the Virgin Creek section of the Virgin Valley, 41.7939° N –119.0977° W.

Epithet: The species is named in honor of Sam L. Van Landingham, diatomist and friend.

Distribution: *Aulacoseira vanlandinghamii* was common to abundant in three white diatomite strata in the Lower Virgin Valley (Table 3). *Aulacoseira royalpeacockii* and *A. virginvalleyana* were also common or abundant co–occurring taxa in the three collections.

Comments: *Aulacoseira vanlandinghamii* is closely related to *Aulacoseira scalaris* (Grunow in Van Heurck) Houk, Klee et Passauer, and to a lesser extent to *Aulacoseira iwakiensis* H. Tanaka (Houk et al. 2017). Like *A. vanlandinghamii*, *A. scalaris* and *A. iwakiensis* have valves of similar size, with a similar mantle height to valve diameter, straight striae, a wide ringleiste, an areolated valve face, and a ring of rimoportula with tubes that lie on and open onto the top of the ringleiste, often terminating near the inner ringleiste margin. In addition, *A. scalaris* is a fossil taxon originally described from Oregon (USA) and reported from other localities in the western USA, and *A. iwakiensi* was found in a Miocene deposit in Japan. The main differences between *A. vanlandinghamii* and *A. scalaris* lie in the morphology of the spines and rimoportulae. The spatula–shaped linking spines, and the rectangular–shaped separating spines found on *A. vanlandinghamii* specimens are not reported for *A. scalaris*, and spines of the latter taxon are mostly with pointed apices. The broader type of separating spine found on *A. vanlandinghamii* specimens is also not reported for *A. scalaris*. In fact, *A. vanlandinghamii* is believed to be the only *Aulacoseira* species known with multiple types of separating spines. The rimoportulae openings on *A. vanlandinghamii* specimens never reach the middle of, or farther out onto, the ringleiste as they do on *A. scalaris* specimens. The areolation pattern of the valve face, spine morphology, and the structure of the rimoportulae all differ on *A. iwakiensis* compared with *A. vanlandinghamii*. The rimoportula on *A. vanlandinghamii* specimens consists of the circular opening of the end of the tube on the ringleiste, but with a labia on *A. iwakiensis* specimens. Despite these differences, all three species appear to have been closely aligned.

Although the structure and arrangement of rimoportula found on *Aulacoseira vanlandinghamii*, *A. scalaris* and *A. iwakiensis* are not known on all but one modern *Aulacoseira* taxa, it was a more common feature of fossil species, especially ones in Miocene deposits. Coupled with this character is the presence of a wide ringleiste, often extending deep into the cell. This pair of features is also found on *A. solida* (Eulenst. in Van Heurck) Krammer, *A. californica* v. *haitensis* (Grunow in Van Heurck) Houk, Klee et H. Tanaka (synonym *A. solida* var. *haitensis* (Grunow in Van Heurck) Houk, Klee et Passauer), *A. procera* (Ehrenberg) Houk et Klee, *A. spiralis* (Ehrenberg) Houk et Lee, *A. krammeri* Edgar, Kociolek et Edgar, *A. temperei* (Pantocsek) Ognjanova–Rumenova et Crawford, and an undescribed species, *A*. sp. 5, reported by Houk & Klee (2007). Like *A. vanlandinghamii*, *A. scalaris* and *A. iwakiensis*, *A. solida*, *A. spiralis*, *A. krammeri* and *A*. sp. 5 were also described from fossil localities in the western USA, including Nevada, Oregon and California, and primarily from Miocene–aged deposits (Bradbury 1991; Edgar et al. 2004; Houk & Klee 2007). *Aulacoseira californica* v. *haitensis*, *A. procera* and *M. temperei* were originally described in fossil deposits from Haiti, Ireland and Hungary, respectively. One additional species, *Aulacoseira houkii* Tanaka was reported from an early Miocene deposit in Japan (Tanaka & Nagumo 2022), has a few rimoportula that open on the mantle near the ringleiste. However, this species differs from the other fossil taxa in also possessing rimoportulae on the valve face. Although the length, terminal structure and position of the rimoportula tubes, and whether they are straight or curved, differ between all of these taxa, they are similar in the fact that the rimoportulae are directly associated with a wide ringleiste. As we learn more about fossil taxa, it may be appropriate to assign different names to rimoportulae that open internally as circular tubes, as opposed to the more common morphology consisting

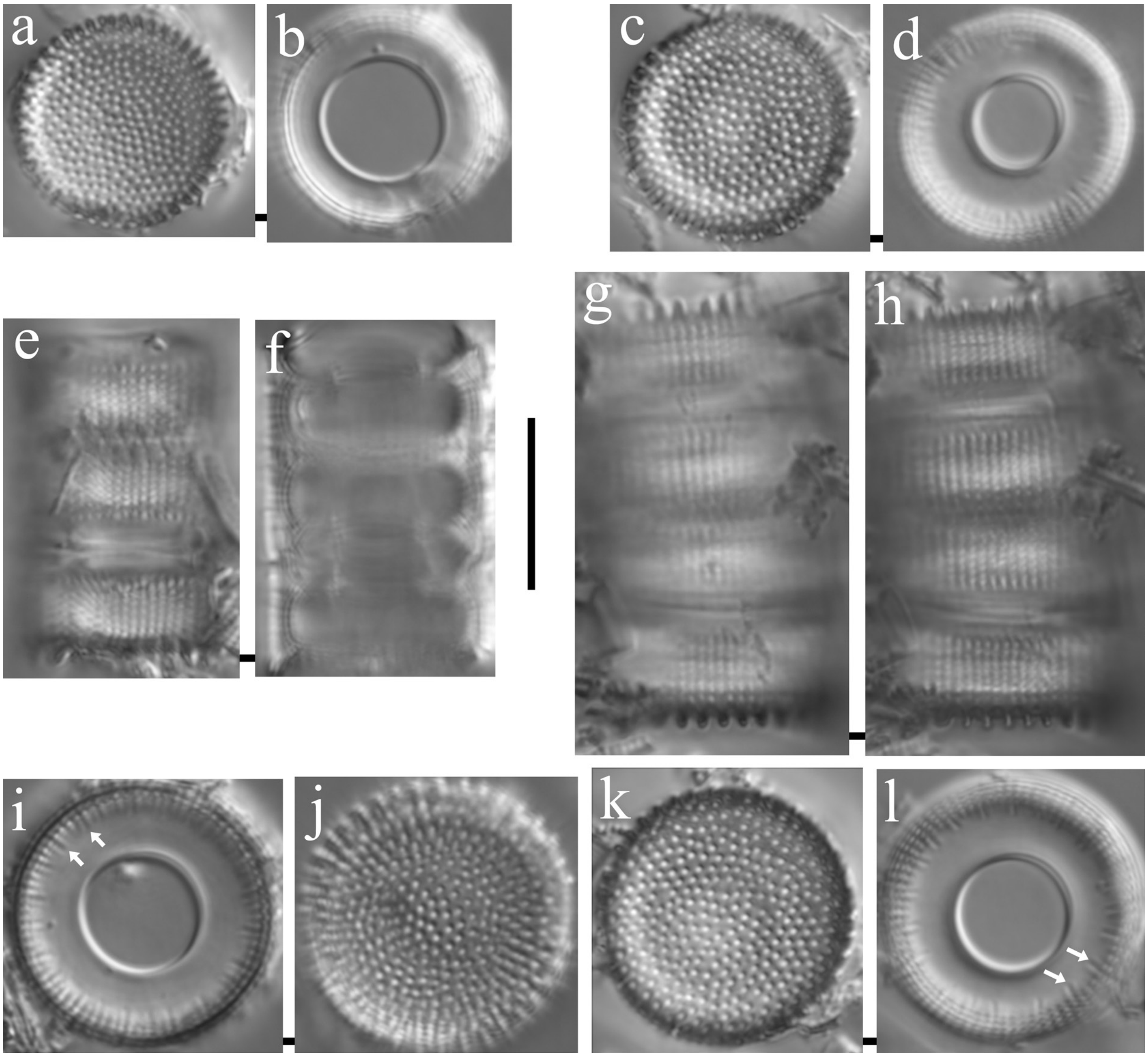

Fig. 6. Light micrographs of six specimens of *Aulacoseira vanlandinghamii* from the Miocene Virgin Valley Formation, each illustrated at different focal planes focused on the valve face and ringleiste: images connected with a horizontal black bar represent the same specimen; note the areolated valve face (a, c, j, k), the wide ringleiste protruding deep into the cell (b, d, i, l), the straight mantle striae consisting of small areolae, and the rimoportula tubes situated on top of the ringleiste (white arrows on i and l); a short filament is depicted in (e–h); the type and isotype specimens are illustrated in (k–l) and (i–j), respectively. Scale bar 10 µm.

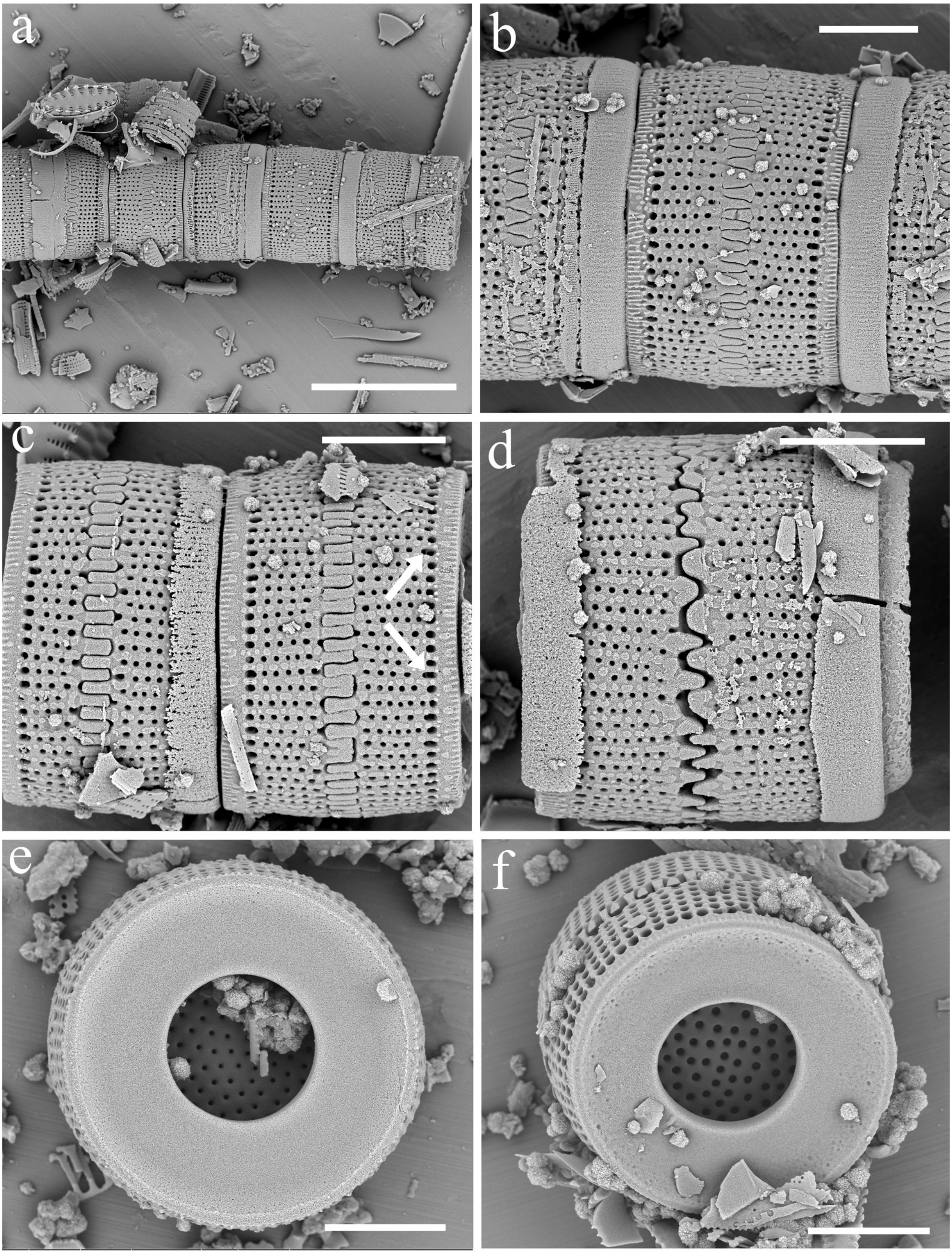

Fig. 7. Scanning electron micrographs of *Aulacoseira vanlandinghamii* from the Miocene Virgin Valley Formation: (a) filament showing details of the mantle striae, linking spines, and low height to diameter ratio of valves; (b) close–up of the specimen in (a) depicting the triangular to spatula–shaped linking spines, straight striae and the pervalvar costae with slightly raised and flat nodules; (c–d) specimens depicting rectangular–shaped (c) and rounded (d) separating spines; note the external openings to the rimoportula within terminal areolae of some striae (arrows); (e–f) specimens showing the large ringleiste extending close to ⅔ of the valve diameter; note the inside view of the areolated valve face. Scale bars 5 µm (b–f) and 20 µm (a).

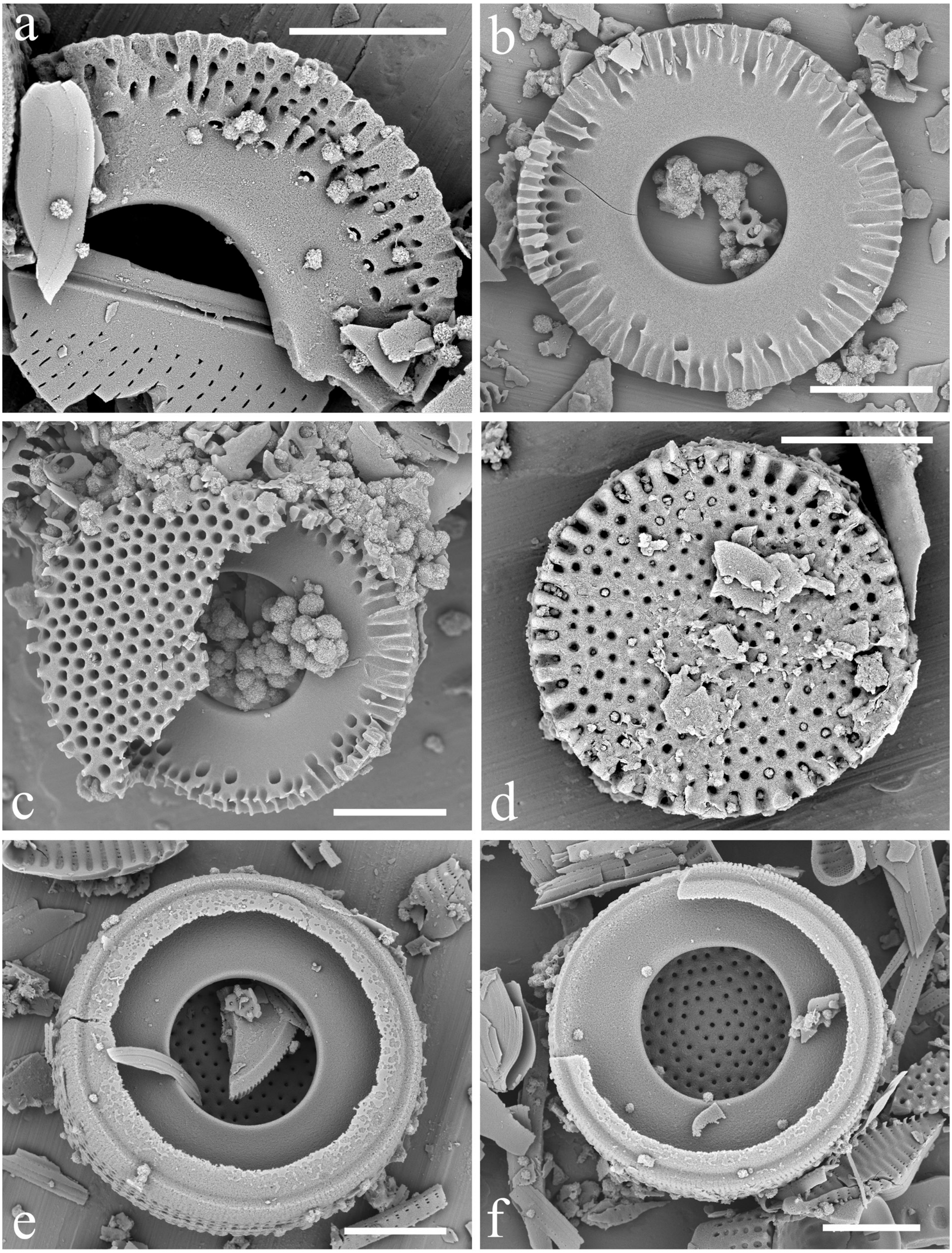

Fig. 8. Scanning electron micrographs of *Aulacoseira vanlandinghamii* from the Miocene Virgin Valley Formation: (a–c) inside views of the upper surface of the ringleiste showing details of the ring of rimoportula; note that each rimoportula consists of a simple straight tube extending a short distance on, and opening on top of the ringleiste; part of the areolated valve face is depicted on (c); (d) areolated valve face; (e–f) inside views of specimens showing the deep ringleiste and details of the valvocopula. Scale bars 4 µm (a) and 5 µm (b–f).

of a flattened tube with two oppressed lips.

Aulacoseira nipponica (Skvortzov) Tuji, originally described as a variety of *A. solida* (*Melosira solida* var. *nipponica* Skvortzov) from Lake Biwa, Japan, is an exception in being a contemporary species with rimoportula associated with the ringleiste (Tuji 2002). Tuji (2002) reported that the rimoportula on *A. nipponica* valves differed from those of *A. solida* in being straight and not strongly curved. As a result of this and several other differences, Tuji (2002) raised the former taxon to the species rank. What is more interesting is that *A. nipponica* is an extant species believed to be endemic to Lake Biwa (Tuji & Houki 2001; Tuji 2002). Perhaps, *A. nipponica* is better described as a paleo–relic, or paleoendemic (Siver et al. 2019).

***Aulacoseira royalpeacockii* sp. nov. Siver (Figs 9–11)**
Description: Valves small, square to rectangular–shaped, with a mantle height ranging from 2.9–5.2 µm, a diameter ranging from 4.9–7.6 µm, and a mean mantle height to valve diameter of 0.69 (Table 2; Figs 9a–l; 10a–e). Striae straight and composed of large circular–shaped areola. Most specimens had striae with three to five areolae, but up to seven were observed. Areolae are variably spaced, and sometimes not aligned in horizontal rows between the striae. Areolae are occluded with a complex volae consisting of a series of ribs or rotae attached to the sides of the foramina and recessed slightly from the external surface (Fig. 10b, f). The internal surface is covered with a thin layer of silica (Fig. 11c). Pervalvar costae are smooth and unornamented. The valve face is flat, smooth, and largely unornamented except for a marginal ring of large pores (Fig. 11d–f). Each pore is situated between two spines and is aligned with a mantle stria (Fig. 11d). Smaller pores of uneven diameters and randomly–spaced can be found on an otherwise smooth valve face (Figs 9d; 11f). The column is wide, approximately 35% of the mantle height, smooth, and flush with the mantle costae (Fig. 10c, e). Spines are of even lengths, wider at the base, tapered, and with variable–shaped apical ends that range from bluntly rounded to slightly anchor–shaped (Fig. 10a–e). A spine terminates each pervalvar rib. The ringleiste is bell–shaped in cross section, broad, and shallow, extending only a short distance into the cell (Figs 9m; 11a–c). Rimoportulae were not observed. Filaments of three to five frustules were commonly observed.

Holotype: Circled specimen on prepared slide labeled “V V 25 C, D” deposited at the Canadian Museum of Nature, CANA 131186. The holotype specimen is illustrated in Fig. 9i–j.
Isotype: Circled specimen on prepared slide labeled “Virgin Valley 25, Slide A” deposited at the California Academy of Sciences, CAS (slide number 223050). The isotype specimen is illustrated in Fig. 9a–c.

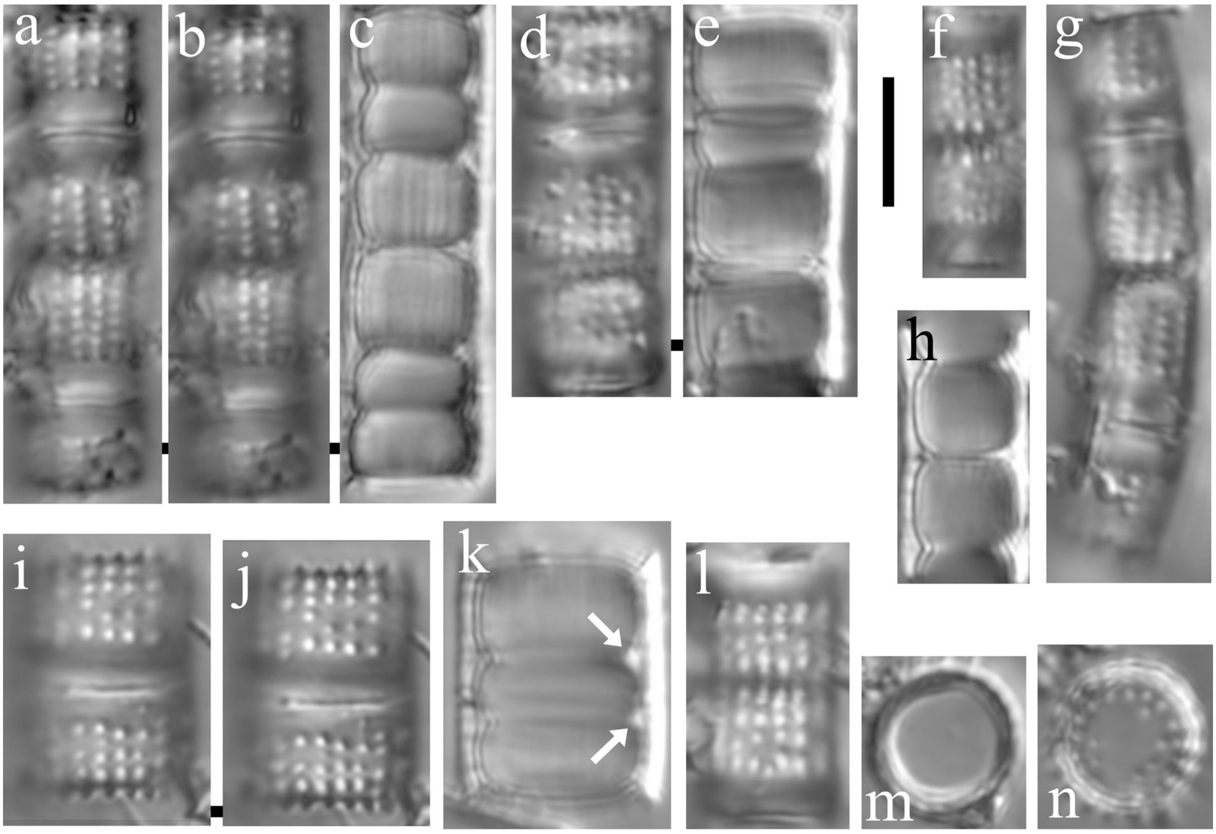

Fig. 9. Light micrographs of *Aulacoseira royalpeacockii* from the Miocene Virgin Valley Formation: images linked with a horizontal black bar (a–c, d–e and i–j) represent the same specimens taken at different focal planes; note the short and straight mantle striae composed of large and circular–shaped areolae and the shallow and bell–shaped ringleiste (c, e and k; white arrows), and the short filament consisting of two frustules (g); valve view of the valve face and ringleiste are depicted in (n, m), respectively; the type and isotype specimens are illustrated in (i–j) and (a–c), respectively. Scale bar 10 µm.

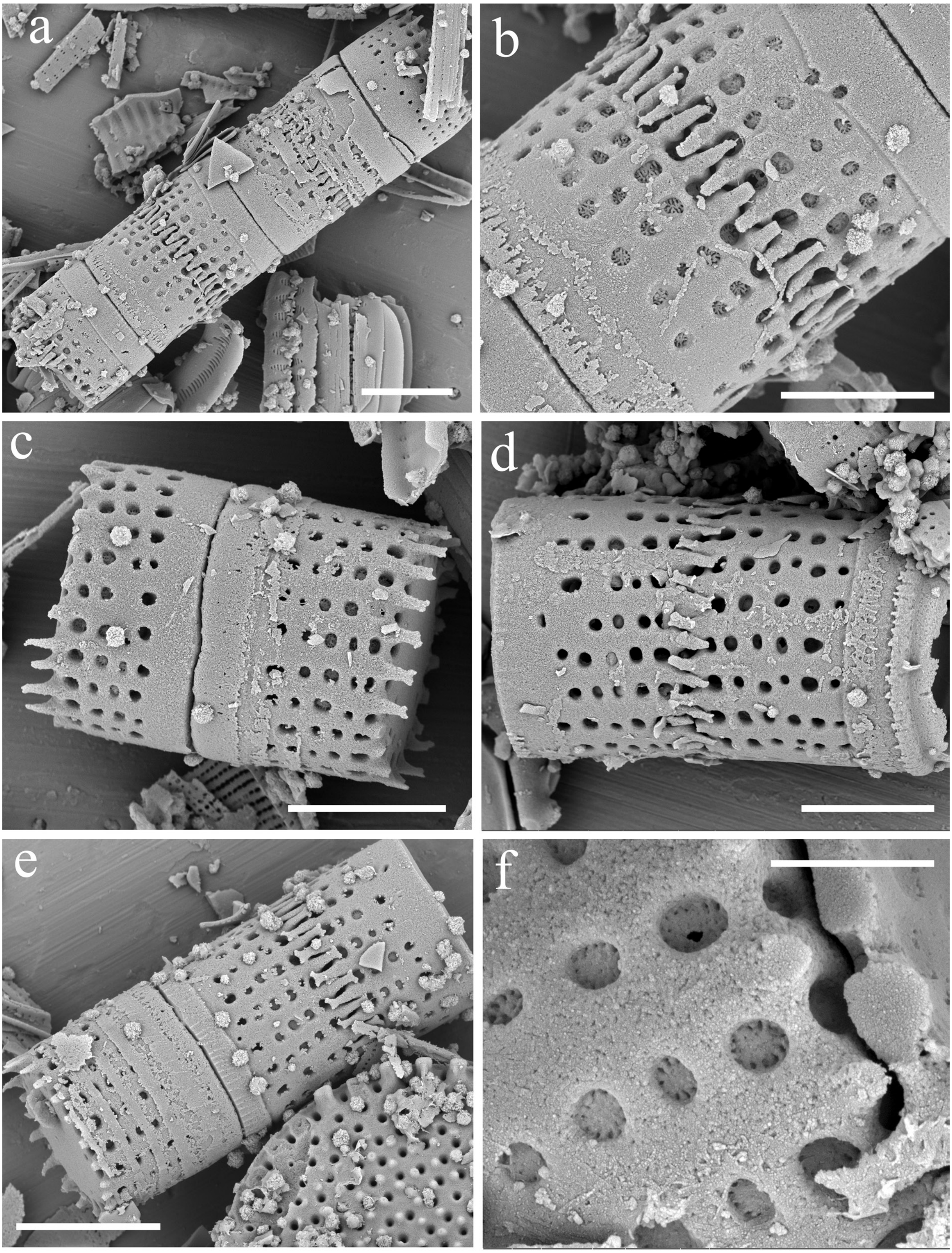

Fig. 10. Scanning electron micrographs of *Aulacoseira royalpeacockii* from the Miocene Virgin Valley Formation: (a) short filament showing details of the spines, straight mantle striae, large areolae and column; (b) close–up of the specimen in (a); note the complex volae occluding each areola, and the smooth and unornamented pervalvar costae, each bearing a spine; (c–e) specimens with different valve lengths; note the remains of girdle bands on some valves and the slender anchor–shaped spines on the specimen in (e); (f) close–up depicting the details of the recessed volae. Scale bars 1 µm (f), 3 µm (b, d), 4 µm (c) and 5 µm (a, e).

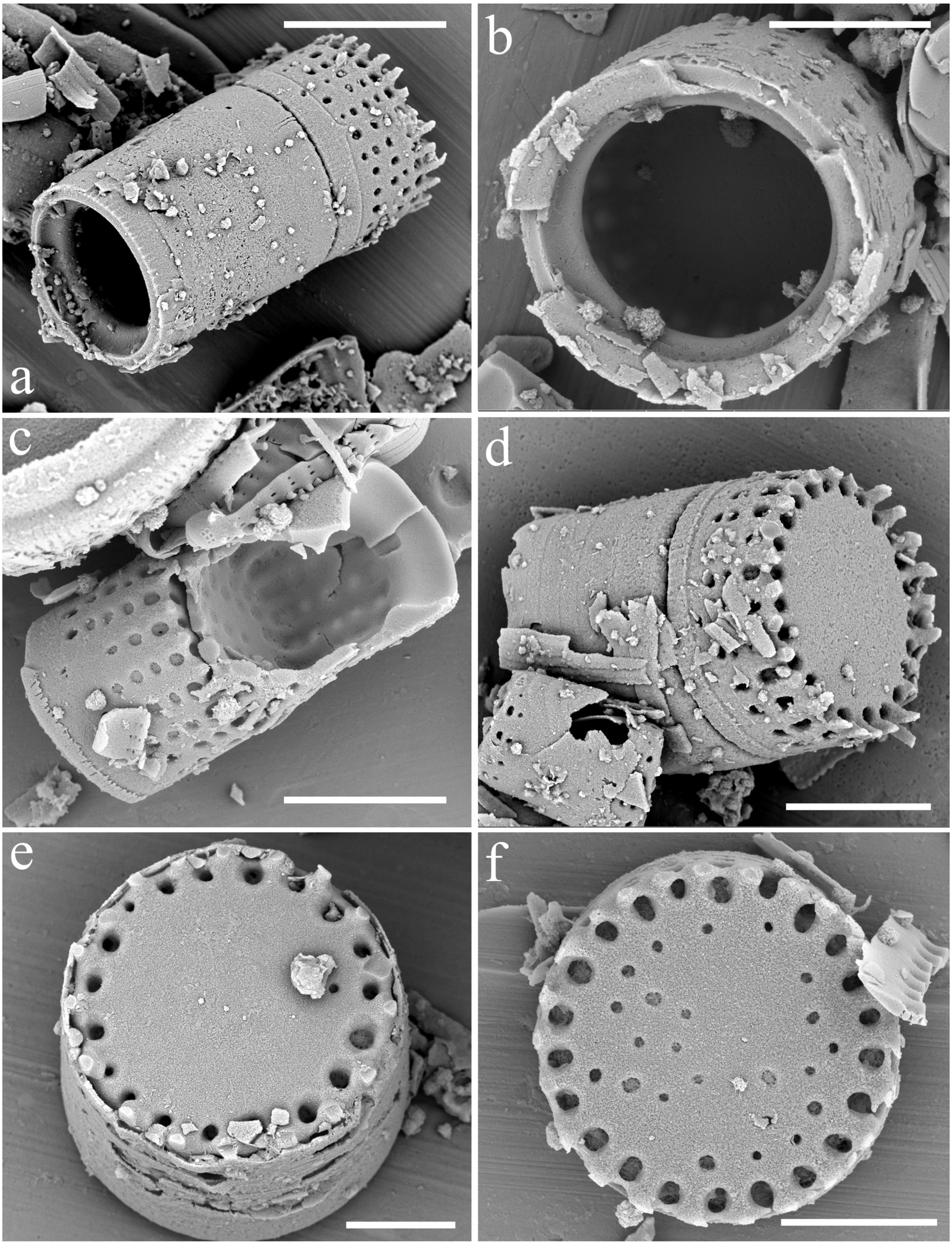

Fig. 11. Scanning electron micrographs of *Aulacoseira royalpeacockii* from the Miocene Virgin Valley Formation: (a–c) internal views depicting details of the broad and relatively shallow ringleiste; note the broad and bell–shaped cross–sectional design in (c); (d–f) views of the smooth and flat valve face and depicting the marginal ring of large pores; a few randomly spaced pores can be seen on the specimen in (f). Scale bars 2 µm (e), 3 µm (b, f) and 4 µm (a, c–d).

Type material: Diatomite material taken from the Lower Virgin Valley outcrop at the Royal Peacock Opal mine and deposited at the Canadian Museum of Nature, CANA 131186. The material was collected by P.A. Siver, and represents sample #25 in his collection.
Type locality: Royal Peacock Property located in the Virgin Creek section of the Virgin Valley, 41.7939° N –119.0977° W.
Epithet: The species is named after the Royal Peacock Opal Mine, the type locality.
Distribution: *Aulacoseira royalpeacockii* was common to abundant in three white diatomite strata in the Lower Virgin Valley (Table 3). *Aulacoseira virginvalleyana* and *A. vanlandinghamii* were also common or abundant co–occurring taxa in the three collections.

Comments: *Aulacoseira royalpeacockii* is similar to *Aulacoseira tethera* Haworth, *A. minuscula* Tremarin, Torgan et Ludwig, and *A. pardata* English et Potapova. *Aulacoseira tethera* was described from multiple acidic and poorly buffered tarns in Cumbria, UK (Haworth 1988), and further discussed by Krammer (1991a). Valves of both *A. royalpeacockii* and *A. tethera* have a mantle height to valve diameter < 1, possess striae with large areolae, a shallow ringleiste, a marginal ring of large areolae on the valve face, and a spine on each pervalvar rib. However, the size of *A. royalpeacockii* valves differs in having a longer mantle height, a significantly smaller valve diameter (Fig. 12), and a lower striae density. In addition, the mantle striae on *A. royalpeacockii* valves are never diagonally positioned, and the collum is wider, comprising a larger percentage of the mantle height relative to *A. tethera* valves.

Aulacoseira minuscula was originally reported from several shallow and eutrophic waterbodies in Brazil (Tremarin et al. 2014), and *A. pardata* from a wetland in Montana, USA (English & Potapova 2009). Valves of both *Aulacoseira royalpeacockii* and *A. minuscula* are small with striae composed of large and circular–shaped areolae, a similar bell–shaped ringleiste, and a wide collum. In addition, both species have similar areolae coverings that are recessed within the foramin. However, they differ in several important ways. First, the valve face on *A. minuscula* valves is covered with areolae, and lacks the marginal ring of large areolae found on *A. royalpeacockii* valves. Second, the spines on *A. minuscula* valves differ in shape and are positioned on every second or third costae, whereas on *A. royalpeacockii* valves spines are found on every costa. Lastly, although both taxa are small, those of *A. royalpeacockii* are wider and with a longer mantle height (Fig. 12).

With respect to overall valve appearance, specimens of *Aulacoseira royalpeacockii* appear most similar to those of *A. pardata*. Both species have valves with straight striae consisting of large and circular areolae, spines on the ends of each pervalvar costae, a shallow and bell–shaped ringleiste, a wide and smooth collum, and a peripheral ring of areolae on the valve face. Although the fine structure of the areolae occlusions was not described by English & Potapova (2009), they do appear to be recessed within the foramin. However, valves of these two species differ in several important characteristics. First, in addition to the marginal ring of large areolae found on the valve face, valves of *A. royalpeacockii* can have additional smaller and randomly scattered pores. Second, *A. pardata* possesses two types of spines, including ones with pointed apices and distinctly serrated margins that are not found on *A. royalpeacockii* valves. Lastly, although there is overlap with respect to valve size, those of *A. pardata* are larger than those of *A. royalpeacockii* (Fig. 12).

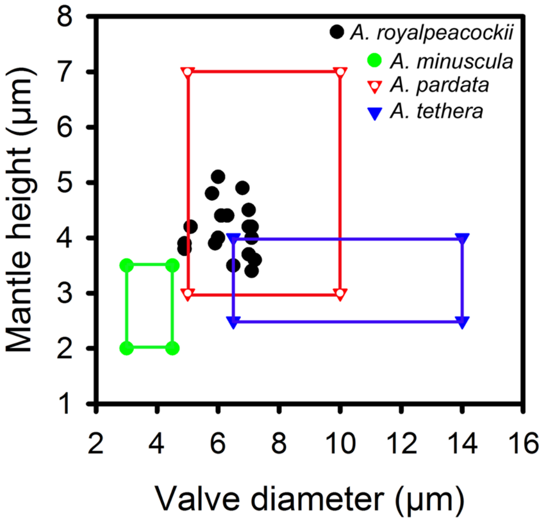

Fig. 12. Mantle height versus valve diameter for *Aulacoseira royalpeacockii* specimens (isolated circles), and ranges for *A. minuscula*, *A. pardata*, and *A. tethera* based on the original descriptions (rectangular boxes).

***Aulacoseira lohmanii* sp. nov. Siver (Figs 13–15)**
Description: Valves large, robust, with a mantle height ranging from 9.4–24.8 µm, and a diameter from 3.9–17 µm, yielding a wide range in height to diameter ratio of 0.64 to < 6 (Table 2; Figs 13–14). Striae straight, 7–8 per 10 µm, evenly–spaced, and consisting of large square to rectangular–shaped areolae that are mostly aligned between neighboring striae forming both horizontal and vertical rows (Figs 13a–i; 14). Areolae are occluded with complex volae that are slightly recessed from the external surface, and connected to the sides of the areolae with a series of mostly radially aligned rotae (Fig. 14b, d). Internally, each areola is covered with a thin hymen that is flush with the inner valve surface (Fig. 15d). The pervalvar costae and ribs connecting adjacent costae are thick and form square–shaped frames around each areola (Fig. 14b, d). The large areola terminating each stria at the top of the mantle are readily observed from the valve face (Fig. 15e, f). There is a series of small areolae near the margin of the valve face often forming a ring (Fig. 15e, f). Otherwise, the valve face is smooth. Both linking and separating spines are

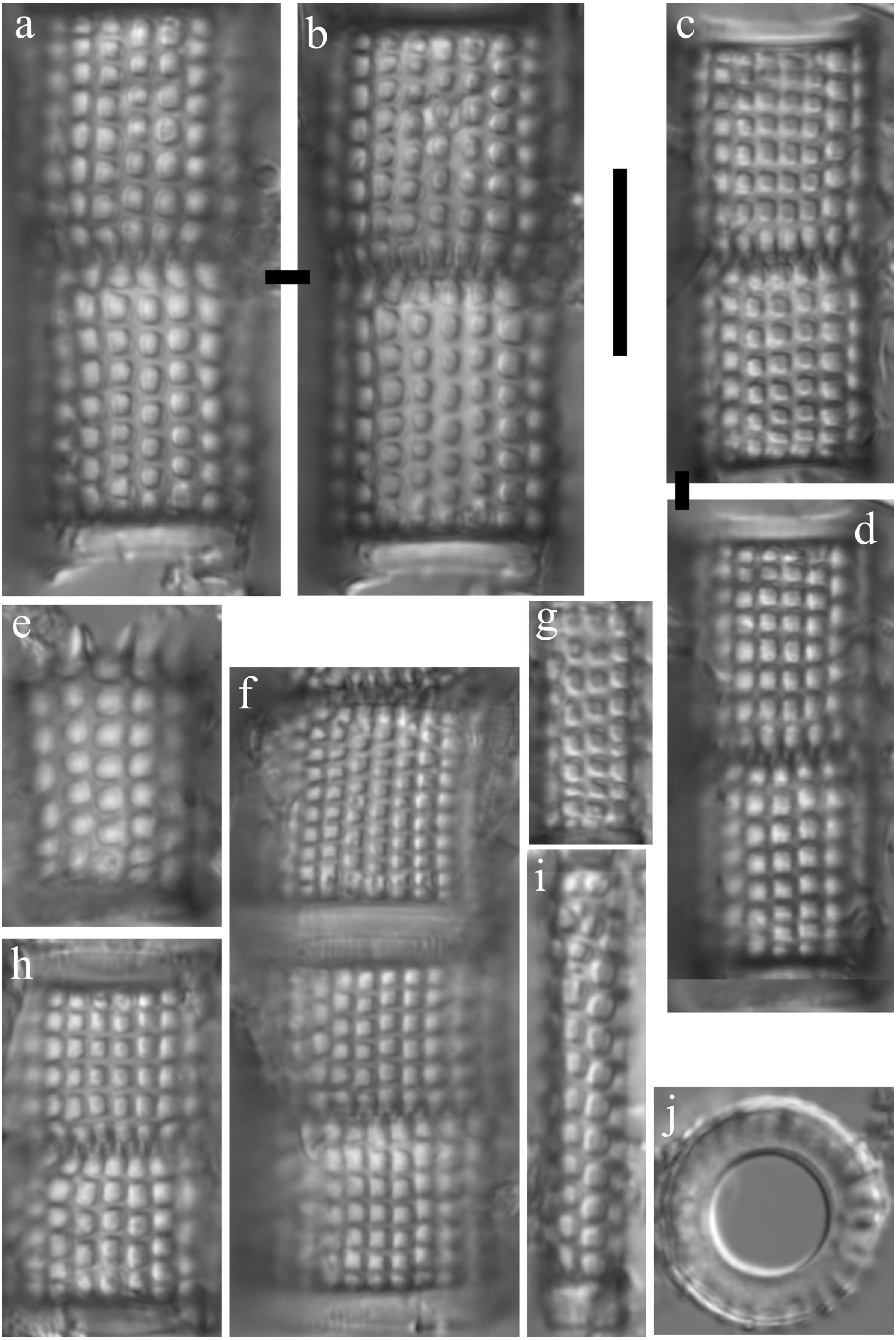

Fig. 13. Light micrographs of *Aulacoseira lohmanii* from the Miocene Virgin Valley Formation, including specimens with valves ranging in height to diameter ratio from close to one (e.g. f) to five (e.g. i); note the straight mantle striae consisting of large and distinctively square areolae, ringleiste (j), and separating spines on (d); the type and isotype specimens are illustrated in (a–b) and (c–d), respectively. The specimen in (f) depicts three valves. Scale bar 10 µm.

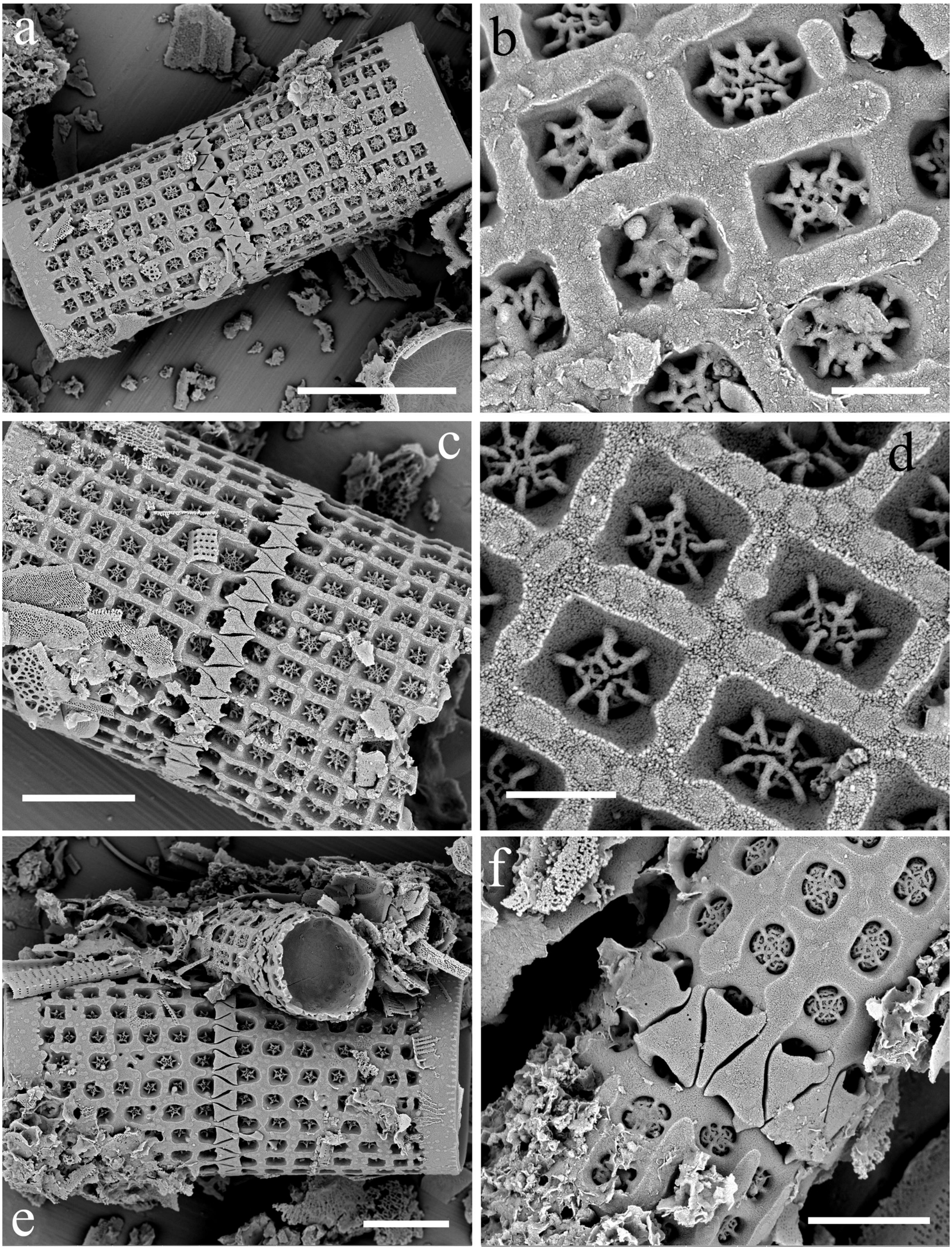

Fig. 14. Scanning electron micrographs of *Aulacoseira lohmanii* from the Miocene Virgin Valley Formation: (a, c) two valves adjoined with linking spines; note the straight striae composed of large and distinctively square areolae, thick pervalvar costae and connecting ribs, triangular–shaped linking spines and well–defined collum; (b, d) close–ups of the specimens in (a) and (c), respectively, showing details of the areolae, each of which is occluded with a recessed circular vola with a set of radiating rotae attached to the areola walls; (e) two specimens illustrating the range in valve diameter; note the triangular–shaped linking spines on the wider specimen; (f) close–up of the linking spines on a narrow specimen. Scale bars 1 µm (b, d), 2 µm (f), 5 µm (c, e) and 10 µm (a).

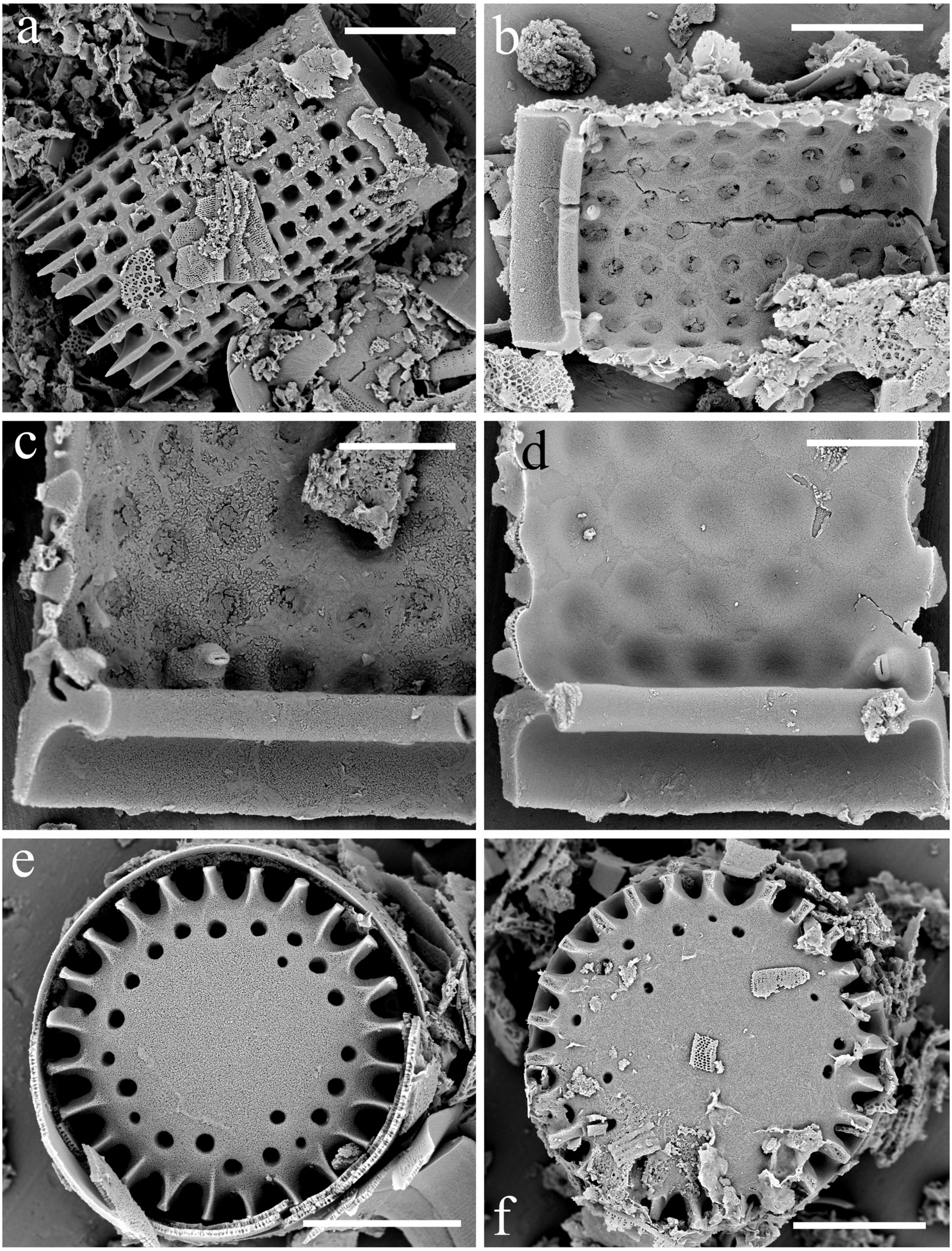

Fig. 15. Scanning electron micrographs of *Aulacoseira lohmanii* from the Miocene Virgin Valley Formation: (a) valve with separating spines; (b–d) inside views depicting the ringleist with a thickened margin with a circular cross–sectional design, and details of the rimoportulae located just about the ringleiste and attached to the mantle walls; the rimoportulae are stalked, sometimes slightly twisted, and terminate as a small slit bordered by a simple pair of lips; (e–f) views of the valve face; note the smooth surface, randomly–spaced marginal pores, and the large openings to the terminal mantle areolae; the large areolae terminating each stria at the top of the mantle are readily observed from the valve face; there is a series of small areolae near the margin of the valve face often forming a ring (e); otherwise, the valve face is smooth. Scale bars 2 µm (c–d) and 5 µm (a–b, e–f).

present. Linking spines are short, of even length, triangular to spatula–shaped with a straight or U–shaped apical end, and collectively form a tight zipper–like arrangement (Fig. 14a, c, e–f). Separating spines are narrow with straight sides and sharply pointed apices (Fig. 15a). As a result of the large spaces formed by the areolae at the juncture of the mantle and valve face, the separating spines appear as spokes radiating from the valve face when viewed in valve view (Fig. 15e, f). In both cases, spines are found on each pervalvar costa. The ringleiste is wide, extends inward approximately 1–2 µm, and with a thickened and rounded marginal rim (Figs 13j; 15b–d). There are multiple rimoportulae widely positioned in a ring on the mantle wall slightly above the ringleiste, and mostly spaced every 3–4 µm (Fig. 15b–d). The rimoportulae are slightly twisted or curved, stalked, and terminate internally with a small slit bordered by a simple pair of lips. The collum is well defined with a mean length of 1.9 µm, mostly smooth and with a row of short and closely–spaced ribs along the base (Fig. 14a, e).

Holotype: Circled specimen on prepared slide labeled "CAS 3540, Siver 1" deposited at the Canadian Museum of Nature, CANA 131185. The holotype specimen is illustrated in Fig. 13a–b.
Isotype: Circled specimen on prepared slide labeled "CAS 3540, Siver 3" deposited at the California Academy of Sciences, CAS (slide number 223049). The isotype specimen is illustrated in Figs 13c–d.
Type material: Diatomite material archived at the Canadian Museum of Nature, CANA 131185. The diatomite material used to describe this species was originally collected by Kenneth Lohman (his sample USGS 3540) and archived at the California Academy of Sciences (CAS accession number 601516). The sample used in the current study, and archived at the Canadian Museum of Nature, was a subsample of the original Lohman material.
Type locality: Upper Virgin Valley outcrop along the Virgin Creek section of the Virgin Valley.
Epithet: The species is named in honor of Kenneth Lohman for his work on fossil diatoms in the western United States.
Distribution: *Aulacoseira lohmanii* was uncovered in two samples from the Upper Virgin Valley, both consisting of white diatomite (Table 3). It was most abundant in material originally collected by Lohman (USGS 3540), along with *A. ponderosa*. However, it was not found in other collections dominated by *A. ponderosa*.

Comments: *Aulacoseira lohmanii* is closely related to *A. canadensis*, and more so to *A. ponderosa*. The primary difference between *A. lohmanii* and *A. ponderosa* is the distinctive square shape of the areolae coupled with the thick pervalvar costae on valves of the former species. In addition, the shapes of spines differ slightly in these two taxa. However, similarities in the structure and position of the rimoportula, the valve face, and the areolae occlusions indicate a close connection between *Aulacoseira lohmanii* and *A. ponderosa*. In addition to the distinctive differences in areola shape, valves of *A. canadensis* possess an areolated valve face and rimoportula associated with the ringleiste instead of being positioned on the mantle wall easily distinguishing if from *A. lohmanii*.

Based on the similarities of *A. ponderosa* and *A. lohmanii* with *A. canadensis*, especially with respect to the large areolae common among the three species as observed with light microscopy, it is possible that some of the previous reports of *A. canadensis* (see Bahls et al. 2009) may represent one or more of these three species. This would require a reexamination of the material from each site, especially with respect to the distribution and structure of the rimoportulae and features of the valve face and areolae, to be sure. Although Lohman apparently was not aware of Hustedt's 1952 paper describing *A. canadensis* at the time he wrote his thesis, he clearly concluded that the suite of specimens he examined from a wide range of samples from Virgin Valley represented multiple taxa.

In addition to *M. ponderosa*, Lohman (1957) proposed two organisms as varieties of the type, *M. ponderosa* v. *curta* and *M. ponderosa* v. *elongata*. He further postulated that this suite of organisms evolved from *M. granulata*, primarily based on the large areolae. Lohman (1957) distinguished *M. ponderosa* v. *curta* from the type by having a smaller height to diameter ratio and square to rectangular puncta. Interestingly, Lohman (1957) also described what he referred to as an "optical dot" in the center of each areolae on *M. ponderosa* v. *curta* specimens. Although he was unaware of the intricate structure of the areolae, his "optical dot" was most likely the result of the complex volae being suspended by the radiating rotae in the center of the areola. Although I did not observe *A. lohmanii* (or *M. ponderosa* v. *curta*) in collections I made, it was abundant in Lohman's USGS 3540 from the Upper Virgin Valley which is the type material I am using to officially describe this species. On the other hand, the samples I examined from different outcrops of the Upper Virgin Valley that were dominated with *A. ponderosa*, lacked *A. lohmanii*. Because the thickness of the formation comprising the Upper Virgin Valley extends close to 100 m, it is reasonable to conclude that the samples Lohman and I retrieved were from different strata. Perhaps a study with close–interval sampling over the entire sequence would yield additional information on the distribution and possibly the evolutionary sequence of these closely related species similar to the study by Theriot et al. (2006). Unfortunately, I did not know of Lohman's thesis work before I made the collection trip.

Although a very different taxon in many aspects, the square–shaped areolae found on *A. lohmanii* share a resemblance to those found on *Aulacoseira polispina* H. Tanaka.

***Aulacoseira virginvalleyana* sp. nov. Siver (Figs 16–17)**

Description: Valves have a shallow mantle ranging in height from 2.3 to 5.8 µm, a diameter ranging from 8.8 to 16.5 µm, yielding a mean height to diameter ratio of 0.29 (Table 2; Figs 16; 17a–e). On most valves there are two circumferential rows of areolae on the mantle, one at the base of the mantle next to the collum, and one at the top near the valve face (Figs 16c–d, g–h; 17a–d). The areolae on the top row are situated between the spines. Additional random areolae may be found between the two circumferential rows on the mantle, and on some specimens the bottom row may be lacking. There are 11–14 areolae per 10 µm. The areolae are circular to irregularly–shaped, open and lack a covering externally, but are covered with a hymen that is flush with the inner mantle wall (Fig. 17f). The remainder of the external mantle surface is smooth and pervalvar costae are not evident. Internally, there are slightly thickened ribs situated between the areolae on the mantle that extend a short distance onto the valve face (Fig. 17f). There are scattered areolae on the valve face, mostly in the peripheral region (Fig. 17e). The valve face areolae are not aligned with the mantle areolae. The collum is short and lined with closely–spaced ribs that are parallel with the pervalvar axis (Fig. 17b, d). Both linking and separating spines are present, and are of similar lengths with means of 1.7 µm and 1.6 µm, respectfully. Linking spines have a flat outer surface flush with the mantle, increase in width from the base to the proximal end, and with highly variable–shaped apices often curving into small spaces and covering an areola on the complementary valve (Fig. 17a–c). Separating spines are wider at the base, tapered, with either pointed or with a slight dichotomous tip (Fig. 17d). A spine is found between each pair of areolae aligning the top of the mantle. The ringleiste is very shallow to lacking and difficult to discern on most specimens (Fig. 17f). There are multiple simple rimoportulae, with three or more per valve, found at the junction of the valve face and mantle (Fig. 17f). Each rimoportula ends in a reinforced circular pore (white arrows on Fig. 17f), and are connected to a wide rib that runs the length of the mantle (black arrows on Fig. 17f). It is not clear if the rib is solid or hollow and tube–like.

Holotype: Circled specimen on prepared slide labeled "Virgin Valley 25, Slide B" deposited at the Canadian Museum of Nature, CANA 131189. The holotype specimen is illustrated in Fig. 16g–h.

Isotype: Circled specimen on prepared slide labeled "V.V. 25 C, C" deposited at the California Academy of Sciences, CAS (slide number 223053). The isotype specimen is illustrated in Fig. 16c–e.

Type material: Diatomite material taken from the Lower Virgin Valley outcrop at the Royal Peacock Opal mine and deposited at the Canadian Museum of Nature, CANA 131189. The material was collected by P.A. Siver, and represents sample #25 in his collection.

Type locality: Royal Peacock Property located in the

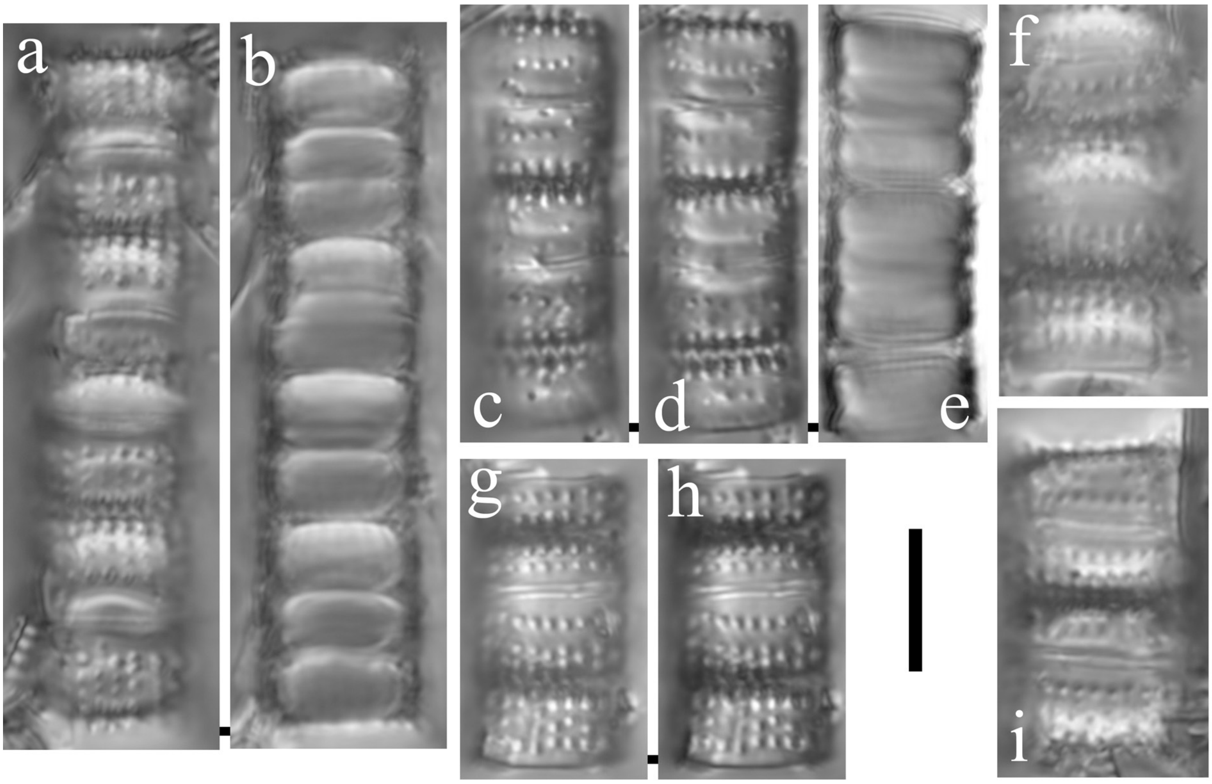

Fig. 16. Light micrographs of *Aulacoseira virginvalleyana* from the Miocene Virgin Valley Formation: note the shallow mantle height, small height to diameter ratio, apparent lack of a ringleiste, and the rows of mantle areolae; specimens (a–b, c–e; isotype) and (g–h; type) represent the same specimen at different focal planes. Scale bar 10 µm.

Fig. 17. Scanning electron micrographs of *Aulacoseira virginvalleyana* from the Miocene Virgin Valley Formation: (a–d) specimens with frustules aligned in short filaments; each valve has two circumferential rows of irregularly–shaped areolae on opposite ends of the short mantle, and a short collum with a set of parallel ribs; additional random valves may also be found; note the details of the linking spines on (a) and (c), the separating spines on (d); (b) close–up of the specimen in (a) showing the details of linking spines; distinct pervalvar costae are not present; (e) specimen showing the flat valve face with randomly scattered pores; (f) internal view depicting three rimoportulae terminating in a small pore and positioned at the mantle/valve face juncture (white arrows), internal costae (ribs) that align the mantle and terminate a short distance onto the valve face, and hymen coverings over the areolae and valve face pores; each rimoportula is positioned on a wide rib (black arrows) that is possibly tubular in nature. Scale bars 3 µm (b), 5 µm (d–f) and 10 µm (a, c).

Virgin Creek section of the Virgin Valley, 41.7939° N –119.0977° W.
Epithet: The species name is derived from the Virgin Valley Formation.
Distribution: *Aulacoseira virginvalleyana* was common to abundant in three white diatomite strata in the Lower Virgin Valley (Table 3). *Aulacoseira royalpeacockii* and *A. vanlandinghamii* were also common or abundant co–occurring taxa in the three collections.

Comments: The distinctive nature and distribution of mantle areolae suggest that *A. virginvalleyana* is morphologically closely related to *Aulacoseira lirata* var. *biseriata* (Grunow) Haworth, recently raised to the species level as *A. biseriata* Houk, Klee et H. Tanaka (Houk et al. 2017). As the name implies, *A. biseriata* specimens possess two circumferential rows of mantle areolae in a similar arrangement as found on *A. virginvalleyana* specimens (Houk 2003; Houk et al. 2017). This characteristic yields a similar mantle view for both taxa. In addition, both taxa form tightly linked chains of frustules. However, *A. virginvalleyana* and *A. biseriata* differ in several key characteristics. First, based on the available records, *A. biseriata* specimens possess a well formed and thick ringleiste (Houk et al. 2017; Enache et al. 2022). Krammer (1991a) further noted that this species (when described as a subspecific taxon of *A. lirata*) had a well formed and thick ringleiste, and he further pictured an image of the lectotype (fig. 7 in Krammer 1991b) with a distinct ringleiste. This is very different from specimens of *A. virginvalleyana* that lack a well–defined ringleiste that is often hard to distinguish. In addition, *A. biseriata* specimens are larger, have a smooth valve face with a distinct marginal ring of areolae, and rimoportulae near the ringleiste on the mantle. It is worth noting that because the presence of a ringleiste is a character used to define *Aulacoseira*, there is a question of whether *A. virginvalleyana*, with its shallow and slight ringleiste, truly belongs in the genus. However, because the suite of characters as a whole match those associated with *Aulacoseira*, *A. virginvalleyana* is being assigned to this genus. Lastly, other species of *Aulacoseira*, namely *A. pfaffiana* (Reinsch) Krammer, *A. nivalis* (W. Smith) English et Potapova, and *A. akitaensis*, were also found to each have an undeveloped and non–evident ringleiste (Houk et al., 2017).

Three other species, *Aulacoseira newjerseyana* Enache et al., *A. samariana* Tremarin, Torgan et Ludwig, and *A. akitaensis* H. Tanaka, are worth noting with respect to *A. virginvalleyana*. *Aulacoseira newjerseyana* valves also may have two circumferential rows of mantle areolae, with one always lining the top of the collum, and a second one sometimes found near the top of the mantle (Enache et al. 2022). However, *A. newjerseyana* valves have a longer mantle height, an areolated valve face, a shallow but distinct ringleiste, and rimoportulae positioned just above the ringleiste. Valves of *A. samariana* also possess two circumferential rows of mantle areolae positioned as found in *A. virginvalleyana*. However, *A. samariana* specimens have conical and pointed spines spanning 2–3 pervalvar costae, a smooth valve face with a marginal ring of areolae, a distinct ringleiste, and a ring of 6 or more rimoportulae on the mantle near the top of the ringleiste. In addition, the areolae coverings are significantly different when compared to *A. virginvalleyana*. Valves of *A. akitaensis* also have a shallow mantle, two circumferential rows of areolae, similar linking spines and a poorly developed ringleiste, showing some similarities to *A. virginvalleyana*. However, the areolation pattern of the valve face and position of the rimoportulae are significantly different. While the peripheral ⅔ of the valve face possesses areolae, the central region is smooth. A group of rimoportula are found on the valve face, usually arranged in a ring bordering the non–areolate portion of valve face, each connected to a tube that connects to the margin of the valve face (Houk et al. 2017).

***Aulacoseira moralesii* sp. nov. Siver (Figs 18–20)**
Description: Valves robust, thick–walled, and with large, wide, and mostly rounded linking spines (Figs 18; 19a–b, 20e). Valves range in diameter from 8 to 21.5 µm, in mantle height from 8.5 to 24.3 µm, and have a mean height to diameter ratio of 0.97 (Table 2). The majority of valves have striae that are sinistrorse, curving or slanting slightly to the left when traced from the collum to the top of the mantle (Figs 18a–b; 19a–b, d; 20a, c). Fewer valves have striae that are more or less straight and parallel with the pervalvar axis (e.g. Fig. 19c). Areolae are small and range in shape from elongate to circular, with the former type more often found on the lower half of the mantle (e.g. Figs 19c–d). On some specimens, the areolae are less dense, more widely spaced, or even lacking near the top of the mantle (Figs 19a–e). On specimens that possess spines, the valve face is either slightly convex or concave, presumably forming complimentary valves. The width to length ratio of a linking spine is roughly equal to one, and spines originate on every three to four pervalvar costae (Figs 19a–b; 20c–e). The collum is wide, accounting for approximately 30% of the mantle height, is largely hyaline except for a row of thin ribs along the base (Figs 19a–d; 20c). The ringleiste is broad and bell–shaped in cross section, and extends only a short distance into the valve interior (Figs 20c–d). Internally, the juncture of the mantle and valve face is thick and gently curved (Fig. 20c). Girdle bands are wide, open, and with rounded ends (Figs 19c; 20e). The presence of rimoportulae was not confirmed.

Resting spores were common in the population from the type locality, representing approximately ⅓ of all specimens (Figs 18a–b, g–j; 19c, e–f; 20a–b, f). The valve face on the spore valves is highly convex, dome–shaped, and most often covered with numerous small–diameter pores (Figs 18a–d; 19c, e–f; 20a). A distinct ridge encircles the top of the mantle, above which is often a zone of incomplete or more random deposition of silica that forms the connection with the convex valve face (Figs 18a–d; 19e–f; 20a). Most specimens were isolated spore valves, or valves attached to vegetative valves. Only one specimen (Fig. 20b) was thought to contain two domed and convex valves.

Holotype: Circled specimen on prepared slide labeled "CAS 3536 Siver 3" deposited at the Canadian Museum of Nature, CANA 131188. The holotype specimen is illustrated in Fig. 18a–d.

Isotypes: Circled specimen on prepared slide labeled "CAS 3536, Siver 1" deposited at the California Academy of Sciences, CAS (slide number 223052). The isotype specimen deposited at CAS is illustrated in Fig. 18g–h. A second isotype is maintained in Siver's personal collection and illustrated in Fig. 18i–j.

Type material: Diatomite material archived at the Canadian Museum of Nature, CANA 131188. The diatomite material used in this study was originally collected by Kenneth Lohman (his sample USGS 3536) and archived at the California Academy of Sciences (CAS accession number 601514). The sample used in the current study, and archived at the Canadian Museum, was a subsample of the original Lohman material.

Type locality: Outcrop along Opal Creek of the Lower

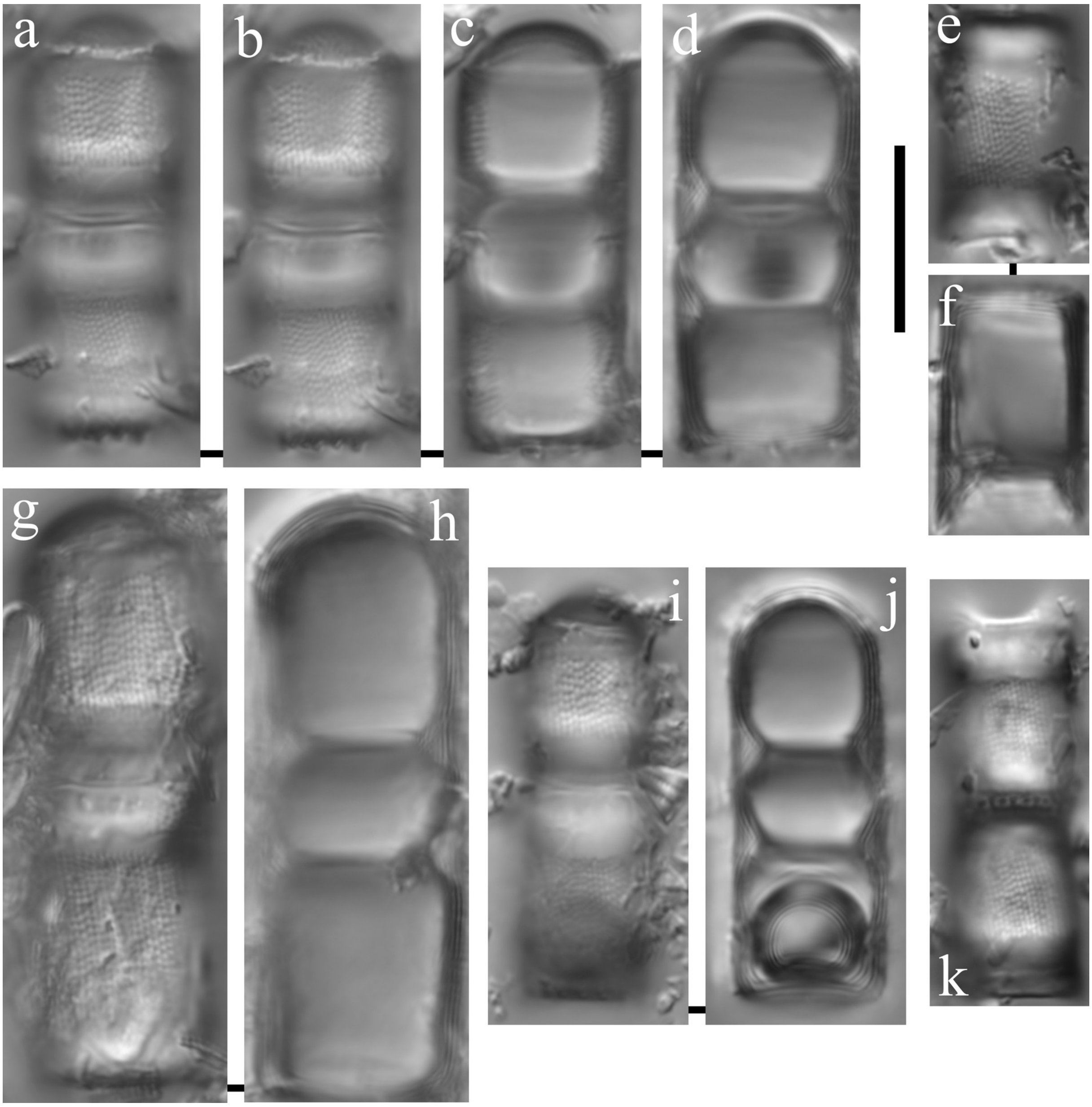

Fig. 18. Light micrographs of *Aulacoseira moralesii* from the Miocene Virgin Valley Formation: specimens connected with a horizontal black bar (a–d, f–g, h–i) are the same ones at different focal planes; the specimens in (a–d) and (f–i) represent intact resting spore frustules where the valve on the top has a domed cap, and the bottom valve a flat valve face; note the slightly sinistrorse striae composed of small elongate–shaped areolae that are often lacking near the top of the mantle, the distinct ridge between the top of the mantle and domed cap (a–b), and the broad and bell–shaped ringleiste on the specimens illustrated in (c–d) and (i); the type and isotype (deposited at the CAS) specimens are presented in (a–d) and (g–h), respectively; a second isotype specimen shown in (h–i) will be maintained in P.A. Siver's personal collection. Scale bar 10 µm.

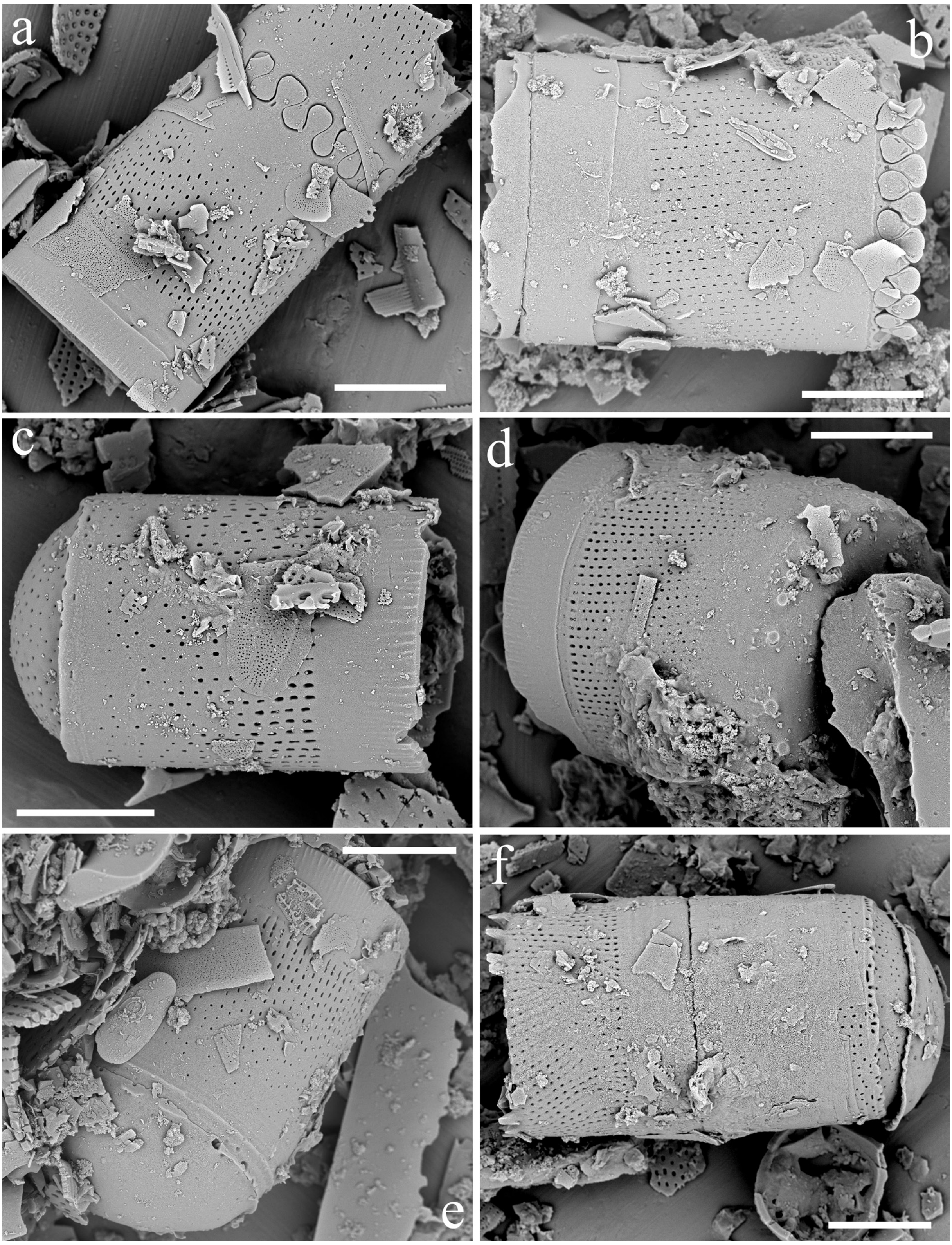

Fig. 19. Scanning electron micrographs of *Aulacoseira moralesii* from the Miocene Virgin Valley Formation: (a–b) valves of vegetative cells illustrating the large, wide and rounded linking spines, sinistrorse mantle striae composed of small areolae, and the wide and smooth collum; note the lack of areolae along the top ⅓ of the mantle; (c, e–f) valves of resting spores denoting the domed–shaped and highly convex valve face, and the distinctive ridge connecting the mantle to the margin of the domed valve face; the dome cap is with small and widely–spaced pores on the specimens in (c) and (f), but smooth on the specimen in (e); a broken piece of the end of a girdle band, depicting the wide and rounded nature of the structure can be seen on the specimen in (c); the sinistrorse mantle striae and wide collum can be seen on each specimen; remains of the complementary concave valve face of the adjacent valve is depicted on the specimen in (f); (d) a specimen with a smooth and convex valve face; note the thick and broken bases of the marginal spines. Scale bars 4 µm (c) and 5 µm (a–b, d–f).

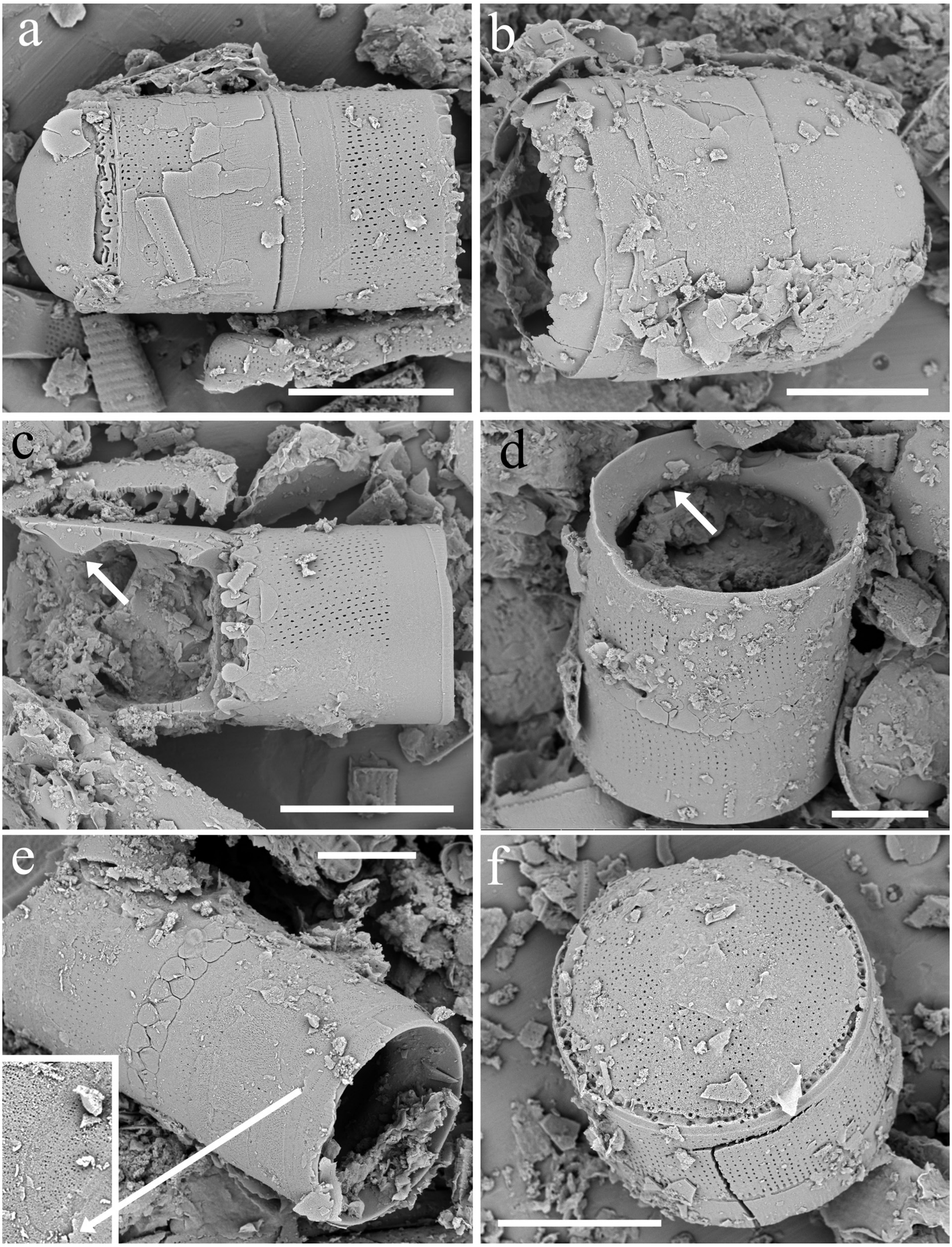

Fig. 20. Scanning electron micrographs of *Aulacoseira moralesii* from the Miocene Virgin Valley Formation: (a) resting spore frustule depicting the domed valve face (left valve), sinistrorse mantle striae, and wide collum (right valve); note the ridge with incomplete deposition of silica that connects the top of the mantle to the convex dome; the wide and rounded end of an open girdle band can be seen on the left–side valve; (b) a rare and fully formed resting spore; (c–d) internal views depicting the thick nature of the valve, and the broad and bell–shaped nature of the ringleiste (white arrows); (e) specimen with two valves attached with evenly–spaced, wide and rounded linking spines; the insert is a close–up of the wide and rounded end of an open girdle band; (f) valve view of a resting spore with a dome covered with small pores; note the distinctive ridge connecting dome with the top of the mantle. Scale bars 5 µm (d–e) and 10 µm (a–c, f).

Virgin Valley portion of the Virgin Valley Formation.

Epithet: The species is named in honor of Eduardo Morales, diatomist, teacher and close friend.

Distribution: *Aulacoseira moralesii* was found in three samples originally collected by Kenneth Lohman and archived at the California Academy of Sciences, USGS 3527, USGS 3530 and USGS 3536 (Table 3). All three samples were derived from strata of the Lower Virgin Valley part of the formation situated in the Opal Creek section of the Virgin Valley (Table 1). Two of the samples, USGS 3527 and USGS 3536, were characterized as brown lignite diatomite, and the third as white punky diatomite. *Aulacoseira italica* was a co–occurring species in all three samples.

Comments: Some diatoms produce resting spores that help them perennate and aid in survival during periods of unfavorable conditions (Edlund et al. 1996; Jewson et al. 2008; Kaczmarska et al. 2013). Typically, the valves of resting spores are morphologically distinct from vegetative cells, more heavily silicified, and often with highly convex valves. Semi–endogenous resting spores are ones where the hypovalve of the spore is contained within the original parent frustule, but the epivalve is outside of the parent frustules and exposed to the elements (Kaczmarska et al. 2013). Semi–endogenous resting spore formation has not been reported for most *Aulacoseira* taxa, but it is well documented for *Aulacoseira italica* and related species (von Stosch 1967; Edlund et al. 1996; Edlund personal communication). The vast majority of resting spore specimens observed for *A. moralesii* were either isolated valves, or valves attached to a morphologically distinct vegetative valve, presumably covering the spore hypovalve. Thus, the resting spores of *A. moralesii* clearly represent the semi–endogenous type. Lastly, although differences in the linking spines of *A. italica* and *A. moralesii* easily distinguish between the two taxa, other features are markedly similar and suggest that *A. moralesii* is in the *A. italica* complex. Both species have large linking spines, a wide and distinctive collum, sinistrorse striae composed of elongate to circular areolae, and a similar shaped ringleiste. In addition, valves of *A. italica* are also thick and possess a valve face with randomly–spaced tiny pores.

The three rock strata containing *Aulacoseira moralesii* also contain healthy populations of *A. italica*, indicating that both species are found under similar environmental conditions. However, resting spores of *A. italica* were not observed, perhaps suggesting that *A. moralesii*, but not *A. italica*, was being stressed in these specific habitats. *Aulacoseira italica* is commonly reported from wetlands and shallow ponds (Siver & Hamilton 2011). Other microfossils found in these strata, including multiple *Pinnularia* Ehrenberg species, synurophyte taxa, and euglyphid remains, coupled with the high organic content, supports the concept of a shallow, slightly acidic and humic–stained waterbody.

Other important species:

***Aulacoseira italica* (Ehrenberg) Simonsen (Figs 21–23)**

Because *A. italica* was found as a common component of the diatom flora in a number of Virgin Valley samples, and is closely aligned with *A. moralesii*, a description of the specimens is given here.

Description: Valves robust, thick–walled, and with large spatulate–shaped linking spines (Figs 21; 22a–e; 23f). Valves range in diameter from 7 to 10.4 µm, in mantle height from 7 to 12 µm, and the height to diameter ratio ranges from 0.73 to 1.5 (Table 2). Striae are sinistrorse, curving to the left when traced from the collum to the top of the mantle, to more or less straight. Longer valves tend to display the sinistrorse design (e.g. 21a–c; 23f), whereas those with smaller height to diameter ratios tend to have less sinistrorse to straight striae (e.g. Fig. 22e; 23b). Areolae are elongate–shaped, and relatively evenly spaced within a stria (Fig. 22a–f). Externally, the areolae are covered with a thin siliceous layer containing a thin elongate slit in the center and often smaller slits at each end forming an I–shape (e.g. Fig. 22a–c). Internally, each areola is covered with a complex vola that may extend onto the mantle wall (Fig. 23b, d). Randomly and widely–spaced pores, each with a diameter much smaller than an areola, are found on the valve face (Fig. 23a–b). The valve face pores are occluded internally with a few rotae. Internally, the junction of the mantle and valve face is rounded and slightly curved (Fig. 23b, e). The linking spines are long, robust, of even length, and often with small siliceous nodules along the shaft (Figs 22a–f; 23c). The base of the spine spans two, sometimes three, pervalvar costae, and the terminal areola of the middle stria usually extends onto the spine shaft (e.g. Figs 22d; 23c). Occasionally, two neighboring spines originating from the same valve, and lacking a complimentary spine in between them, are observed, giving the appearance of a double spine (Fig. 23b). The collum is well defined, wide, mostly hyaline, with a row of short and parallel ribs along the base (Figs 21a–e; 22c–d; 23f). A step is often observed midway on the collum. The ringleiste, situated on the top of the collum, is broad and bell–shaped in cross section and extends only a short distance into the valve interior (arrow on Figs 22d; 23c–d (left arrow)). There is one, possibly two, large rimoportula per valve positioned on the mantle approximately 3–4 areolae above the ringleiste (Figs 23c–d (right arrow on d)). The slit (lips) of a rimoportula is more or less parallel with the long axis of the mantle, and connected to a wide, straight, and flat tube that runs perpendicular to the mantle. The rimoportula can be attached near the center of the horizontal tube, or more often closer to one end of the tube. The external opening of the rimoportula is usually aligned with the areolae of a stria (arrow on Fig. 22c).

Distribution: Specimens of *Aulacoseira italica* were uncovered in six collections investigated in this study, all from the Lower Virgin Valley (Table 3), and ranging from rare to very common. The samples containing *A. italica* were characterized as brown or chocolate diatomite, lignite diatomite, or with significant lignite matter, and the strata are easy to distinguish in the field from the extensive deposits of pure white diatomite (Fig. 2b, e).

Comments: The highly distinctive rimoportula, coupled with a very shallow ringleiste, have also been reported by Houk et al. (2017), and are key characters of *A. italica*. However, *Aulacoseira italica* is closely related to *A. valida* (Grunow) Krammer and *A. crenulata* (Ehrenberg) Thwaites, two species also possessing the characteristic large spatulate–shaped linking spines (Krammer 1991b; Siver & Hamilton 2011; Houk et al. 2017). The primary trait originally used to distinguish between all three species was the character and direction of the pervalvar striae. The striae are sinistrorse on *A. italica* specimens (Houk 2003; Siver & Hamilton 2011; Houk et al. 2017), although they can also be re-

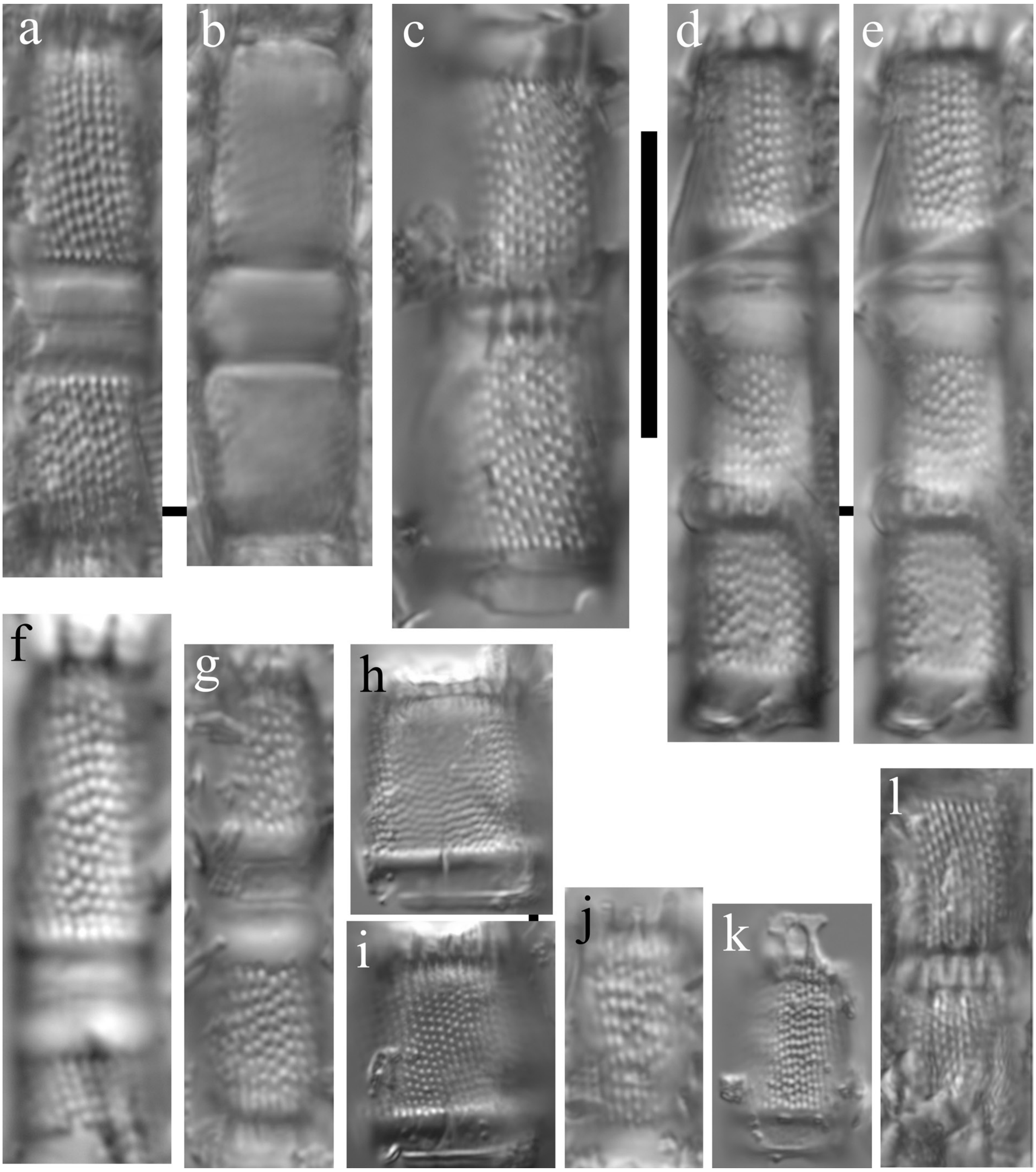

Fig. 21. Light micrographs of *Aulacoseira italica* from the Miocene Virgin Valley Formation: note the sinistrorse striae composed of elongate–shaped areolae, the wide collum; details of the ringleiste and linking spines are illustrated in (h–i) and (k), respectively; specimens connected with a horizontal black bar (a–b) and (d–e) are the same ones at different focal planes. Scale bar 10 µm.

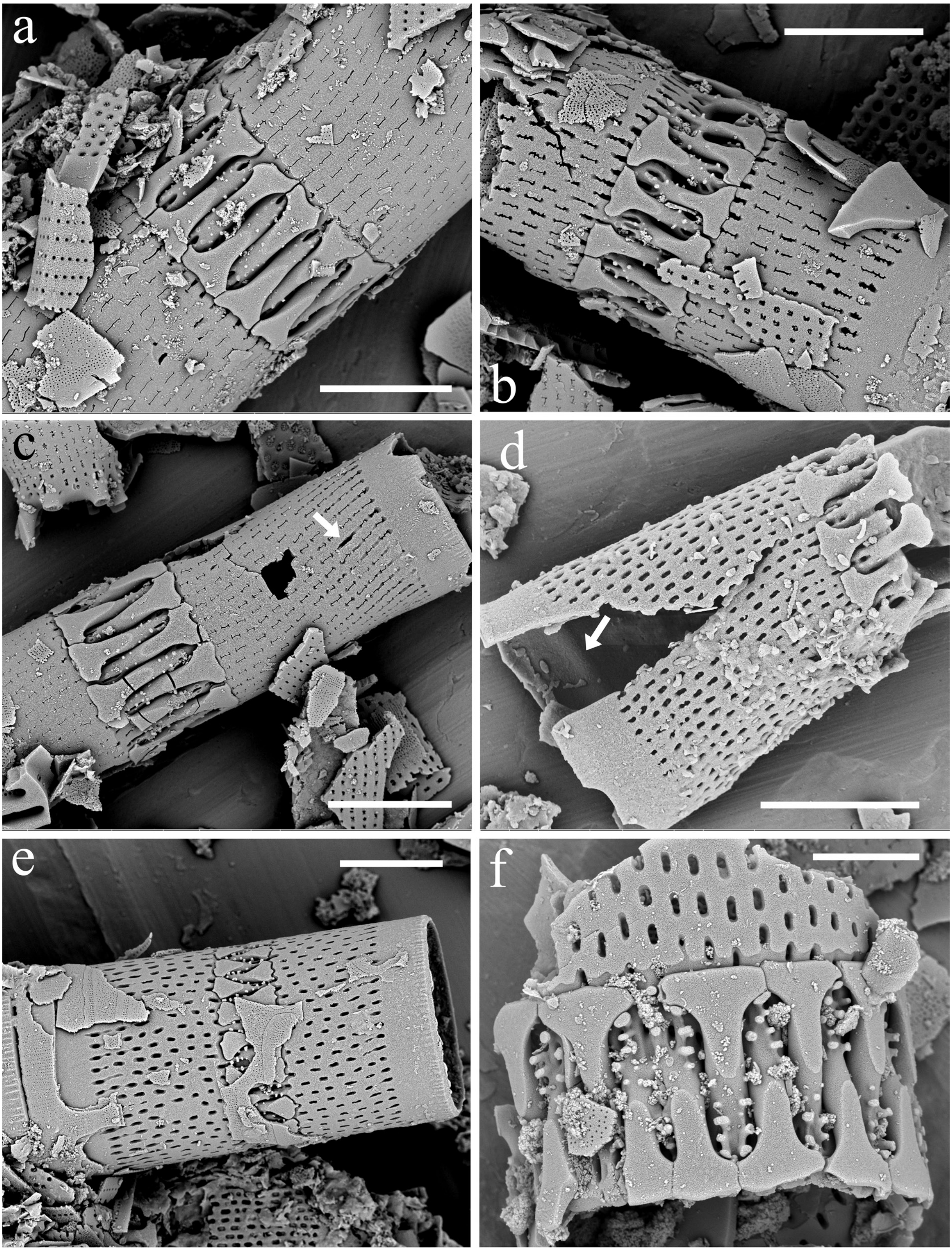

Fig. 22. Scanning electron micrographs of *Aulacoseira italica* from the Miocene Virgin Valley Formation: (a–e) specimens depicting details of the striae, the large spatulate–shaped linking spines, and the wide collum; the striae on specimens in (a) and (c–e) are sinistrorse, while the ones in (b) are more or less straight; note the elongate–shaped areolae with the I–shaped external coverings on specimens (a–c); the external opening of the rimoportula is depicted by the arrow in (c); (f) close–up showing details of the linking spines; note the widened and flat distal end and the papillae on the spine shaft. Scale bars 2 µm (f), 4 µm (a–b) and 5 µm (c–e).

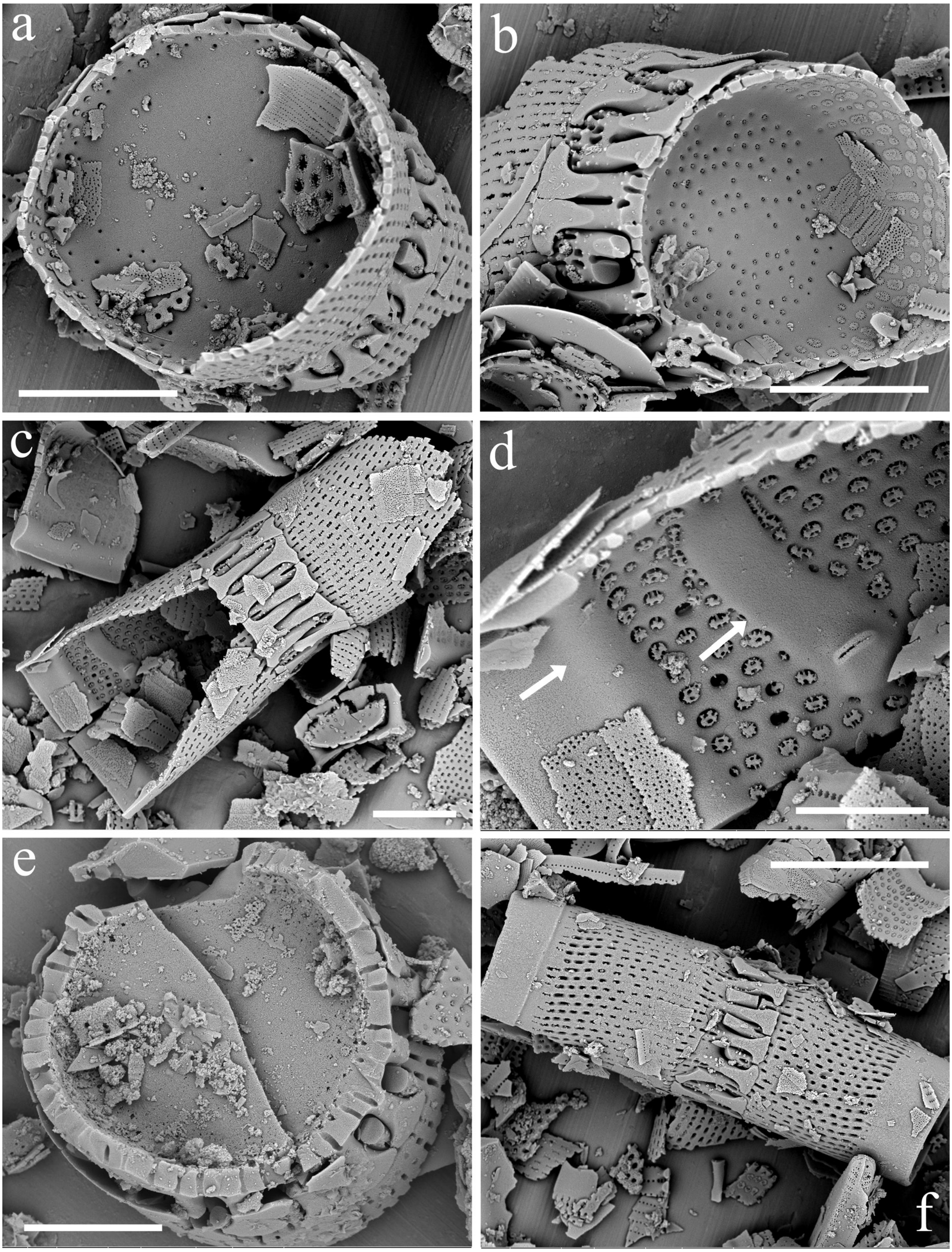

Fig. 23. Scanning electron micrographs of *Aulacoseira italica* from the Miocene Virgin Valley Formation: (a–b) inside views of the randomly areolated valve face; note the internal coverings of the areolae on (b); (c) internal view of the wide and shallow ringleiste, and a mantle rimoportula; (d) close–up of the specimen in (c) depicting the shallow ringleist (left arrow), remains of areola coverings, and the rimoportula (right arrow); note the extensive, wide and flat tube running perpendicular to the mantle height and slit situated close to one end of the tube; (e) inside view of a broken and thick–walled valve; note the interlocking nature of the linking spines; (f) specimen depicting the sinistrorse striae and the wide and smooth collum. Scale bars 2 µm (d), 4 µm (e), 5 µm (a–c) and 10 µm (f).

latively straight, or parallel with the mantle. In contrast, the striae on *A. valida* valves curve strongly to the right (dextrorse), and they are never sinistrorse (Houk 2003; Houk et al. 2017). The striae on *A. crenulata* specimens were characterized as sinistrorse to straight (Houk 2003), leaving this character a more difficult one to use in order to separate it from *A. italica*. In fact, Houk's (2003) descriptions of *A. italica* and *A. crenulata* were virtually identical. Crawford et al. (2003) addressed this issue through an investigation of type material from the Ehrenberg collection. These authors verified that striae on *A. italica* valves were sinistrorse, opposite that of *A. valida*. In addition, upon examination of the type material for *A. crenulata* (*Gaillonella crenulata* Ehrenberg), they concluded this taxon was conspecific with *A. italica*. However, because of differences in the shape and position of the rimoportulae, and the number of striae between adjoining spines, Houk et al. (2017) concluded that *A. crenulata* should be maintained as a separate species. Interestingly, the type localities for *A. italica* and *A. crenulata* are both fossil sites, the former species described from a deposit in Santa Fiora, Italy (Lectotype in BRM collection), and the latter taxon in diatomite from West Point, N.Y. (Crawford et al. 2003; Houk et al. 2017). In addition, *A. valida*, has also commonly been observed in fossil material (Houk 2003).

Two additional taxa, *Aulacoseira multistriata* (Patrick) Houk, Klee et H. Tanaka described from Brazil and *A. tsugaruensis* H. Tanaka described from Japan, are worth noting with respect to *A. italica*. Originally described as a variety of *A. italica* (*Melosira italica* v. *multistriata* Patrick), Houk et al. (2017) raised this taxon to the species rank because of a higher striae density and a larger number of rimoportulae per valve. Although the linking spines and sinistrorse nature of the striae found on the Miocene *A. tsugaruensis* valves are similar to those of *A. italica*, the rimoportula tube is positioned obliquely to vertically on the mantle.

A common denominator with the collections containing *A. italica* is that they all represented shallow waterbody environments, high in organic content, and primarily acidic. The light to dark brown nature of the rocks, especially those containing moderate levels of lignite material, are indications of higher organic content. In addition, samples from these rocks required longer treatments under stronger oxidation conditions to remove enough of the organic material for proper observation. The remains of multiple species of *Pinnularia* and *Eunotia* Ehrenberg also found in these samples, genera rare or missing from the pure white diatomite strata, are indicative of more acidic environments with higher dissolved humic content (Camburn & Charles 2000; Siver & Hamilton 2011; Costa et al. 2017). In addition, numerous testate amoebae plates were also present in some of the collections adding further evidence of shallow and acidic environments (Siver et al. 2020).

Aulacoseira laevissima (Grunow in Van Heurck) Krammer (Figs 24–26)

Aulacoseira laevissima was another common species found in strata of the Virgin Valley Formation. Because of its overall importance in the diatom flora, a description of the specimens uncovered is given here.

Description: Valves square to rectangular–shaped, relatively small (Table 3), often with a height to diameter ratio close to, or slightly lower than 1, and with closely–spaced rows of straight mantle striae (Figs 24; 25a, c–f; 26c). Most of the specimens derived from the rocks represented whole frustules (e.g. Figs 24h–i; 25a) or short filaments of two to five frustules (Figs 24a; 25e). Striae are composed of small, square to ovate–shaped areolae that are usually covered externally by a flat hymen covering attached by one part to the rim of the areola, often yielding a thin and C or crescent–shaped appearance (Figs 25a, c–d). Often, a thin siliceous layer can cover the stria areolae (Fig. 26a) and these specimens appear to have slightly thicker pervalvar costae. Linking spines are short, slender, of similar length, found on each pervalvar costa, and with variable–shaped apices ranging from small anchor to a more pronounced antler–shape (Figs 25e–f; 26c). Separating spines are shorter and tooth–shaped (Fig. 25d). The collum is relatively wide, and either smooth or consisting of a series of parallel struts believed to be formed through contact with the cingulum band, which leaves a distinct groove with the remaining portion of the mantle (Figs 25d; 26a). The valve face is flat, smooth and sometimes with a marginal ring of small pores (Figs 26a–d). The ringleiste is robust, extends inward approximately 1/9 of the valve diameter, and possesses a thickened margin (Figs. 26e–f). Despite a long search, rimoportulae were not observed.

Distribution: *Aulacoseira laevissima* was rare to common in 10 of 11 of the collections from the Lower Virgin Valley (Table 3). The collections included brown and white diatomite, and one described as a grey diatomite.

Comments: Based on available information, the species uncovered in Virgin Valley strata best fit previous reports of *A. laevissima*. According to Houk & Klee (2007), *A. laevissima* valves range in size from 6–10 µm (mantle height) × 10–17 µm (valve diameter), with straight striae composed of fine areolae, a well–defined collum that can be smooth or patterned with ribs, and a flat and smooth valve face often with a marginal ring of pores. Although the Virgin Valley specimens are on the lower end of the size range, this suite of characters fits that reported here for *A. laevissima*. In addition, the size, shape and arrangement of spines is virtually the same for both taxa. It is also noteworthy that, as found in the current study, neither Houk & Klee (2007), nor Houk et al. (2017), mention rimoportulae for *A. laevissima*. However, the two species do show slight differences in several charac-

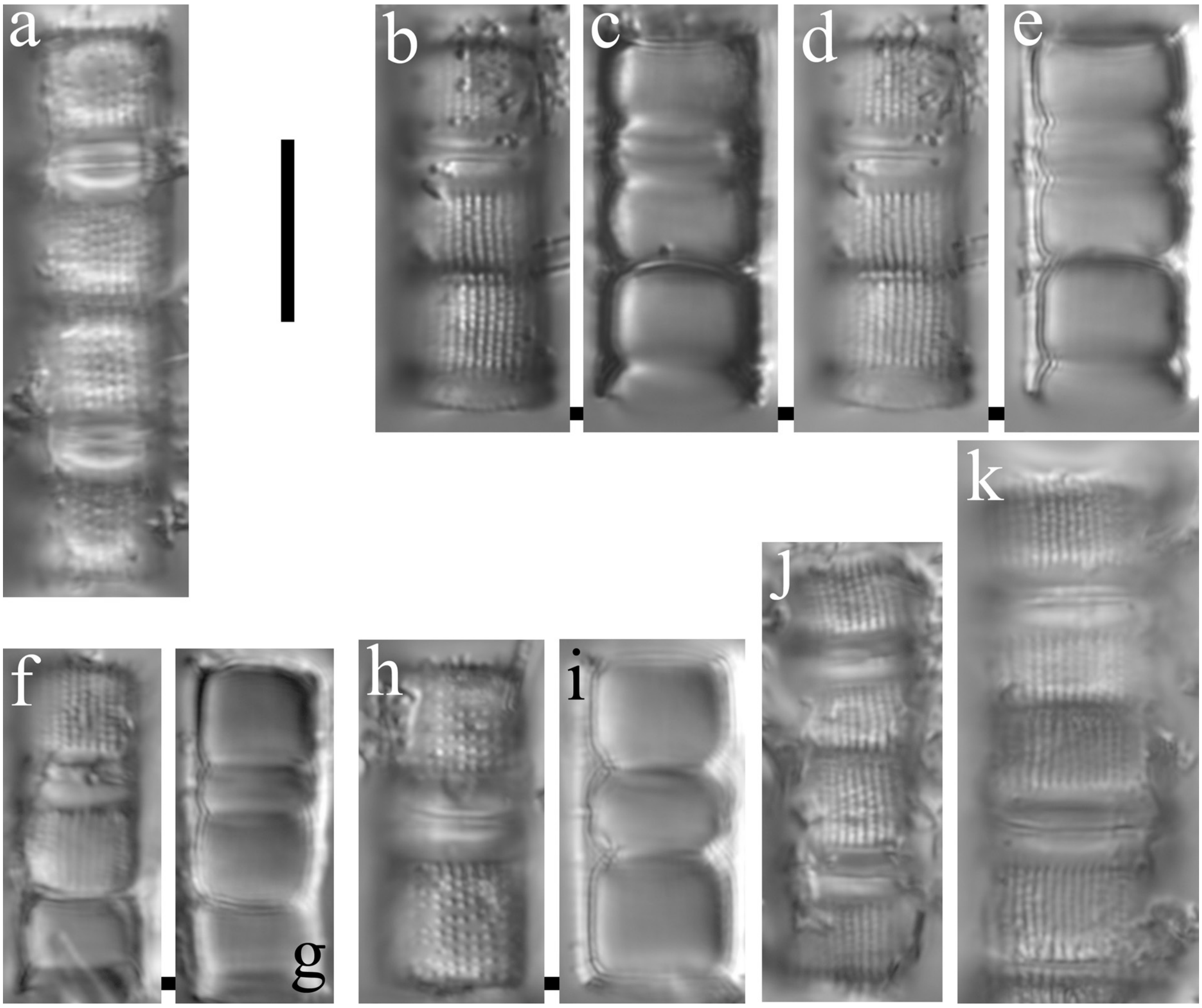

Fig. 24. Light micrographs of *Aulacoseira laevissima* specimens from the Miocene Virgin Valley Formation: specimens connected with a horizontal black bar (b–e, f–g and h–i) are the same ones at different focal planes; all specimens depict girdle views of frustules within short filaments; note the straight and dense mantle striae composed of small and circular–shaped areolae, and the shallow and the V–shaped nature of the ringleiste (e, g and h); complimentary pair of concave/convex valves is illustrated in (c). Scale bar 10 µm.

ters. Although the stria density of Virgin Valley specimens is slightly smaller than that reported by Houk & Klee (2007), there is overlap between the two taxa. In addition, Houk & Klee (2007) stated that the ringleiste of *A. laevissima* was V–shaped in cross section, but poorly developed. However, they do not illustrate ringleiste details with SEM images. Although the ringleiste in Virgin Valley specimens does not extend far into the cell interior, I would not refer to it as poorly developed. Perhaps with further study, these two taxa will be closely related, but different.

Haworth's (1988) description of *A. laevissima* shares some similarities to those described by Houk & Klee (2007) and to specimens in the current communication, but differ significantly with respect to features of the valve face. The distribution of spines also differs, and according to Haworth (1988) the valve face is areolate with a "*distans* pore pattern." Differences in these two features clearly indicate different taxa. Lastly, *Aulacoseira nygaardii* valves share some similarities with those of *A. laevissima*, including valve size, stria features and overall appearance. In addition, fig. 5 on Tab XCI of Houk & Klee (2007) depicting *A. laevissima* is very similar to *A. nygaardii*. In an earlier communication, Houk (2003) even commented on the similarities of the two taxa, and suggested they may be the same species. However, the distribution of spines on *A. nygaardii* is on every 2–3(4) mantle costae, which is very different from that of *A. laevissima* (Siver & Hamilton, 2005).

Discussion

Comparisons with Lohman (1957). In his thesis on diatoms from fossil localities in the Great Basin, Lohman (1957) described 11 new taxa of *Melosira* from the Virgin Valley, six species and five varieties. One additional species, *M. micropunctata*, described from a different formation was also reported by Lohman (1957) as common

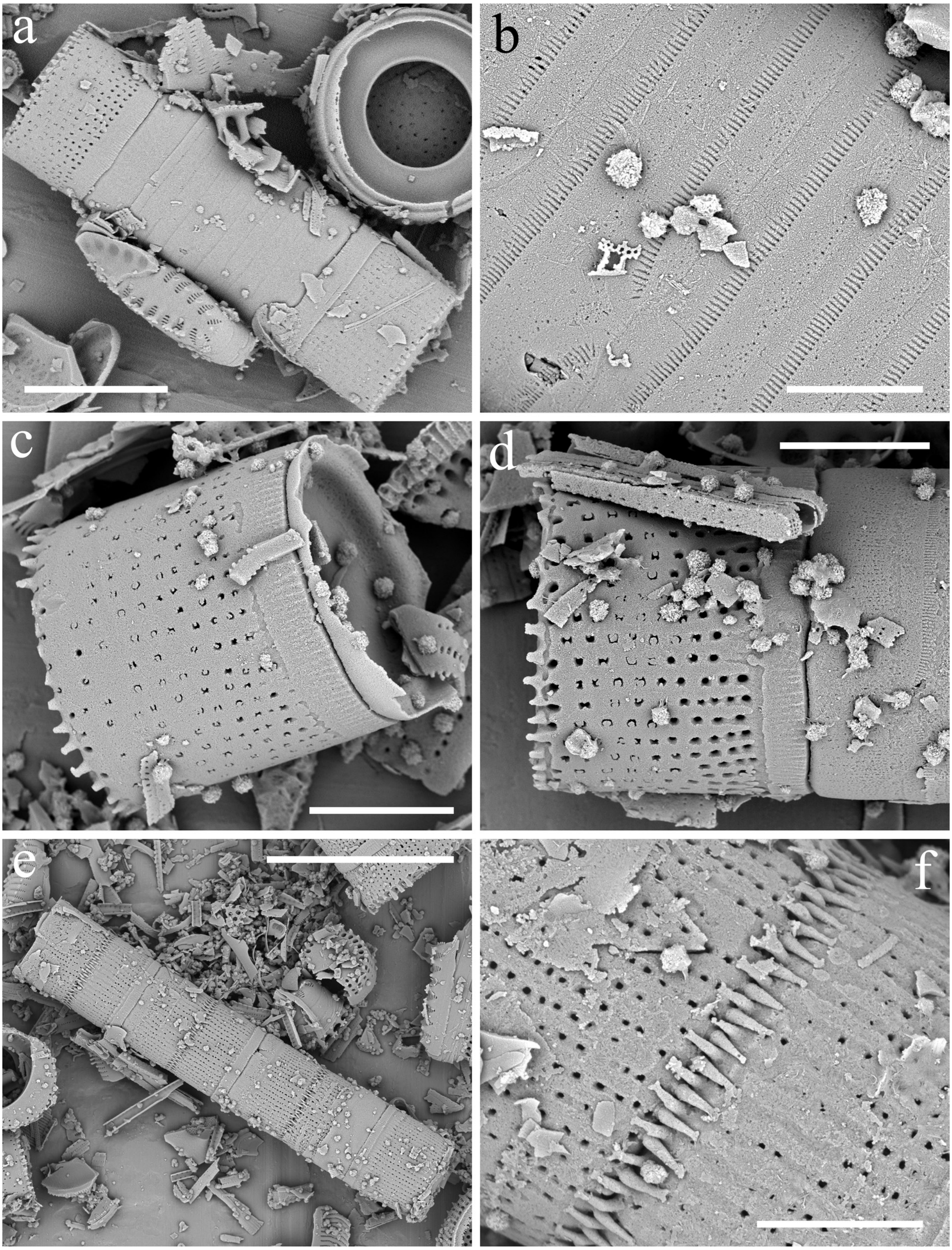

Fig. 25. Scanning electron micrographs of *Aulacoseira laevissima* specimens from the Miocene Virgin Valley Formation: frustule (a), valves (c–d) and a short filament (e) showing details of the striae, spines and collum; (b) close–up of (a) depicting the girdle bands; details of the c–shaped hymen covering the external surface of the areolae can be seen in specimens c–d; (f) close–up of the specimen in (e) showing details of the linking spines. Scale bars 2 µm (b), 3 µm (f), 4 µm (c–d), 10 µm (a) and 20 µm (e).

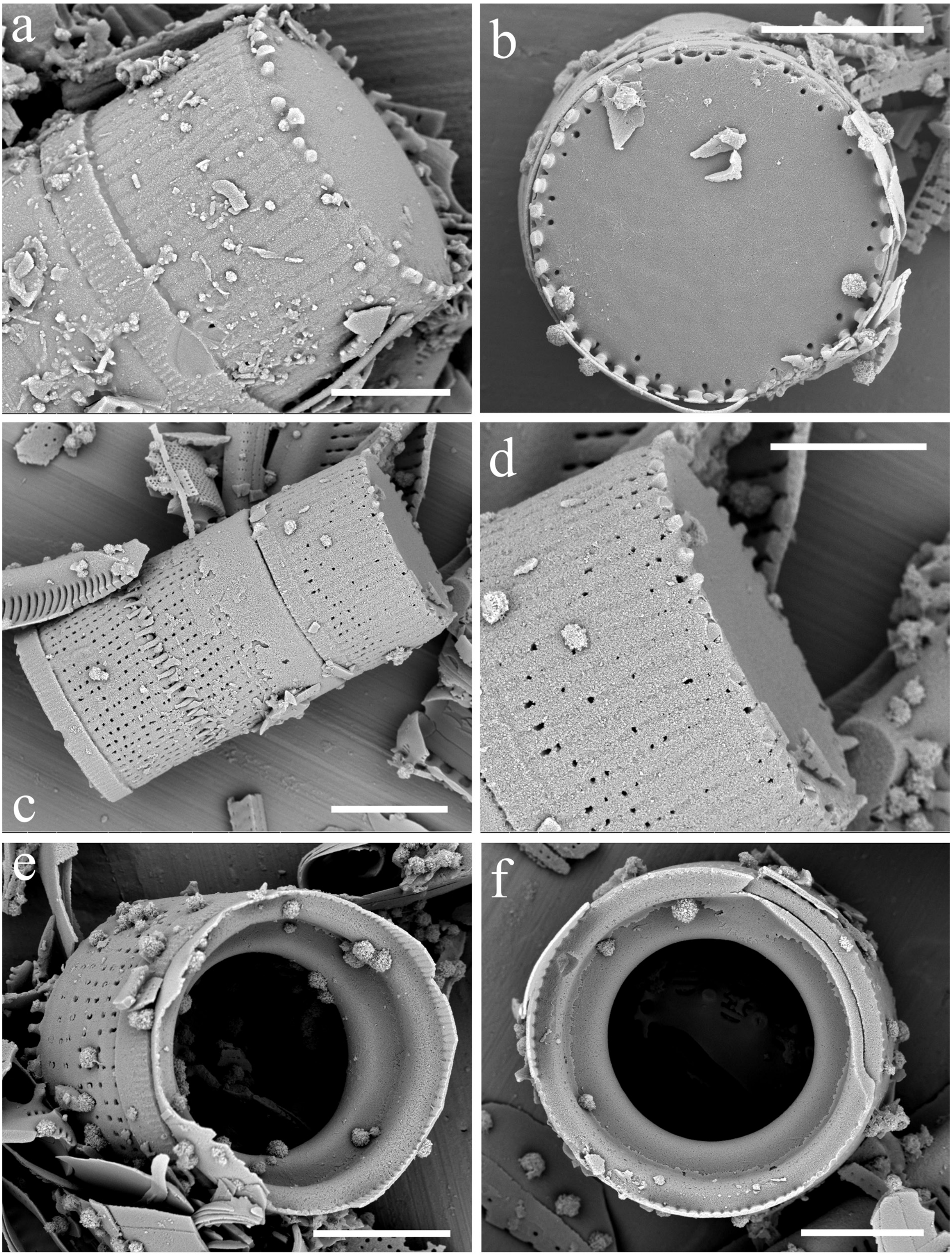

Fig. 26. Scanning electron micrographs of *Aulacoseira laevissima* specimens from the Miocene Virgin Valley Formation: (a) valve depicting a thin siliceous covering over the strial areolae, and the smooth valve face; (b) valve view showing the smooth valve face and a marginal ring of small pores close to the spines; (c) specimen showing the straight mantle striae and linking spines; (d) close–up of the specimen in (c) depicting the thin siliceous covering over most mantle areolae; (e–f) specimens depicting the well–developed ringleiste and the thickened inner marginal rim; the valvocopula is still attached on both specimens. Scale bars 3µm (a, d, f), 4 µm (b, e) and 5 µm (c).

in Virgin Valley samples. Today, all 12 taxa would be classified within *Aulacoseira*. As noted, unfortunately, Lohman's findings were never officially published and his suggested names are not valid. Lohman's (1957) descriptions are mostly brief and accompanied with only 1–2 images each. In addition, there is a lack of detail for key structures that today are best studied with SEM. Despite these drawbacks, I was able to find, confirm, and further examine nine of the 12 taxa in both his samples and ones I collected.

Perhaps the easiest taxa to confirm were *A. ponderosa* and *A. lohmanii* because of their large and distinctive areolae. I consider two of Lohman's taxa, *Melosira ponderosa* and *M. ponderosa* v. *elongata*, to fit within the description for *A. ponderosa*. The variety was separated on the sole basis of possessing longer valves with a smaller diameter. Because both taxa were always found together, I believe the smaller diameter valves represent one end of the size range for *A. ponderosa*. The new species described here as *A. lohmanii* was mentioned by Lohman as a variety of *M. ponderosa*, *M. ponderosa* v. *curta*, separated on the basis of having a larger diameter to mantle height ratio, and with square areolae each of which contained an "optical dot" in the center of the structure. The optical dot is formed by the structure of the complex volae within the areolae that is attached by the radiating rotae, a feature that could not be fully resolved by Lohman with light microscopy.

In addition to *Melosira italica*, Lohman (1957) reported two taxa closely aligned to it, *M. italica* v. *irregularis* and *M. micropunctata*. The former taxon differed from *M. italica* is being wider at the base of the mantle than at the valve face. However, in the samples from which Lohman reported *M. italica* v. *irregularis*, I uncovered numerous specimens that had been partially flattened causing the discrepancy in diameter between the two parts of the valve. Otherwise, these specimens were identical to the *M. italica* specimens also in the samples. *Melosira micropunctata* was reported to be similar to *M. italica*, but with slightly smaller punctae and spines with shorter stalks. I observed such specimens and believe them to be within the range of those representing *A. italica*. All of these taxa were restricted to samples from brown lignite diatomite strata.

The species reported by Lohman (1957) as *Melosira denticulata*, *M. triannula* and *M. punctissima*, correspond nicely to the species of *Aulacoseira* reported here as *A. virginvalleyana*, *A. royalpeacockii* and *A. laevissima*, respectively. Like *A. virginvalleyana*, *M. denticulata* valves are much wider than long, contain one to two circumferential rows of mantle areolae, and are commonly found in filaments containing 2–8 frustules. *Melosira triannula* was described as having small–diameter valves, large and coarse areolae in three rows, a shallow ringleiste, and a slightly convex valve face. This suite of characters, and the samples in which it was reported, nicely match those of *A. royalpeacockii*. Characteristics of *Melosira punctissima* and *M. punctissima* v. *curvata* discussed by Lohman (1957), including valve size and shape, a moderate ringleiste, and straight rows of striae consisting of very fine punctae, matched those for *A. laevissima*. In addition, I readily found specimens in the samples in which this species was listed by Lohman (1957) as being abundant, further supporting this match. I found it difficult to separate *M. punctissima* from another species (and a variety) described by Lohman (1957), *Melosira margaritata*. It is very likely that this species also represents *A. laevissima*, which I found to be abundant in multiple samples.

Discussion on Paleoecology. Several conclusions can be made regarding the paleoecological conditions of the aquatic environments archived in Virgin Valley rock strata based on findings made in this investigation and those from Lohman (1957). All of the evidence indicates that either different waterbodies existed at this locality over long periods of time, or that the conditions of a single waterbody significantly changed over time. Given the extensive beds of fossils, these aquatic environments were very productive, and often contained a high diversity of organisms. In addition to *Aulacoseira* taxa, strata from the LVV often contained a fair number of pennate and benthic diatoms, especially small fragilarioid species, suggesting a shallow lake environment. Periods where the concentrations of *Aulacoseira* increased relative to benthic pennate forms, and resulted in bright white diatomite layers, were likely correlated with a deeper waterbody and increased wind mixing, conditions that would favor planktic forms. These strata were mostly dominated by *Aulacoseira ponderosa*, one of the species capable of forming long filaments.

Other strata found in the LVV consisted of brown lignite/diatomite. These strata contained a very different compliment of pennate diatoms, including taxa belonging to *Eunotia*, *Oxyneis*, and numerous species of *Pinnularia*, suggesting a shallow, acidic waterbody with elevated concentrations of humic compounds (Flower 1989; Camburn & Charles 2000; Melo et al. 2010; Siver & Hamilton 2011). *Aulacoseria italica*, *A. moralesii*, *A. laevissima*, *A. virginvalleyana* and *A. royalpeacockii* were consistently uncovered in these brown diatomite layers, often in large numbers, and these strata lacked *A. ponderosa*.

Species of *Tetracyclus* Ralfs first appeared in strata found towards the end of the LVV and in lower sections of the UVV. Lohman (1957) also reported that specimens of *Tetracyclus* were abundant in his samples from this part of the formation, and believed their presence signaled a cooling environment. My observations confirm the presence of *Tetracyclus* in these samples. At least some modern species of *Tetracyclus* have also been associated with cooler environments. For example, Bishop & Spaulding (2015) described *T. hinziae* from cool streams in the western Cascade Mountains in Washington. The hypothesis that the environment was cooling during the period represented at the LVV to

UVV boundary corresponds nicely with the transition from the MMCO to the MMCT, when the global mean annual temperature was beginning to decline. Shortly after the arrival of *Tetracyclus*, extensive deposits of white diatomite are found in the UVV that contained massive concentrations of *Aulacoseira ponderosa*. The populations of *A. ponderosa* found in these deposits contain valves with a wide range in diameter, including a large number of small–diameter specimens with long mantle heights. In a recent study, SIVER et al. (2021) successfully correlated mean valve diameter for *Aulacoseira ambigua* (Grunow) Simonsen over ~120 years in a shallow lake with population growth. Increased growth caused by enhanced concentrations of nutrients resulted in a significant decline in mean valve diameter. Applying the findings of SIVER et al. (2021) to *A. ponderosa* in the Virgin Valley strata supports the hypothesis that populations of this species had high rates of growth over an extended growing season. Given its robust frustules, the large concentrations of *A. ponderosa* represented in the UVV strata also imply a high degree of mixing of the water column. Further, the disappearance of *Pinnularia* taxa and other acidic diatom taxa signals an increase in pH coupled with a decline in dissolved humic content.

The centric diatom genus *Actinocyclus* Ehrenberg was a dominant component of many lake systems in western North America over an approximately 10 Ma period during the Middle Miocene (BRADBURY & KREBS 1995). *Aulacoseira* was also reported as a co–dominant in many of these waterbodies, prompting BRADBURY & KREBS (1995) to suggest that the ecological conditions of these two centric diatom genera were similar. They further pointed out that many of the lakes harboring both genera were likely to have been warm monomictic systems, allowing for mixing to continue throughout the winter months which would favor planktic diatoms. The abundance of *Aulacoseira* species in Virgin Valley remains supports the idea that diatoms were maintained in the water column for extended periods of time. Interestingly, the dominance of *Actinocyclus* declined precipitously near the end of the MMCO (KREBS et al. 1987), concurrent with declining temperatures (ZACHOS et al. 2008). In fact, although numerous *Actinocyclus* taxa thrived during the Miocene, only one species, capable of tolerating a range of salinities, is found in freshwater ecosystems today (BRADBURY & KREBS 1995). In contrast, *Aulacoseira* continued to diversify after this time period, and today remains an important component of numerous freshwater ecosystems. Although a few samples from Virgin Valley contained *Actinocyclus*, it was very rare in each of these samples, further supporting the concept of a cooling environment.

It is interesting to note that recent studies suggest that climate warming has caused a decline in *Aulacoseira* across expansive regions of North America, often in favor of smaller centric diatom genera such as *Cyclotella* (Kützing) Brébisson and related genera (reviewed by RÜHLAND et al. 2015). Simply stated, the concept is that recent warming has resulted in greater water column stratification coupled with less mixing, including less mixing with depth. This change favored smaller and less silicified diatoms, such as single–celled *Cyclotella* organisms, while heavier *Aulacoseira* cells would tend to drop out of the mixing zone. The result would be an increase in cyclotelloid–taxa relative to *Aulacoseira*, and this change would be reflected in lake sediment archives. Of course, as RÜHLAND et al. (2015) and others (SAROS et al. 2011, 2012) point out, water temperature is only one of a number of interacting variables resulting in apparent shifts in the complement of planktic species.

Despite the recent decline in relative importance of *Aulacoseira* across North America, it is certainly interesting that this genus was so abundant in waterbodies in the same geographic region during the Miocene when temperatures were significantly warmer that today (BRADBURY & KREBS 1995; ZACHOS et al. 2008; DILLHOFF et al. 2009). Annual mixing patterns are likely one factor responsible for the observed difference. As suggested by BRADBURY & KREBS (1995), many of the lake systems in western North America that favored large growths of *Aulacoseira* would have been warm monomictic systems due to the lack of winter freezing. This means the water column continued to circulate from fall, through the winter, and until summer stratification, potentially yielding favorable growth conditions over a large portion of the year. In contrast, many, if not all, of the lakes where the relative abundances of *Aulacoseira* have recently declined are temperate dimictic lakes where winter ice cover would effectively reduce the period of time mixing would aid heavy celled–organisms to be maintained in the water column. Based on this hypothesis, if continued warming were to result in shorter periods of ice cover, or none at all, the abundance of *Aulacoseira* could once again increase. A closer examination of fossil localities that harbored *Aulacoseira* during both warm and cooler climates could prove valuable in our understanding of current and future shifts in the composition of planktic communities.

In summary, the extensive fossil deposits found in the Virgin Valley Formation indicate that this region sustained freshwater aquatic environments for an extended time period in the Miocene when the global mean temperature was at a peak and then began to cool (ZACHOS et al. 2008). The aquatic environments contained a diverse flora of diatoms, largely dominated with *Aulacoseira* taxa, including six species described herein as new. The *Aulacoseira* species include a wide range of morphological types, especially regarding rimoportula, ringleiste and areolae structure. *Aulacoseira* is among the oldest known diatoms to inhabit freshwaters, dating to at least the Cretaceous, and becoming more diversified and widespread during the Cenozoic (SIVER & VELEZ 2023). Documentation of the fossil *Aulacoseira* species represented in the Miocene deposits of the Virgin Valley adds to our knowledge of this important genus, including its paleoecology, and will ultimately aid in furthering our understanding of diatom evolutionary history.

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