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Middle Miocene *Aulacoseira khankaica* sp. nov. (Bacillariophyta), a new centric diatom from the Russian Far East

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Abstract

The present paper describes the diatom species *Aulacoseira khankaica* sp. nov. based on detailed light and scanning electron microscopy observations. Its morphological features are compared with those of similar *Aulacoseira* species. The new species is described from the Middle Miocene sediments of the Khanka Basin, Primorsky Krai (Russian Far East). *Aulacoseira khankaica* is characterized by short chains joined by spatulate spines, straight rows of small areolae on the valve mantle, a narrow ringleiste and sessile rimoportulae located on the valve rim. The finding of *A. khankaica* provides additional information on the distribution of centric diatoms in the Middle Miocene.

Key words: Bacillariophyta, fossil, morphology, ultrastructure, palaeoecology, Miocene Climatic Optimum, Primorsky Krai

Introduction

The genus *Aulacoseira* Thwaites is one of the largest centric diatom genera, comprising over two hundred species, varieties, and forms. These taxa are widely distributed worldwide in ecologically diverse lacustrine and lotic waters (Guiry & Guiry 2025). Approximately 20% of the known species within this genus are extinct (Edgar 2003; Siver & Velez 2023; Edgar & Theriot 2004).

Originally described by Thwaites (1848), *Aulacoseira* was established to accommodate species formerly assigned to *Melosira* C. Agardh that exhibited distinct valve morphology. However, the name *Aulacoseira* was not widely adopted until 1979, with most taxa continuing to be classified under *Melosira*. Simonsen (1979) subsequently reinstated the genus and transferred numerous species to it. Later, based on unique diagnostic features, Moisseeva and Nevretdinova (1990) established the genus *Alveolophora* Moisseeva & Nevretdinova by separating it from *Aulacoseira*.

Historically, the identification and description of *Aulacoseira* taxa have focused on the ornamentation of the siliceous cell walls. Most morphological characteristics used in these descriptions are equally accessible for examination in both fossil and extant taxa (Edgar 2003).

Many attempts to describe or to differentiate species, or species groups, have relied on valve shape in girdle view, specifically the height to diameter ratio: those with a ratio ≥ 1 and those with a ratio < 1 (Hustedt 1942; Krammer & Lange-Bertalot 1991). Additionally, three diagnostic characteristics, the presence of a ringleiste, rimoportulae, and collum, help to further define the genus and facilitate interspecific differentiation (Siver 2025).

The Middle Miocene fossil diatom flora of the Khanka Basin, located in Primorsky Krai (Russian Far East), has been a subject of research for over 70 years, beginning with the pioneering work of Jouse (1952). These studies were subsequently advanced by Moisseeva (Moisseeva 1971, 1995), Tsarko (Moisseeva & Tsarko 1990), Pushkar, Cherepanova, Likhacheva (Pavlyutkin *et al.* 1993; Pavlyutkin *et al.* 2004; Likhacheva *et al.* 2009), and Avramenko (Likhacheva *et al.* 2021). The Middle Miocene diatom flora is characterized by the dominance of centric *Aulacoseira*

taxa belonging to the “prae” group, which inhabited lacustrine environments during the Middle Miocene Climatic Optimum (MMCO) in the region (Likhacheva *et al.* 2021). The Early Middle Miocene (14.5–17 Ma) global warming event was one of the most conspicuous climate changes of the Neogene Period. This warming peaked at approximately 16 Ma, with marine and terrestrial temperatures exceeding current levels and reaching their highest point since the Eocene (Tanai & Huzioka 1967; Kennett 1982; Tsuchi & Ingle, 1992; Oleinik *et al.* 2008; Zachos *et al.* 2008). Similar climate changes were also established for Primorye (Korotky *et al.* 1996; Pavlyutkin & Petrenko 2010; Pushkar *et al.* 2019), where the Middle Miocene climate was identified as typical subtropical (Korotky *et al.* 1996). Abundant precipitation and a monsoon regime led to the development of a dense river system and numerous lakes. These conditions, combined with relatively mild winters, likely extended the growing season, resulting in high diatom productivity (Avramenko & Pushkar 2023).

The purpose of the present paper is to describe *Aulacoseira khankaica*, a new species from the Middle Miocene sediments in Primorsky Krai. This description is based on a detailed morphological analysis using light and scanning electron microscopy. Furthermore, we compare the new species with morphologically similar taxa and discuss its systematic position within the Aulacoseiraceae.

Materials and methods

The investigated samples were collected from the Middle Miocene diatomite bearing deposits in the Khanka Basin, Primorsky Krai, Russian Far East (Fig. 1). The sections are located on the western shore of Lake Khanka, between the settlements of Turiy Rog and Novokachalinsk (northwestern Khanka Basin). Five samples were obtained from two nearby sections (Fig. 1): L-03/2 (45°09'14.3"N, 132°00'23.3"E) and L-04/1 (45°09'11.8"N, 132°00'12.6"E).

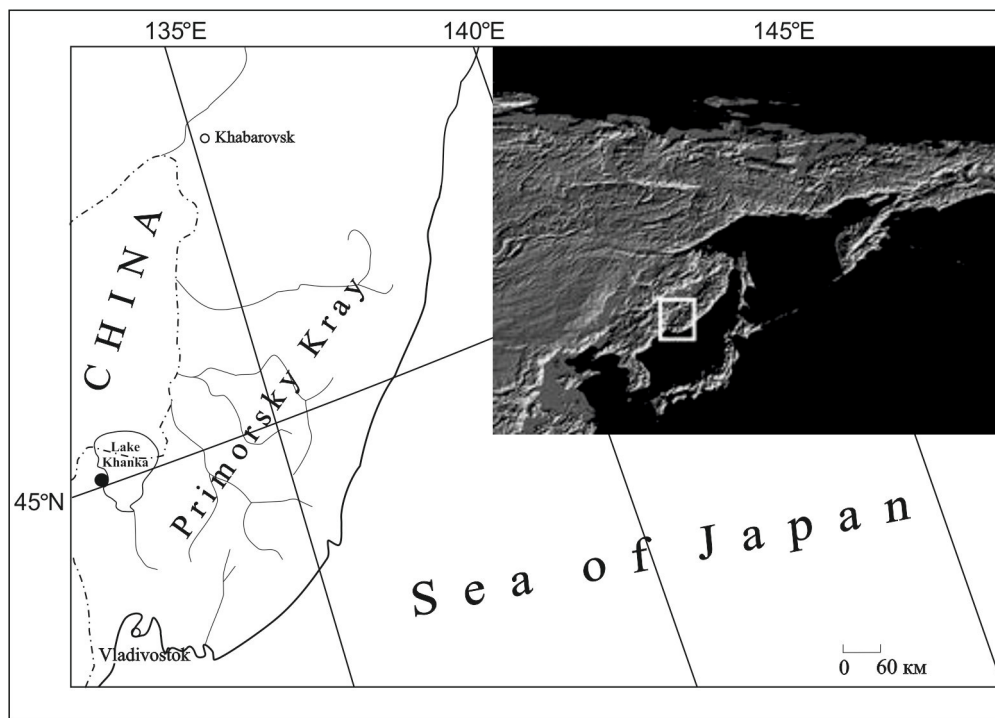


FIGURE 1. Sampling site of *Aulacoseira khankaica* (indicated by black dot) on the western shore of Lake Khanka, Primorsky Krai.

The shoreline consists of an abrasion scarp with a narrow strip of sand and a pebble beach (Fig. 1). The deposits comprise pebbles, sandstones, thin-layered tuffaceous siltstones and diatomite. These sedimentary strata belong to the Novokachalinskaya Formation (Pavlyutkin *et al.* 2004), which is overlain by Upper Pliocene clays and underlain by Upper Oligocene coal-bearing beds. Based on fossil spores, pollen, leaves, and diatom data, the Novokachalinskaya Formation is assigned to the Middle Miocene (Pavlyutkin *et al.* 2004, Pavlyutkin 2005). Volcanic rocks from this Formation have been dated to 18.1–14.9 Ma (Pavlyutkin *et al.* 1993; Likhacheva *et al.* 2009).

Samples for diatom analysis were processed following standard methods using hydrogen peroxide (H₂O₂) (Proshkina-Lavrenko 1974). Light microscopy (LM) observations were conducted using a Zeiss Axioskop 40 (Carl

Zeiss, Germany) equipped with an oil immersion objective. For scanning electron microscopy (SEM), the cleaned material was dried onto aluminium stubs, sputter-coated with Pt–Pd. Observations were performed using a Merlin (Carl Zeiss, GmbH, Jena, Germany). Additional observations were carried out using a ThermoScientific, Quattro S (Brno, Czech Republic) microscope.

Taxonomic analysis followed the criteria of Krammer & Lange-Bertalot (1991), focusing on rimoportulae morphology, the distribution and frequency of valve features, valve dimensions, and the mantle height-to-diameter ratio. Morphometric data were obtained from 100 valves.

Morphological terminology follows Crawford (1981), Round *et al.* (1990), Siver & Kling (1997) and Houk *et al.* (2017).

Results

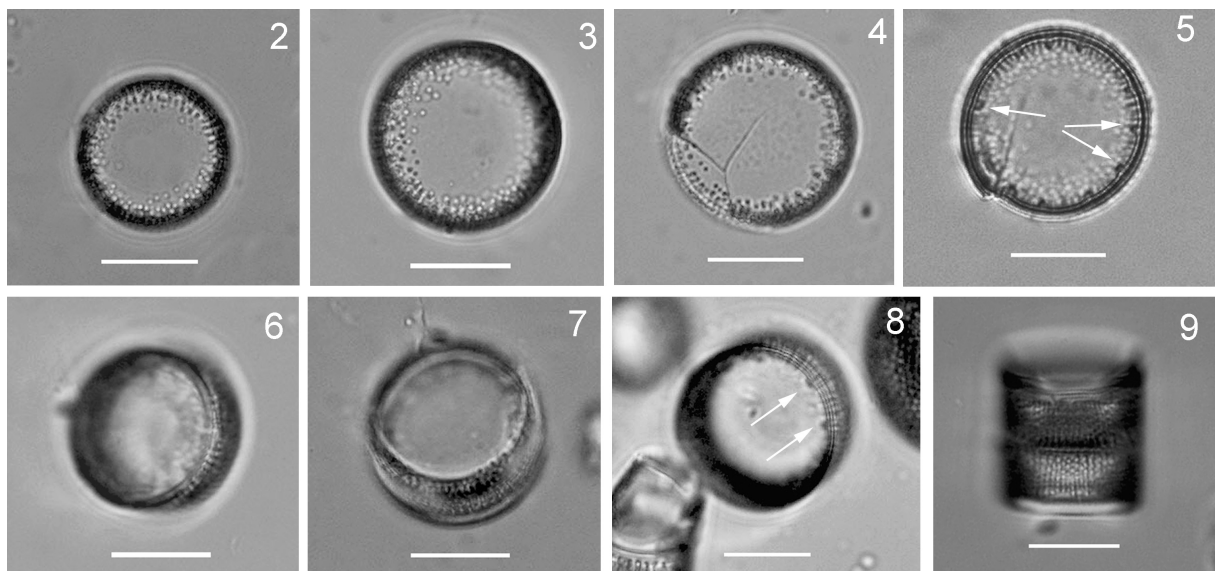
Overview: All samples from the Novokachalinskaya Formation contained taxa of the Aulacoseiraceae, represented by the genera *Aulacoseira* and *Alveolophora*. Within this material, *Aulacoseira* species show significant morphological variability, making small valves difficult to distinguish from *Alveolophora* under LM.

Among the identified taxa, *Aulacoseira* contributed more than 90% of the total number. This genus was represented by six taxa belonging to *A. praegr anulata* group. The latter included one species, three varieties, and six forms, including: *A. praegr anulata* var. *praeislandica* f. *praeislandica* (Jousé) Moisseeva, *A. praegr anulata* var. *praeislandica* f. *curvata* (Jousé) Moisseeva, *A. praegr anulata* var. *praegr anulata* f. *praegr anulata* (Jousé) Simonsen, *A. praegr anulata* var. *praegr anulata* f. *curvata* (Jousé) Simonsen, *A. praegr anulata* var. *praeangustissima* f. *praeangustissima* (Jousé) Moisseeva, and *A. praegr anulata* var. *praeangustissima* f. *curvata* (Jousé) Moisseeva (Likhacheva *et al.* 2021). One of the encountered species did not show sufficient similarity to any previously known species and is therefore described in detail below as a new species.

Descriptions of new species

Aulacoseira khankaica Avramenko & Cherepanova *sp. nov.* (Figs 2–26)

Holotype. Slides L-03/2 and L-04/1, deposited in collection of Far East Geological Institute, Far East Branch of the Russian Academy of Science, Vladivostok, Russia.

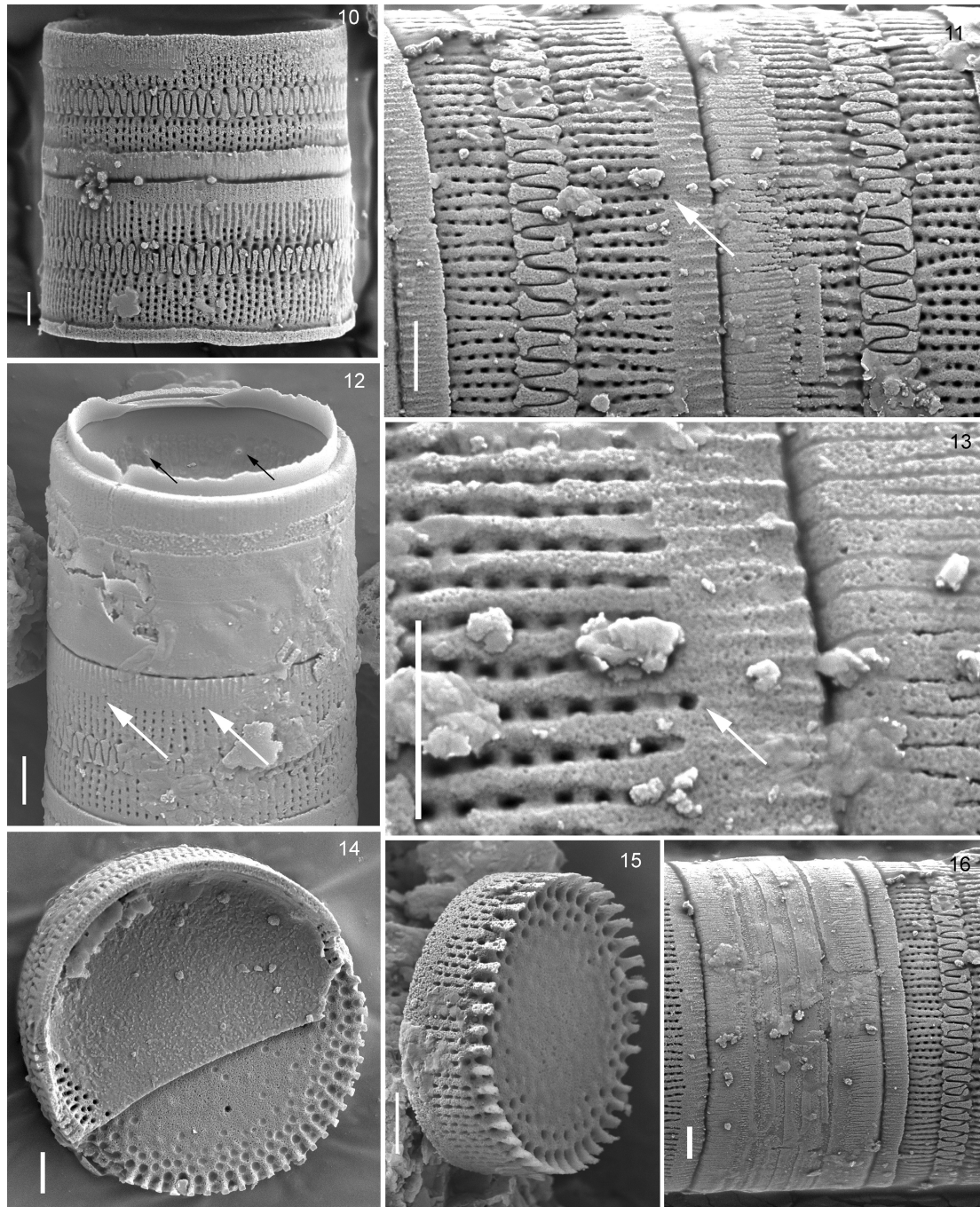


FIGURES 2–9. *Aulacoseira khankaica*, LM. Scales: 10 μ m. Figs 2–5. Valve views: 4—Valve view of the two linked cells, 5—Arrows indicate the tubes of rimoportulae. Figs 6–8. Oblique view, 7—Arrows indicate the tubes of rimoportulae. Fig. 9. Girdle views of two linked valves.

Type locality. Russia, Primorsky Kray, western shore of Lake Khanka, northwestern Khanka Basin; Novokachalinskaya Formation, Middle Miocene.

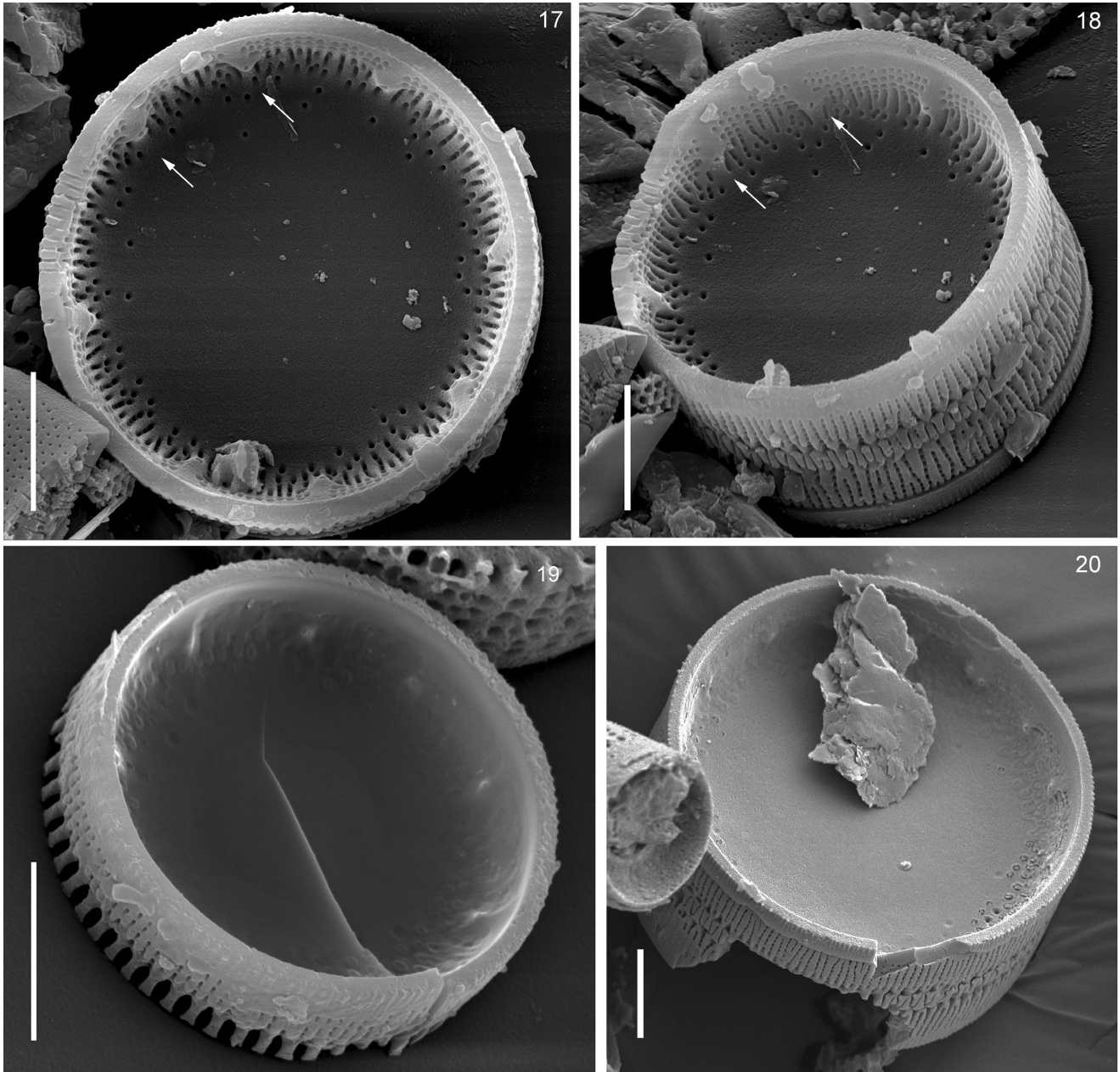
Description. LM (Figs 2–9). Cells joined by spines, usually forming short chains of 2–4 cells. Frustules short, cylindrical, round in valve view. Valve have shallow, mantle height 2.8–7.1 μm , valve diameter 9.8–20.2 μm . Mantle height/diameter ratio 1.6–4.6 (mean=2.36). Ringleiste narrow with a circular opening. Rimoportulae (8–10 per valve) located near the valve face/mantle junction, forming a ring.

SEM. External views (Figs 10–16). Valve face flat, ornamented with a variable number of round areolae located mainly along the margin; valve center usually lacking areolae. Pervalvar rows of areolae straight, 18–27 in 10 μm , 20–24 areolae/10 μm in a row, deeply recessed within the valve mantle. Areolae small ($d=0.10\text{--}0.4$, $h=0.13\text{--}0.19$ μm). Linking spines relatively short, 1.27–3.13 μm in length (mean=2.43 μm), spatula-shaped with a broader distal end. External opening of rimoportula rounded. Collum structureless, internally with a poorly developed ringleiste. Girdle smooth, composed of several copulae.



FIGURES 10–16. *Aulacoseira khankaica*, SEM, external view. Scales: 2 μm . Fig. 10. Mantle of the linking valves. Fig. 11. Mantle of the linking valves and location of external rimoportula openings (white arrow) and detail of the linking spines. Fig. 12. Mantle of the linking valves and location of external rimoportulae openings (white arrows) and internal rimoportulae openings (black arrows) on the ringleist. Fig. 13. External rimoportula openings (white arrow). Fig. 14. External valve view. Fig. 15. Oblique view of the linking valves. Fig. 16. Detail of girdle with copulae.

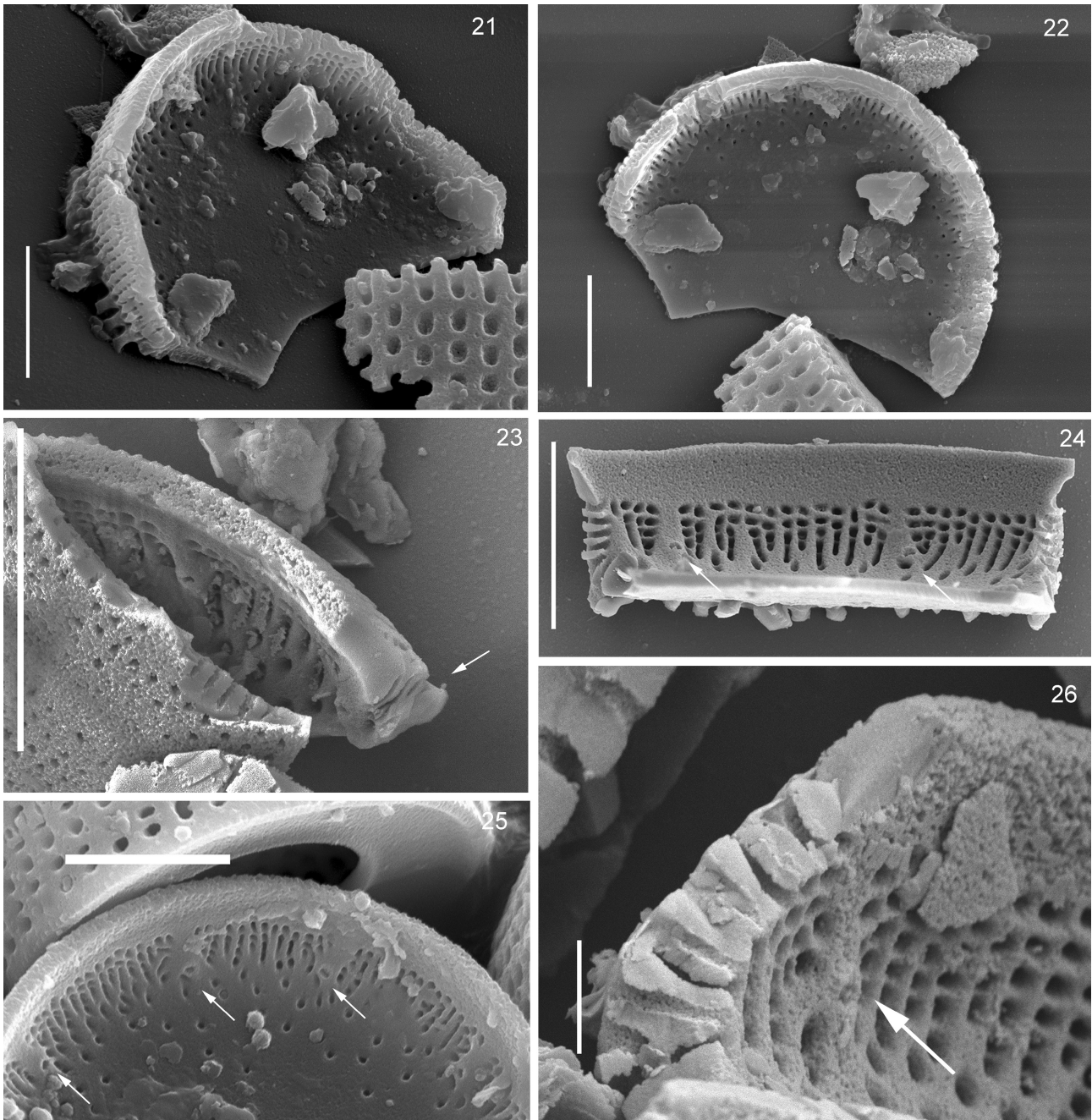
SEM. Internal views (Figs 17–26). Inner mantle surface with straight perivalvar rows of areolae. Areolae circular to irregularly shaped, open, lacking external coverings, though covered by a thin silica layer in some specimens. External mantle surface otherwise smooth, without discernible perivalvar costae. Rimoportulae (8–10 per valve) located on the middle of the mantle forming a ring. Internal opening of each rimoportula: circular opening of the tube on the ringleiste, connected to a wide rib running the length of the mantle. Rimoportulae sessile, radiately oriented in relation to the valve margin. The ringleiste narrow and shallow. Internal valve surface occasionally covered by a thin silica layer.



FIGURES 17–20. *Aulacoseira khankaica*, SEM. internal view. Scales: 5 μm . Fig. 17. Internal whole view of valve: rimoportulae (white arrows). Fig. 18. Oblique view of Fig. 17. Fig. 19. Valve covered by a thin silica layer. Fig. 20. Broken valve, cross section areolae.

Etymology. This species name refers to the area of its discovery—the Lake Khanka coast in Primorsky Kray, Russian Far East.

Distribution. As yet known only from the type locality.



FIGURES 21–26. *Aulacoseira khankaica*, SEM. Scales: 5 μm (Figs 21, 22, 24–26), 1 μm (Fig. 23). Fig. 21. Broken valve, showing cross section of areolae. Fig. 22. Internal view of valve. Fig. 23. Broken valve, rimoportula and cross section of its canal (arrow). Figs 24, 26. Broken valve, showing cross section of areolae; rimoportulae (white arrows). Fig. 25. Internal view of valve; rimoportulae (white arrows).

Discussion

Aulacoseira khankaica sp. nov. is mainly characterized by short filaments, fine areolae represented in deeply recessed pervalvar rows, spatulate linking spines, a narrow ringleiste, and a ring of rimoportulae. The combination of rimoportulae located near the valve face/mantle junction and areolae arranged in deep rows appears to be distinctive to this species.

Several species share a narrow ringleiste and rimoportulae located on the valve face, e.g., the fossil *Aulacoseira akitaensis* H. Tanaka and *A. virginvalleyana* Siver, as well as subfossil to modern *A. laevissima* (Grunow) Krammer, *A. tenella* (Nygaard) Simonsen, modern *A. perglabra* (Østrup) Haworth and others (Table 1).

TABLE 1. Morphological comparison of *Aulacoseira khankaica* sp. nov. and similar species.

	<i>Aulacoseira khankaica</i> sp. nov.	<i>Aulacoseira akitaensis</i>	<i>Aulacoseira virginvalleyana</i>	<i>Aulacoseira laevissima</i>	<i>Aulacoseira tenella</i>	<i>Aulacoseira perglabra</i>
Valve diameter, μm	9.8–20.2	10–18	8.8–16.5	6–17	5.1–5.9	8–17
Mantle height, μm	2.8–7.1	2.5–3	2.3–5.8	5–10	3.0–4.2	3–4
Height: Diameter range/mean, μm	1.6–4.6/2.36		0.17–0.54/0.29			
Areolae on valve face	randomly distributed	randomly distributed	randomly distributed	fine, irregularly spaced pori	randomly distributed	from one ring at the valve margin to pattern consisted of coarser puncta on the whole surface
Linking spines	short, length of 1.27–3.13 (mean 2.43), spatulate, widened on tops	short spatulate interlocking	flat outer surface flush with the mantle, increase in width, length of 1.7	back-hooked linking spines	shot conical	short, pointed
Pervalvar rows of areolae (in 10 μm)	18–27	12		22–28		20–28
Areolae in a row (in 10 μm)	20–24	2–3	11–14	23–30		
Orientation of the pervalvar rows of areolae	straight	straight	straight	straight (or slightly dextrorse)	straight	straight
Number of areolae per stria	1	1	1	1	1–2	1
Areolae shape	rounded, fine areolae	rounded	circular to irregularly-shaped	rounded, very fine areolae	rounded to elliptical	rounded
Ringleist	narrow and shallow	narrow and shallow	very shallow to lacking and difficult to discern on most specimens	poorly developed ringleiste internally	shallow	
Rimoportula number and position	8–10 near the valve face mantle junction	4–7 in a submarginal zone forming a ring	multiple simple rimoportulae, with 3 or more per valve, found at the junction of the valve face and mantle	not observed	1–2 near the ringleiste	1 small internal slit of sessile rimoportula
Chain length	2–4 cells		long filaments	tightly linked into shorter or longer chains	2 cells	long chain
Location; age	Russia, Khanka Basin, Primorsky Krai; fossil, Novokachalinskay Formation, Middle Miocene	Japan, Hinokinaimata-Zawa, Senboku City, Akita; Fossil, Pliocene	USA, Nevada; fossil, Virgin Valley Formation Middle Miocene	Romania, Scotland Germany, Bavaria, modern	Germany, Lake Gribso, Denmark; subfossil-modern	Germany, Lake Madum, Denmark; modern
Reference	this study	Houk <i>et al.</i> 2017	Siver 2025	Buczkó <i>et al.</i> 2010	Houk <i>et al.</i> 2017	Buczkó <i>et al.</i> 2010

Among these, *Aulacoseira khankaica* is most morphologically similar to *A. akitaensis* (Houk *et al.* 2017) and *A. virginvalleyana* (Siver 2025). These three species appear to be closely aligned, sharing similar valve size, straight striae, a shallow ringleiste, and a ring of rimoportulae with tubes. Both *A. akitaensis* (Pliocene, Japan) and *A. virginvalleyana*

(Middle Miocene, Nevada, USA) are fossil taxa, which further aligns them with the Miocene *A. khankaica*. The main differences between *A. khankaica* and *A. akitaensis* lie in the morphology of the spines, the morphology of the areolae on the mantle and the rimoportulae. The relatively short and spatula-shaped spines with a broadened distal end linking spines observed in *A. khankaica* specimens have not been reported for *A. akitaensis* or *A. virginvalleyana*. However, *A. virginvalleyana* specimens have separating spines that are wider at the base and tapered, with either a pointed or slightly dichotomous tip. In contrast, the spines of *A. akitaensis* specimens are more variable in shape, being basically spatulate, but sometimes quite slender.

The areolation pattern of the valve face is significantly different. Valves of *A. khankaica* have small areolae representing deep rows (18–27 rows in 10 µm, 20–24 areolae in 10 µm per row). Most valves of *A. akitaensis* and *A. virginvalleyana*, typically feature only two circumferential rows of areolae on the mantle. While the general organization of the rimoportulae is comparable among these species, their precise position differs. The rimoportulae openings on *A. khankaica* specimens (8–10 per valve) were located in the middle of the mantle, but rimoportulae on *A. akitaensis* (4–7 per valve) were located on the valve face, usually in a submarginal zone, and *A. virginvalleyana* (3 or more per valve) was found at the junction of the valve face and mantle.

In *A. khankaica*, the rimoportula consists of a circular opening at the end of a tube positioned on the ringleiste. In *A. akitaensis*, the rimoportula canals form thick, raised tubes on the inner valve surface that extend toward the valve margin. Each rimoportula in *A. virginvalleyana* ends in a reinforced circular pore and is connected to a wide rib that runs the entire length of the mantle.

It is worth noting that since the presence of a well-developed ringleiste is a defining character for *Aulacoseira*, there is a question of whether *A. khankaica*, with its shallow and slight ringleiste, truly belongs to the genus. However, several other species also exhibit an undeveloped or non-evident ringleiste. These include Miocene taxa such as *A. akitaensis* H. Tanaka, *A. fukushimae* H. Tanaka, and *A. virginvalleyana* Siver, subfossil-modern—*A. laevisissima* (Grunow) Krammer, *A. tenella* (Nygaard) Simonsen, and modern—*A. lacustris* (Grunow in Van Heurck) Krammer, *A. nivalis* (W. Smith) English et Potapova, *A. perglabra* (Østrup) Haworth, *A. pfaffiana* (Reinsch) Krammer (Houk et al. 2017; Siver 2025). Therefore, as the suite of characters as a whole aligns with the diagnosis of *Aulacoseira*, *A. khankaica* is confidently assigned to this genus.

In addition to the fact that both *A. khankaica* and *A. laevisissima* have a slight ringleiste, they have similar, very fine areolae on the external valve view (Buczko et al. 2010; Houk et al. 2017). However, *A. khankaica* specimens are distinguished by areolae arranged in deep rows, and a different form of their spines. Specifically *A. khankaica* is slightly shot, spatulate, and widened on top, linking spines, whereas *A. laevisissima* has back-hooked spines.

Although a shallow ringleiste has also been described in *A. tenella*, *A. perglabra* (Houk et al. 2017) and other species, they are easily distinguished from *A. khankaica* by all other morphological characters.

Furthermore, some genera share a narrow ringleiste and rimoportulae located on the valve face, e.g., such as the fossil genus *Alveolophora* Moisseeva et Nevretdinova. *Aulacoseira khankaica* may be closely related to *Alv. tscheremissinovae* (Khursevich) Khursevich, notably both species occur in the Middle Miocene Novokachalinskaya Formation.

They share similar valve dimensions, a narrow ringleiste as seen under light microscope, and a ring of rimoportulae located near the valve face junction.

However, the diagnosis of *Alveolophora* specifies that alveolae, pseudoalveolae, and costae are visible on the internal valve surface (Moisseeva & Nevretdinova 1990; Usoltseva 2022; Avramenko & Cherepanova 2023). In contrast, *A. khankaica* displays areolae in cross-sections, and no alveolus-like structures are present. *Alveolophora* is an extinct freshwater planktonic genus that existed from the Late Eocene to the end of the Miocene (Moisseeva & Nevretdinova 1990). We suggest that the appearance of the genus *Alveolophora* may indicate a possible evolutionary relationship within the Aulacoseiraceae.

Conclusion

In summary, the abundance of freshwater diatoms in the Novokachalinskaya Formation indicates the widespread presence of fluvial and lacustrine systems in this region during the Miocene. The accumulation of these deposits corresponds to the MMCO, characterized by a peak in global mean temperatures followed by a cooling trend (Zachos et al. 2008; Likhacheva et al. 2009). These aquatic ecosystems supported a diverse diatom flora dominated by representatives of the genus *Aulacoseira*, including the new species described here.

Aulacoseira is among the oldest known freshwater diatom genus, reported to go back at least to the Cretaceous (Khursevich 1995; Krebs 1994), and it became more diversified and widespread during the Cenozoic (Siver & Velez 2023). *Aulacoseira* still remains a taxonomically complex genus due to its relatively limited number of diagnostic characters (Crawford & Likhoshway 2002). Moreover, most of its can be studied using light microscopy (valve diameter, mantle height, orientation of pervalvar rows of areolae, and details of the spines, especially separating spines). However, taxonomically important ultrastructural details, such as the morphology of the valve face, structure of the ringleiste, shape of linking spines, and nature of the mantle areolae, can only be reliably documented using SEM (Krammer 1991). SEM analysis was decisive in establishing of the taxonomic status of *Aulacoseira khankaica* sp. nov.

In conclusion, seven *Aulacoseira* taxa were identified in the Middle Miocene of Primorsky Krai. This study contributes to our understanding of centric diatom diversity during the MMCO. Further observations of fossil taxa will help clarify the phylogenetic relationships, evolutionary processes, and biogeography of this genus.

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