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RESEARCH ARTICLE

Genus *Spiniferomonas* (Chrysophyceae, Chromulinales) in Eastern Siberian reservoirs

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Abstract

Species belonging to the genus *Spiniferomonas* are commonly found in continental reservoirs in northern latitudes and may serve as indicators of climate change. A recent revision of the genus has identified 21 morphologically confirmed species of *Spiniferomonas*, with 17 species inhabiting reservoirs in Eastern Siberia. Detailed descriptions of these species are provided, along with their morphological characteristics supported by microphotographs and original distribution data in Eastern Siberia's reservoirs.

Keywords

Chrysophyceae, *Spiniferomonas*, Eastern Siberia

Introduction

Silica-scaled chrysophytes are a diverse group of heterokont protists including the orders Paraphysomonadales (genera *Lepidochromonas* and *Paraphysomonas*), Chromulinales (*Chrysosphaerella* and *Spiniferomonas*), and Synurales (*Mallomonas*, *Synura*, and *Neotessella*) in the Chrysophyceae class (Škaloudová and Škaloud 2013; Pusztai et al. 2023). The taxonomy of these microeukaryotes is based on the detection of the ultrastructure of siliceous elements (scales, spines, and bristles) using scanning and transmission electron microscopy methods. However, species with less obvious morphological features often require molecular methods for accurate identification. Notably, for the highly diverse genera *Mallomonas* (approximately 220 species), *Synura* (approximately 50 species), and *Paraphysomonas* (approximately 50 species), an agreement between the morphological species concept and molecular phylogenetic data has been demonstrated (Kristiansen and Preisig 2007; Scoble and Cavalier-Smith 2014; Siver et al. 2015; Škaloud et al. 2020). Cultivation challenges have limited the availability of molecular phylogenetic data for the genera *Lepidochromonas* and *Chrysosphaerella*, with only a few species studied (Škaloudová and Škaloud 2013; Scoble and Cavalier-Smith 2014). Recently, molecular phylogenetic data for *Spiniferomonas trioralis* have shed light on the phylogenetic position of the genus *Spiniferomonas* (Pusztai et al. 2023). Thus, Pusztai et al. (2023) provided compelling evidence supporting the differentiation between *Chrysosphaerella coronacircumspina* and *Spiniferomonas trioralis* taxa. Previously, a key criterion for distinguishing these genera was the simpler arrangement of the base plate in *Spiniferomonas* species compared to *Chrysosphaerella* (Takahashi 1973). This distinction is true for most species of the genus *Spiniferomonas*. However, in the genus *Spiniferomonas*, there is variability in the morphology of the spine and its base plate. Spiniferomonas spines can exhibit flattened, tubular, or triangular shaft shapes in the transverse section. According to Voloshko (2008), species have been categorized into three distinct sections – *Tubulares*, *Planae*, and *Trigonae* (Voloshko 2008). However, according to the International Code of Nomenclature, the *Tubulares* section should be renamed *Spiniferomonas* sect. *Spiniferomonas*, since the division of the genus that includes the type (in our case, *S. bourrellyi*) is called the same as the genus. *Spiniferomonas septispina* Nicholls, a member of the *Spiniferomonas* section, possesses a spine base structure resembling that of *Chrysosphaerella annulata* Kristiansen and Tong. Based on this resemblance, Kristiansen and Tong (1989) suggested classifying species with a double base plate or a septum with an adjacent pore, such as *Spiniferomonas septispina*, under the genus *Chrysosphaerella*. Therefore, the phylogenetic placement of these two species remains enigmatic. Without genetic data supporting its classification in the genus *Chrysosphaerella*, we continue to consider it as *Spiniferomonas septispina*.

Owing to their relatively small cell sizes and delicate scales and spines, which may be lost during sampling, data on the distribution of *Spiniferomonas* species remain limited. However, our research highlights their important role in the phytoplankton community of northern latitudes, such as in the lakes of Yakutia, both during the subglacial and open water periods (Bessudova et al. 2019; Bessudova et al. 2023). As mixotrophs, they can thrive under light-restricted conditions under ice, providing them with a competitive advantage amidst changing environmental factors (Bessudova et al. 2023). In a recent study performed in a natural model system with a water temperature gradient – the Lake Baikal–Irkutsk Reservoir – changes in the species composition of silica-scaled chrysophytes were observed, notably owing to the presence of *Spiniferomonas* species. These changes correlated with increasing water temperatures over three seasons. This suggests that certain members of the genus *Spiniferomonas* could serve as indicators of rising water temperatures, a crucial observation in the context of ongoing climate changes. Meanwhile, an intriguing aspect of their distribution is the relatively low species diversity observed in tropical reservoirs (Gusev et al. 2022a; b), contrasted with higher diversity in northern reservoirs (Siver et al. 2005; Bessudova et al. 2022). A previous study performed in northern Russian reservoirs identified 12 species of the genus *Spiniferomonas* (Voloshko 2013). This article presents the results of a floristic study focusing on the species from the *Spiniferomonas* genus from reservoirs in Eastern Siberia. It includes updated descriptions, new micrographs, and distribution data detailing the occurrence of species in reservoirs across Eastern Siberia.

Materials and methods

The species of the *Spiniferomonas* genus described in this study were collected by the author from reservoir samples in Eastern Siberia between 2009 and 2024. To examine the species' distribution, both original data and literature sources on the diversity and distribution of silica-scaled chrysophytes, based on electron microscopy methods, were analyzed (Balonov and Kuzmina 1986; Kristiansen et al. 1997; Gusev 2016; Gusev et al. 2018). The studied reservoirs in Eastern Siberia include reservoirs from temperate, subarctic, and Arctic latitudes.

To detect cells of the genus *Spiniferomonas*, 7–20 mL of a batometric sample was passed through a 13-mm-diameter filter with 0.8 µm pores (Whatman, part of GE HealthCare, Chicago, IL, USA). The filter with the test material was dried at room temperature, attached to SEM stubs using double-sided tape, and stored at room temperature until arrival at the laboratory. The filter was then coated with gold in an SDC 004 vacuum evaporator (SD 004 Balzers, Liechtenstein) and examined using a QUANTA 200 scanning electron microscopy (SEM) instrument (FEI Company, Hillsboro, OR, USA). Transmission electron microscopy (TEM) was also used to detect scales and spines.

Samples were transferred to 1.5 mL Eppendorf tubes and centrifuged at 13,400 rpm for 10 minutes using the MiniSpin centrifuge (Eppendorf, Germany). The supernatant was removed with a pipette, and deionized water was added to the precipitate. This procedure was repeated three times. Then, 30% H_2O_2 was added to the precipitate, and the sample was heated at 80°C for 5 h in a thermostat. Next, the precipitate was washed with deionized water and centrifuged five times. The washed samples were pipetted onto a 3-mm-diameter grid covered with Formvar support, dried at room temperature, and examined using a transmission electron microscope (LEO 906E; Carl Zeiss, Germany).

Results

As a result of the study of the genus *Spiniferomonas* based on the morphology of scales and spines, 17 out of the 21 reliably known species were identified in the reservoirs of Eastern Siberia (Table 1).

Descriptions of these 17 species are provided below. The distribution of species across reservoirs and areas in Eastern Siberia is detailed in Table 2.

Table 1. Alphabetical checklist of all previously described species of the genus *Spiniferomonas*. "*" indicates the species not found in the reservoirs of Eastern Siberia during this analysis.

Taxon	Section	Taxonomic status
S. abei Takahashi 1973	Planae	Accepted
S. abrupta Nielsen 1994	Trigonae	Accepted
*S. alata** Takahashi 1973	Trigonae	Accepted
S. bilacunosa Takahashi 1973	Trigonae	Accepted
S. bourrellyi Takahashi 1973	Spiniferomonas	Accepted
*S. breakneckii** Siver 1987	Trigonae	Accepted
S. cetrata Hansen 1996	Trigonae	no (probably = *S. involuta*)
S. conica Takahashi 1973	Spiniferomonas	Accepted
S. cornutus Balonov 1978	Trigonae	Accepted
S. crucigera Takahashi 1973	Trigonae	Accepted
S. genuiformis Wujek & Bland 1988	Trigonae	no (= *S. alata*; Nicholls 1989)
S. grandis Vigna 1981	–	not valid
*S. hamata** Ito & Takahashi 1982	Trigonae	Accepted
S. heterospina Bessudova, Firsova & Kopyrina 2023	Trigonae	Accepted
S. involuta Jacobsen 1985	Trigonae	Accepted
S. minuta Nicholls 1984	Trigonae	Accepted
*S. nichollsii** Ito & Takahashi 1982	Trigonae	Accepted
S. pectinata Stefanová & Kalina 1992	–	not valid
S. septispina Nicholls 1984	Spiniferomons	Accepted
S. serrata Nicholls 1981	Trigonae	Accepted
S. silverensis Nicholls 1984	Trigonae	Accepted
S. takahashii Nicholls 1981	Trigonae	Accepted
S. triangularis Siver 1988	Trigonae	Accepted
S. trioralis Takahashi 1973	Trigonae	Accepted
S. trioralis f. *cuspidata* Balanov 1978	Trigonae	Accepted

Table 2. Distribution of *Spiniferomonas* in the reservoirs of Eastern Siberia. Descriptions of the areas and reservoirs are provided below

№	Taxon	Area/Reservoir																																				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
1	*Spiniferomonas abei*	+		+				+	+				+										+				+											
2	*S. abrupta*									+			+									+			+	+	+											
3	*S. bilacunosa*		+				+						+				+						+					+		+			+					
4	*S. bourrellyi*			+	+			+	+	+	+	+	+	+				+		+			+		+	+	+	+	+	+			+			+		
5	*S. conica*			+									+	+																								
6	*S. cornuta*			+	+			+		+	+	+	+	+					+	+			+			+	+			+			+					
7	*S. crucigera*																													+								
8	*S. heterospina*												+		+																							
9	*S.* cf. *involuta*							+																														
10	*S. minuta*			+				+																						+			+					
11	*S. septispina*																								+	+												
12	*S. serrata*			+	+	+		+		+			+	+			+	+		+			+				+	+				+	+					
13	*S. silverensis*			+																+			+			+	+											
14	*S. takahashii*			+									+													+	+											
15	*S. triangularis*							+										+	+							+	+			+								
16	*S. trioralis*	+		+	+	+		+	+	+	+	+	+	+		+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
17	*S. trioralis* f. *cuspidata*			+				+			+	+	+	+				+		+			+		+	+	+	+				+	+					
	Total	2	1	10	4	2	1	9	3	5	4	4	11	6	1	1	3	5	3	6	1	1	8	1	6	9	9	5	2	7	1	3	8	1	1	2	1	1

Notes: 1 – reservoirs of Kotelny Island (Bessudova et al. 2023); 2 – the mouth of the Anabar River (Gusev et al. 2018); 3 – the mouth of the Olenek River (Bessudova et al. 2021); 4 – the mouth of the Yana River (Bessudova et al. 2021); 5 – the mouth of the Kolyma River (Bessudova et al. 2021); 6 – Kolyma Reservoir (Gusev et al. 2018); 7 – Sevastyan River basin, Tiksi (Bessudova et al. 2022); 8 – Horogor River basin lake, Tiksi (Bessudova et al. 2022); 9 – Hatys-Yuryakh River basin, Tiksi (Bessudova et al. 2022); 10 – Lake Ulu (Firsova et al. 2024 in press); 11 – Lake Myamichi (Firsova et al. 2024 in press); 12 – Lake Labynkyr (Bessudova et al. 2019; 2023); 13 – Lake Vorota (Bessudova et al. 2019; 2023); 14 – Lake Vodorazdelnoe (Firsova et al. 2024 in press); 15 – Lake Toko (Gusev et al. 2018); 16 – Toko Lake area (Gusev et al. 2018); 17 – the mouth of the Upper Angara River (Bessudova et al. 2018); 18 – the mouth of the Kicher River (Bessudova et al. 2018); 19 – Angara-Kichera Delta (Bessudova et al. 2018); 20 – Frolikha Lake (Gusev 2016); 21 – the mouth of the Barguzin River (Bessudova et al. 2018; 2020); 22 – the mouth of the Selenga River (Bessudova et al. 2018; 2020); 23 – the mouth of the Chikoy River (Bessudova et al. 2020); 24 – Lake Baikal (Bessudova et al. 2017); 25 – Irkutsk Reservoir (Bessudova et al. 2023; 2024 in press); 26 – Boguchany Reservoir (Bessudova and Likhoshway 2017). Continued on the next page.

Continued from the previous page. 27 – The Khantay Reservoir and reservoirs located nearby (Balonov and Kuzmina 1986); 28 – The lower part of the Yenisei River, the Yenisei Bay and the coastal part of the Kara Sea (Bessudova et al. 2015); 29 – an unnamed lake near the mouth of the Bolshaya Denezhkina River, natural monument Ledyanaya Gora, a basin of the Lower Yenisei (Bessudova et al. 2018); 30 – an unnamed lake near the village of Karaul, the basin of the Lower Yenisei (Bessudova et al. 2018); 31 – Belye Peski Lake, Ladyginsky Yary tract, on the right bank of the Yenisei River above the mouth of the Kokora River, the basin of the Lower Yenisei (Bessudova et al. 2018); 32 – lake near the village of Sopochnaya Karga, basin of the Lower Yenisei (Bessudova et al. 2018); 33 – Srednee Lake, Sibiryakova Island (Bessudova et al. 2018); 34 – Engelhardt Lake, Taimyr Peninsula (Kristiansen et al. 1997); 35 – an unnamed lake northwest of the city of Khatanga, Taimyr Peninsula (Kristiansen et al. 1997); 36 – an unnamed lake north of the city of Khatanga, Taimyr Peninsula (Kristiansen et al. 1997); 37 – Lake Taimyr, Taimyr Peninsula (Kristiansen et al. 1997).

Genus *Spiniferomonas* Takahashi 1973: 76

Chromophysomonas Preisig et Hibberd 1982

In water samples observed under a light microscope, spherical cells, 3–12 μm in diameter, were noted with spines extending from them, along with 1–2 chloroplasts, 1–2 contractile vacuoles, and 1 stigma (Voloshko 2013). When observed under an electron microscope, the air-dried cells on filters appear burst and flattened, leaving behind numerous silicon elements of two types: plate scales (which range from circular to elliptical) and spines (which consist of a base plate or funnel-shaped base with an extending shaft). Depending on the shape of the shaft in the transverse section – flattened, tubular, or triangular – the species are divided into three sections.

Section *Planae* Voloshko 2008: 1256

The *Planae* section includes species with a flattened shaft of the spine tapered towards the apex.

Spiniferomonas abei Takahashi 1973: 77 (Figs 1 A–C)
Chrysosphaerellam parva Asmund 1973
Spiniferomonas abei (Takahashi) Preisig et Hibbered 1982

The cell is spherical to ovoid, measuring 3–10 μm in diameter, with numerous 1.5–8.7-μm-long spines. Each spine consists of a flat, circular base plate, 0.55–0.75 μm in diameter, from which a flattened shaft extends, terminating in a sharp apex. There are two types of spines: one with a shaft that tapers abruptly to a sharp apex and extends into a long needle-like extension (up to 3 μm long) and another with a shaft that tapers gradually to a tapered apex. The plate scales are elliptical, measuring 1.3–3 μm in length and 0.7–1.7 μm in width, with thickened margins creating a central elliptical lacuna.

Stomatocysts are spherical, 3–7 μm in diameter (Voloshko 2013).

Section *Spiniferomonas*

The *Spiniferomonas* section includes species with tubular, tapered, and roundish spines when viewed in the transverse section.

Spiniferomonas bourrellyi Takahashi 1973: 76 (Figs 2 A–F)
S. andersonii Green 1979
Paraphysomonas bourrellyi (Takahashi) Preisig et Hibbered 1982

The cells are spherical to oval, measuring 3–10 μm in diameter, with 3–8 straight, cone-shaped spines, 2.2–22 μm long. The funnel-shaped base plate, 1.2–3.6 μm in diameter, tapers distally to a pointed apex or slightly bifurcated tip. The plate scales are flat, ranging from circular to elliptical, 0.7–1.5 μm in length and 0.5–1.0 μm in width, with thickened margins creating a central elliptical lacuna.

Stomatocysts are obovate, measuring 5 μm in length and 7 μm in width. The stomatocyst collar complex consists of a conical pair, 0.5 μm in diameter and 0.3 μm deep, located in a narrow annulus. The primary collar, with a sharp or rounded apex, is 2.6–3.5 μm in diameter. An unornamented transition region separates the primary collar from the low secondary collar, which is 5–6 μm in diameter. Below the secondary collar is a very low, regular reticulum of rounded lacunae measuring 0.5–1 μm in diameter (Voloshko 2013).

Remarks: In TEM images, areas of reduced density with square and rectangular shapes are noticeable at the base of the funnel-shaped plates of some spines (Fig. 2E).

Spiniferomonas conica Takahashi 1973: 78 (Figs 1 G–J)

The cells are spherical, 3–4 μm in diameter, with 2–8 slightly curved, cone-shaped spines that measure 5.9–10.3 μm in length. The bell-shaped base plate, 1.8–2.4 μm in diameter and 1.2–3.6 μm wide, tapers distally to a slightly bifurcated tip. Typically, a curvature of the spine is observed at the transition from the cone-shaped base plate to the shaft. The plate scales are circular or elliptical, 0.65–1 μm in length and 0.45–0.75 μm in width, with thickened margins creating a central elliptical lacuna.

Stomatocysts are unknown.

Remarks: On some spines, located approximately 1.3–1.8 μm from the base plate, there is a rounded pore measuring approximately 0.08–0.25 μm in diameter (Fig. 1 G, H).

Spiniferomonas septispina Nicholls 1984: 104–105, 107 (Figs 2 G–J)
Paraphysomonas spinapunctata Wujek et Gardiner 1985
Chrysosphaerella septispina (Nicholls) Kristiansen et Tong 1989

The cells are spherical, up to 10 μm in diameter, with 5–12 cone-shaped, narrowed spines that measure 6–18 μm in length. Each spine consists of a wide conical base plate, 3–4.5 μm in diameter, separated from the shaft by a septum. Positioned above the septum, in the shaft wall, approximately 0.1–1 μm from the base plate, there is a rounded pore approximately 0.2 μm in diameter. The tip of the spine is bifurcated. The plate scales are flat and elliptical, ranging from 1.5–2.3 μm in length and 2.3–3.5 μm in width, with a thickened rim along the edge measuring 0.05 μm wide. In TEM images, the submarginal ridge is poorly developed and intermittent, with short curved ribs and shallow depressions.

Stomatocysts are spherical, measuring 6.5 μm in diameter (Fig. 2 G). The entire surface is irregularly covered with short, petal-like ridges extending along the apical border (approximately 100 in total), which are 0.4–0.5 μm high and 0.4–1.5 μm long. Additionally, there are small spiny outgrowths (Firsova et al. 2017).

Section *Trigonae* Voloshko 2008: 1256

The *Trigonae* section comprises species with spines that have a triangular shaft in the transverse section (Voloshko 2013).

Spiniferomonas abrupta Nielsen 1994: 478 (Figs 1 D–F)

The cells are spherical, measuring 2.2–4 μm in diameter, with 7–16 slightly curved spines that are 4.3–7 μm long. Each spine consists of a circular, flat base plate, 0.4–0.6 μm in diameter, and a triangular shaft extending from the center of the base plate, abruptly terminating at the apex. The plate scales are circular or slightly elliptical, measuring 0.8–1.8 μm in length and 0.9–2.8 μm in width, with a thickened margin that creates a central circular or elliptical lacuna.

Stomatocysts are unknown.

Spiniferomonas bilacunosa Takahashi 1973: 78 (Figs 3 A, B)
Chrysosphaerella parva Asmund 1973
Chromophysomonas bilacunosa (Takahashi) Preisig et Hibberd 1982

The cells are spherical, 4–6 μm in diameter, with 8–15 straight spines that measure 4–8.4 μm long. Each spine consists of a flat, circular base plate, 1–1.2 μm in diameter, and a triangular shaft extending from the center of the base plate, terminating in a tapered apex. There are two types of plate scales: smaller elliptical scales (0.8–1.1 μm in length and 0.6–0.8 μm in width, with two rounded lacunae separated by a median rib) and larger, circular scales (1–1.4 μm in diameter, with a single lacuna). Some cells also exhibit a third type of scales: small elliptical scales, 0.8–1.1 μm in length and 0.6–0.8 μm in width, with two rounded lacunae separated by a median rib, along with a single small nodule located near the middle of the median rib.

Stomatocysts are unknown.

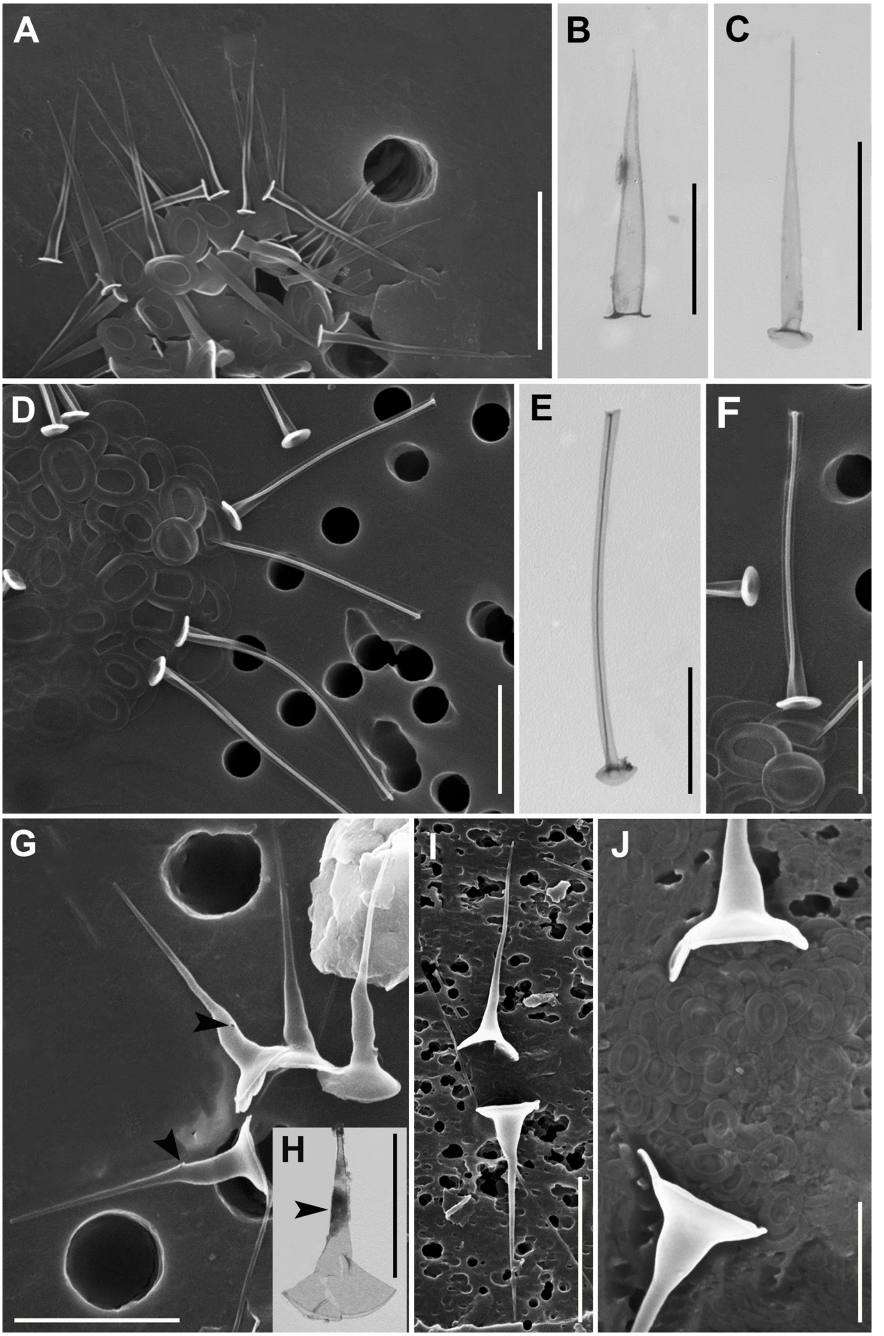

Figure 1. *Spiniferomonas* (**A**, **D**, **F**, **G**, **I**, **J** – SEM; **B**, **C**, **E**, **H** – TEM). **A–C** – *S. abei* (**A** – plate and spine scales; **B**, **C** – individual spines); **D–F** – *S. abrupta* (**D** – plate and spine scales; **E** – single spines; **F** – plate scales and single spine); **G–J** – *S. conica* (**G** – spine scales, on the bell-shaped base plate, the arrow shows the hole, from Lake Labynkyr; **H** – single spine scales with a hole, from the basin of the Ob River; **I** – whole cell with plate and spine scales; **J** – bell-shaped base plate and plate scales). Scale bars: **B**, **C**, **E**, **F**, **H**, **J** – 2 μm; **A**, **D**, **G**, **I** – 5 μm.

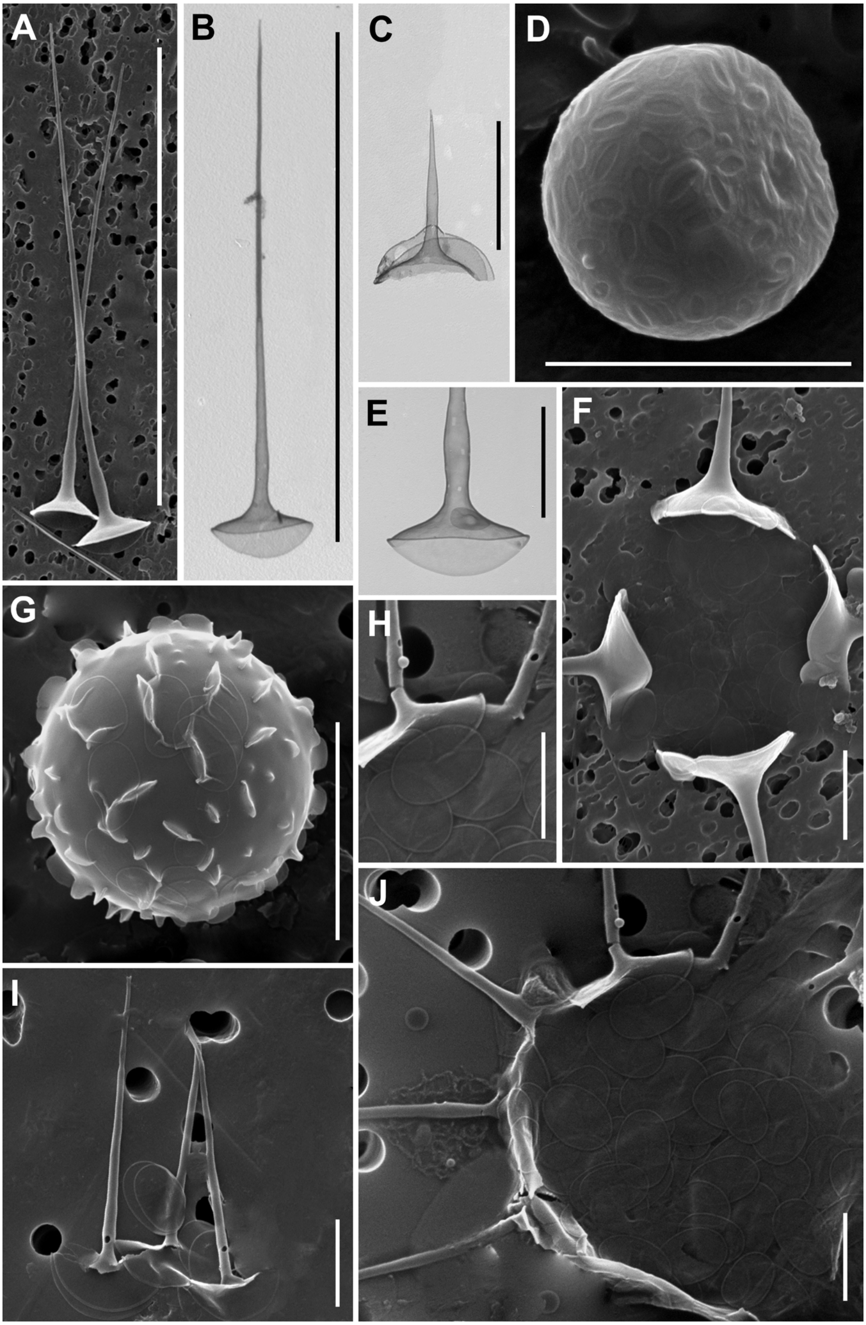

Figure 2. *Spiniferomonas* (**A**, **D**, **F–J** – SEM; **B**, **C**, **E** – TEM). **A–F** – *S. bourrellyi* (**A**, **B** – individual long spines, **C** – individual short spine, from the mouth of the Olenek River; **D** – stomatocyst covered with plate scales; **E** – funnel-shaped base plate with scale, areas of square and rectangular shape with reduced density on the thorn shaft; **F** – plate scales and bases of four spines). Continued on the next page.

Figure 2. Continued from the previous page. **G–J** – *S. septispina* (**G** – stomatocyst covered with plate scales; **H** – plate scales and a funnel-shaped base plate of the spine, an pore on the shaft above the septum is showing; **I** – individual spine and plate scales; **J** – plate and spine scales. Scale bars: **C**, **E**, **F**, **H–J** – 2 µm; **D**, **G** – 5 µm; **A**, **B** – 20 µm.

Spiniferomonas cornuta Balonov 1978: 1644–1645 (Figs 3 C–F)
Chromophysomonas cornuta (Balonov) Preisig et Hibberd 1983

The cells are spherical, 2.5–6 µm in diameter, with 6–14 straight or slightly curved spines that are 4–6 µm in length. Each spine consists of a flat, circular, or saucer-shaped base plate measuring 0.35–0.8 µm in diameter, with a triangular shaft extending from the center of the base plate and terminating in a tapered apex. There are two types of plate scales: smaller elliptical scales (1.1–1.4 µm in length and 0.6–0.8 µm in width, with two lacunae separated by a median rib and two nodules located at each end of the median rib) and larger, elliptical scales (1.8–2.2 µm in length and 1.4–1.6 µm in width, with a single lacuna).

Stomatocysts are unknown.

Remarks: Some cells exhibit a third type of scales—small elliptical, measuring 1.1–1.4 µm in length and 0.6–0.8 µm in width—with two lacunae and a single nodule located on one side of the median rib (Fig. 3 E).

Spiniferomonas crucigera Takahashi 1973: 78 (Figs 4 H, I)

The cells are spherical, measuring 3 µm in diameter, with 4–14 curved spines that are 3–4 µm long. Each spine consists of a flat, circular base plate, 0.4–0.55 µm in diameter, and a triangular shaft extending from the center of the base plate, terminating in a tapered apex. There are two types of plate scales: small, elliptical scales (0.7–1 µm in length and 0.4–0.7 µm in width, with two lacunae separated by a median rib and four nodules—two at each end of the median rib) and large, elliptical scales (measuring 0.7–1.6 µm in length and 0.6–1 µm in width, with a single lacuna).

Stomatocysts are unknown.

Remark: On some plate scales with two lacunae, the number of nodules varies from 4 to 6.

Spiniferomonas heterospina Bessudova, Firsova and Kopyrina 2023: 8 (Figs 5 A–D)

The cells are spherical, 4.5–8.8 µm in diameter, with 14–24 straight spines categorized into two size ranges: shorter ones measuring 0.45–2.7 µm long and longer ones measuring 5.4–8.7 µm long. Each spine consists of a circular base plate, 1.4–2.3 µm in diameter on the apical side, with a thickened margin resembling a lacuna of plate scales, approximately 0.25 µm wide on the basal side, forming a saucer-shaped base. A triangular shaft extends from the center of the base plate, terminating in a tapered apex. The plate scales are elliptical, measuring 0.9–1.1 μm in length and 1.3–1.6 μm in width, with a thickened margin that creates a central elliptical lacuna.

Stomatocysts are unknown.

Spiniferomonas involuta (Jacobsen) Preisig et Hibberd (Fig. 3 G)
Chromophysomonas involuta Jacobsen 1985: 390

The cell measures 3–4.5 μm in diameter when air-dried with many straight spines that are 0.8–1.3 (up to 2.6) μm long. Each spine consists of a circular to slightly elliptical base plate measuring 0.7–1.7 μm in diameter, with a distinct, upturned rim. A short triangular shaft extends from the center of the base plate, terminating in a tapered apex. The plate scales are elliptical, measuring 0.9–1.2 μm in length and 0.7–0.9 μm in width, with a thickened margin that creates a central elliptical lacuna and a thickened border. Occasionally, plate scales with a decentrally placed median rib are observed (Jacobsen, 1985).

Stomatocysts are unknown.

Spiniferomonas minuta Nicholls 1984: 2331 (Figs 4 J–L)

The cell, measuring 2–3 μm in diameter when air-dried, has 5–9 broadly bent spines, each 1.6–2.8 μm long. These spines consist of a circular base plate, 0.3–0.45 μm in diameter, and a triangular shaft that extends from the center of the base plate, bending widely at approximately 2/3 of its length before tapering to the apex. The plate scales are elliptical, measuring 0.6–1.3 μm in length and 0.4–0.8 μm in width, with a thickened margin that creates a central elliptical lacuna.

Stomatocysts are unknown.

Spiniferomonas serrata Nicholls 1981: 112 (Figs 6 A–D, F)
Chromophysomonas serrata (Nicholls) Preisig et Hibberd 1982

The cells are spherical, measuring 5–7 μm in diameter, and have 6–14 straight or curved spines that are 9–15 μm long. Each spine consists of a flat or saucer-shaped base plate, 1.1–1.5 μm in diameter, with a saw-toothed margin, and a triangular shaft extending from the center of the base plate, terminating in a tapered apex. There are two types of plate scales: smaller elliptical scales (1.1–1.4 μm in length and 0.5–1.2 μm in width, with two rounded lacunae separated by a median rib, with a single small nodule positioned near the middle of the median rib) and larger, circular scales (measuring 1.5–2.8 μm in diameter or slightly elliptical, 3–3.2 μm in length and 2.6–3 μm in width, with a single lacuna).

Stomatocysts are unknown.

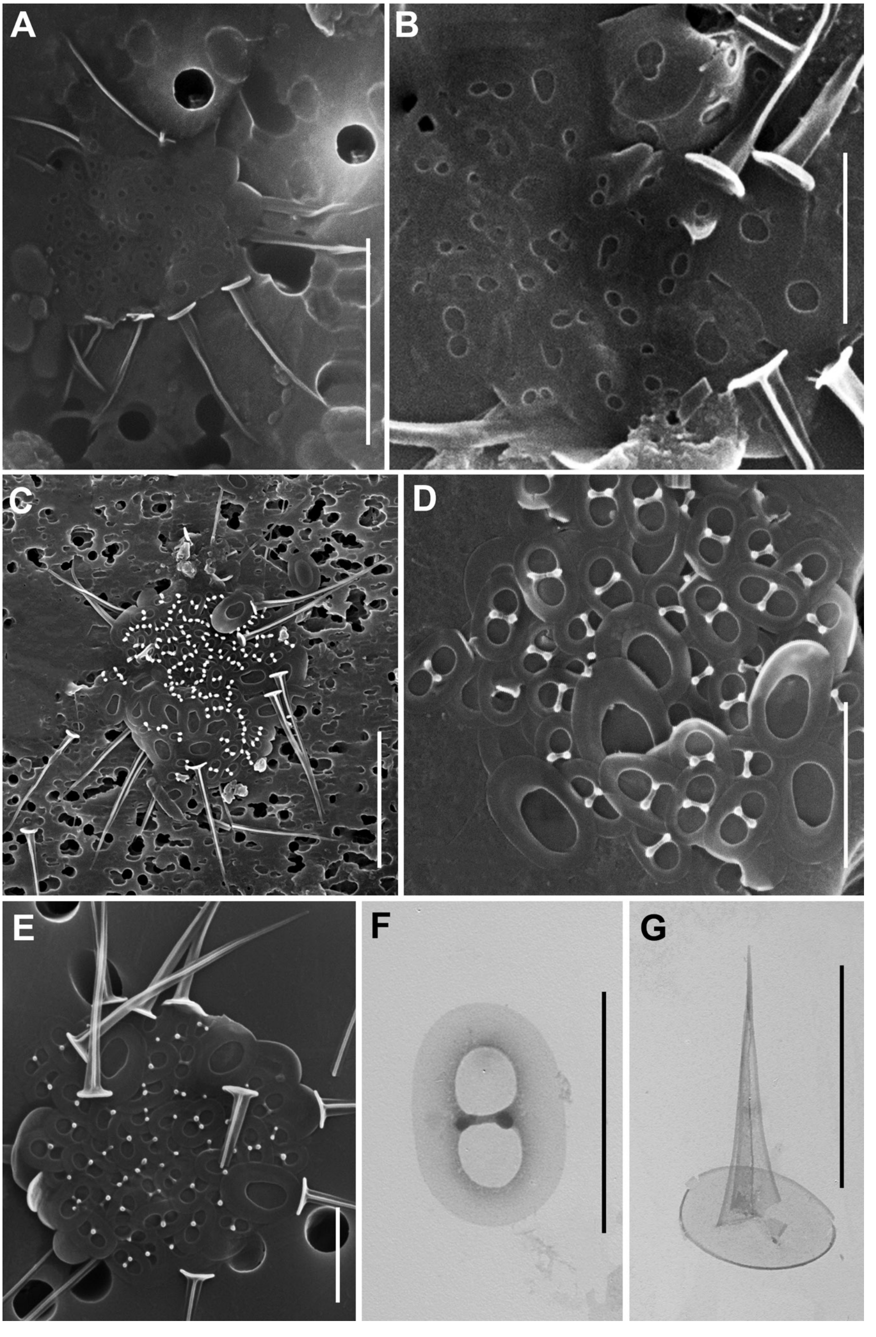

Figure 3. *Spiniferomonas* (**A–E** – SEM; **F**, **G** – TEM). **A**, **B** – whole cells with plate and spine scales *S. bilacunosa*; **C–F** – *S. cornuta* (**C** – whole cell with plate and spine scales of two types; **D**, **F** – individual plate scales; **E** – spine bases and plate scales of three types, from Lake Baikal; **G** – individual spine scale *S.* cf. *involuta*. Scale bars: **B**, **D–G** – 2 μm; **A**, **C** – 5 μm.

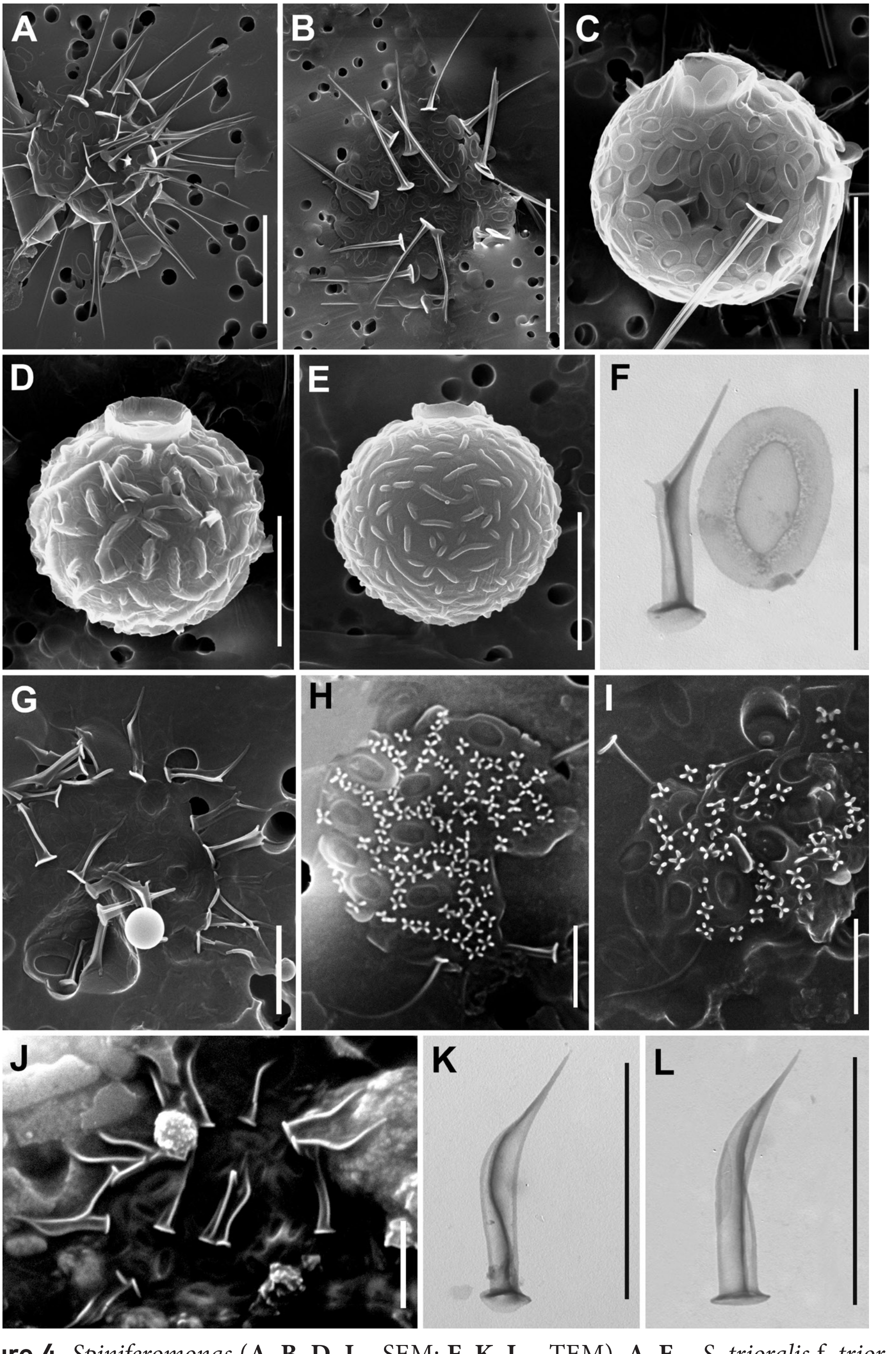

Figure 4. *Spiniferomonas* (**A**, **B**, **D–I** – SEM; **F**, **K**, **L** – TEM). **A–E** – *S. trioralis* f. *trioralis* (**A**, **B** – whole cells with plate and spine scales; **C**, **D**, **E** – stomatocysts covered with plate scales); **F**, **G** – *S. takahashii* (**F** – individual spine and plate scale; **G** – whole cell with plate and spine scales); **H**, **I** – plate and spine scales *S. crucigera*; **J–L** – *S. minuta* (**J** – whole cells with plate and spine scales; **K**, **L** – individual spine scales, the arrow shows the nodule). Scale bars: **F–L** – 2 μm; **A**, **C–E** – 5 μm; **B** – 10 μm.

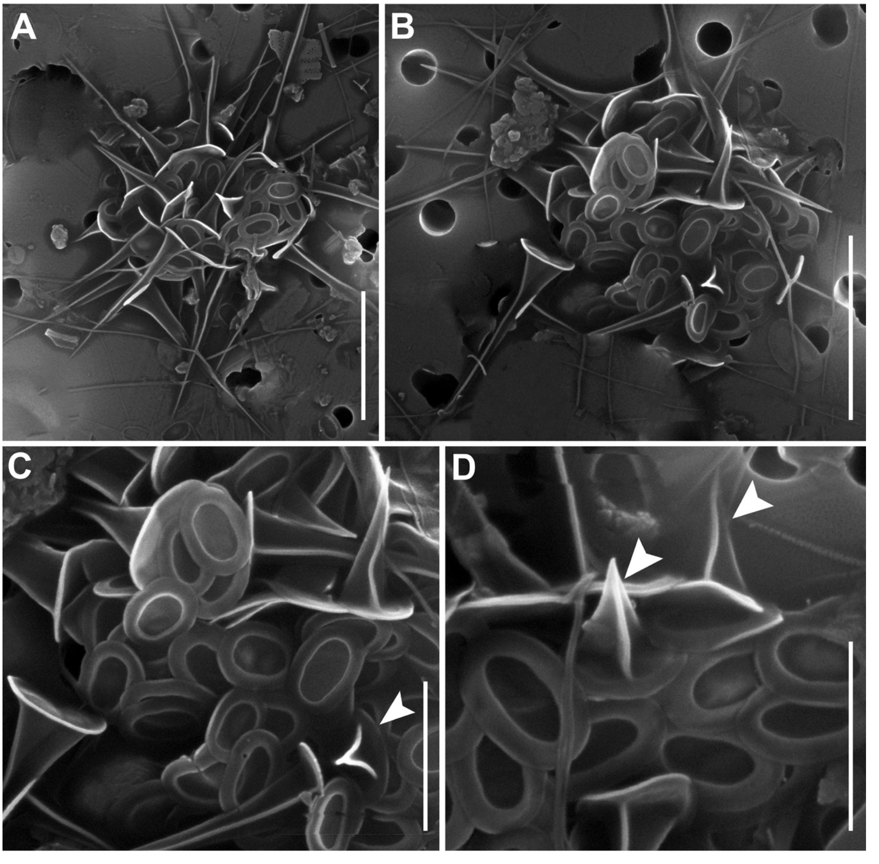

Figure 5. *Spiniferomonas heterospina*. SEM. **A**, **B** – whole cells with plate and spine scales; **C**, **D** – spine bases, plate and spine scales, the arrow shows the short spine scales. Scale bars: **C**, **D** – 2 µm; **A**, **B** – 5 µm.

Spiniferomonas silverensis Nicholls 1984: 2330–2331 (Figs 7 A–F)

The cells are spherical, measuring 4–7 µm in diameter, with 3–13 straight spines that are 9–18.7 µm long. Each spine consists of a large conical base plate, 1.7–2.8 µm in diameter and approximately 1 µm in height, with a triangular shaft extending from the centrally protruding base plate and terminating in a slightly bifurcate tip. The plate scales are elliptical, measuring 1.2–2.4 µm in length and 0.6–1.5 µm in width, with a wide and thickened margin that creates a central elliptical lacuna.

Stomatocysts are unknown.

Remarks: Some cells possess a second type of scales—small elliptical scales, measuring 1.2–2.4 µm in length and 0.6–1.5 µm in width, with a single lacuna and a small nodule up to 0.3 µm high positioned on the rim of the lacuna midway along its long axis (Figs 7 D–F).

Spiniferomonas takahashii Nicholls 1981: 114–115 (Figs 4 F, G)

The cells are spherical, 2.5–5 µm in diameter, with 5–14 curved spines that are 2.2–3.5 µm long. Each spine consists of a flat, elliptical, or saucer-shaped base plate, 0.3–0.5 µm in diameter, with a triangular shaft extending from the center of the base plate. Approximately 2/3 of the way along the shaft, two membranes terminate in short hooks, and the middle rib tapers to a sharp apex. The plate scales are elliptical, measuring 0.6–1.3 µm in length and 0.4–0.8 µm in width, with a wide and thickened margin that creates a central elliptical lacuna.

Stomatocysts are unknown.

Spiniferomonas triangularis Siver 1988: 380–382 (Figs 6 E, G–I)

The cells are spherical, 6–7 µm in diameter, with 5–11 straight spines that are 8–15.3 µm long. Each spine consists of a flat, circular base plate, 1–3 µm in diameter, with a triangular shaft extending from the center of the base plate and terminating in a tapered apex. The plate scales of two types, all with two lacunae: larger scales, almost circular (measuring 1.6–2.2 µm in diameter, with a triangular protrusion midway along the bridge separating the lacunae on most scales) and smaller scales, almost elliptical (measuring 1–1.7 µm in length and 0.5–1 µm in width). Additionally, some cells feature a third type of scales—small elliptical scales, measuring 1–1.7 µm in length and 0.5–1 µm in width, with a triangular protrusion (Fig. 6H).

Stomatocysts are unknown.

Spiniferomonas trioralis Takahashi 1973: 78 (Figs 4 A–E)
Chrysosphaerella parva Asmund 1973
Chromophysomonas trioralis (Takahashi) Preisig et Hibberd
S. trioralis Takahashi f. *trioralis*

The cells are spherical, measuring 4.5–7 µm in diameter, and feature 5–82 straight spines that range from 3–12 µm in length. Each spine consists of a flat, circular base plate, 0.9–1.6 µm in diameter, with a triangular shaft extending from the center of the base plate and terminating in a tapered apex. The plate scales are elliptical or circular, measuring 0.8–1.8 µm in length and 0.7–1.7 µm in width, with a wide and thickened margin that creates a central elliptical lacuna.

Stomatocysts are spherical, with a diameter of 7.6–9.5 µm. The collar is cylindrical with a sloping inner margin and an acute apex that is often irregular. The pore has a regular diameter of 7.6–9.5 µm and is surrounded by a flat annulus that is 1 µm wide. The entire surface of the stomatocyst is adorned with low ridges, measuring 0.2–0.6 µm in height and 0.5–3.2 µm in length, located in different orientations. The number of these ridges ranges from 80 to 115 (Figs 4 D, E) (Firsova et al. 2017).

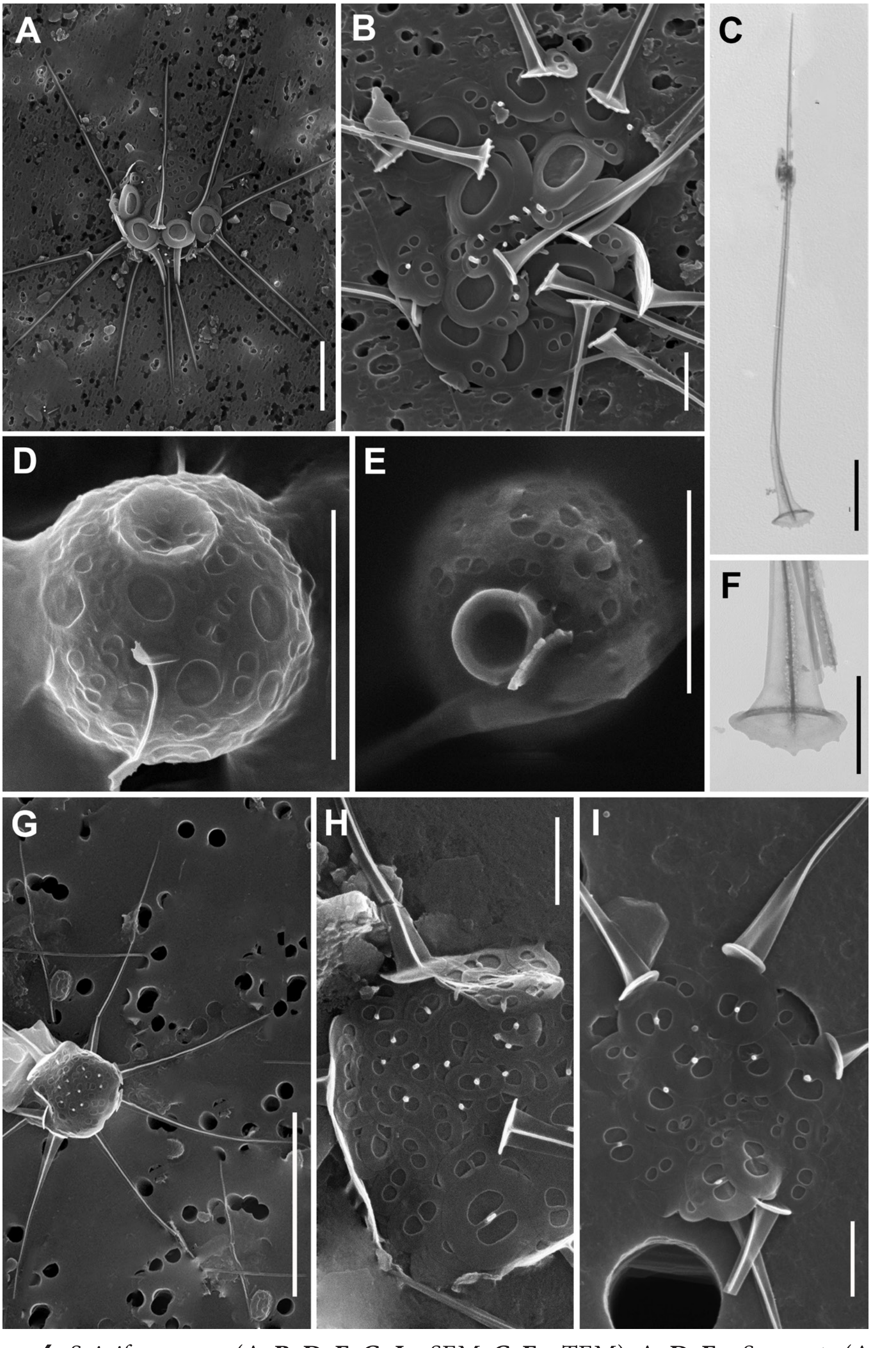

Figure 6. *Spiniferomonas* (**A**, **B**, **D**, **E**, **G–I** – SEM; **C**, **F** – TEM). **A–D**, **F** – *S. serrata* (**A**, **B** – whole cells with spine and plate scales; **C** – individual spine scale; **D** – stomatocyst covered with plate scales; **F** – base plate of spine showing saw-toothed margin on outer rim); **E**, **G–I** – *S. triangularis* (**E** – stomatocyst covered with plate scales; **G** – whole cell with plate and spine scales; **H** – spine bases and plate scales of three types, from Irkutsk Reservoir; **I** – spine bases and plate scales of two types). Scale bars: **F** – 1 μm; **B**, **C**, **H**, **I** – 2 μm; **A**, **D**, **E** – 5 μm; **G** – 10 μm.

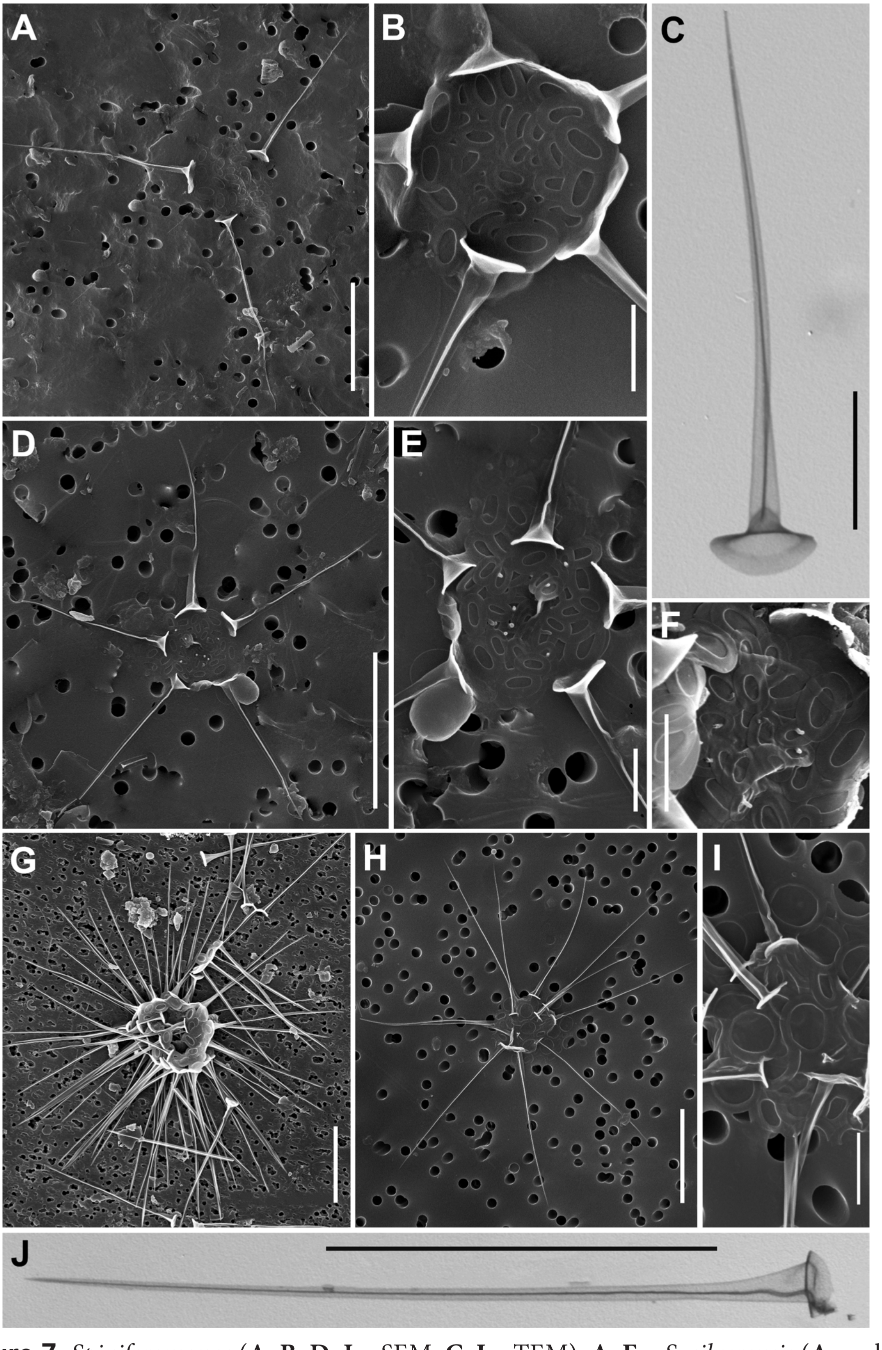

Figure 7. *Spiniferomonas* (**A**, **B**, **D–I** – SEM; **C**, **J** – TEM). **A–F** – *S. silverensis* (**A** – whole cell with plate and spine scales; **B** – spine bases and plate scales of one type; **C** – individual spine scale; **D** – whole cell with plate and spine scales; **E**, **F** – spine bases and plate scales of two types, from Angara-Kichera Delta); **G–J** – *S. trioralis* f. *cuspidata* (**G**, **H** – whole cells with plate and spine scales; **I** – spine bases and circular plate scales; **J** – individual spine scale). Scale bars: **B**, **C**, **E**, **F**, **I** – 2 μm; **A**, **D**, **G**, **H**, **J** – 10 μm.

Spiniferomonas trioralis f. *cuspidata* Balonov 1978: 1646 (Figs 7 G–J)

The cells are spherical, 5–8 µm in diameter, with 5–40 straight spines measuring 14–22 µm in length. Each spine consists of a flat, circular base plate with a diameter of 0.9–1.6 µm and a triangular shaft extending from the center of the base plate to a tapered apex. Additionally, the plate scales are elliptical or circular, measuring 0.8–1.95 µm in length and 0.7–1.8 µm in width, characterized by a wide, thickened margin that creates a central elliptical lacuna.

Stomatocysts are unknown.

Thus, new morphological features have been identified in four species: *S. conica*, *S. cornuta*, *S. crucigera*, and *S. silverensis*. It has been observed for the first time that *S. conica* exhibits a rounded pore on its bell-shaped basal base. Both *S. cornuta* and *S. crucigera* have features in the arrangement of nodules on plate scales. Additionally, *S. triangularis* displays not only the typical two types of plate scales but also three types, which are atypical (Siver 1988). Furthermore, the maximum spine lengths have been increased for *S. silverensis*, *S. serrata*, and *S. triangularis*. For *S. bourrellyi*, both the minimum and maximum spine lengths have been increased.

Discussion

The previous study of Spiniferomonas species in northern Russian reservoirs identified 12 species (Voloshko 2013), 11 of which were observed in this study. However, S. alata was absent in the reservoirs of Eastern Siberia during this revision, although it is found in the northern reservoirs of Western Russia (Voloshko 2013). Additionally, three other species – *S. breakneckii*, *S. nichollsii*, and *S. hamata* currently known in the reservoirs of Eastern Siberia, have also not been found. *S. breakneckii* was originally described from a small body of water in Connecticut, North America (Siver 1987). Later, the species was identified in small reservoirs of Western Greenland (as *S. takahashii*, Figs 55–57; Jacobsen 1985) and in a national park reservoir in Portugal (Santos and Leedale 1993). *S. hamata* and *S. nichollsii* were found in a coastal reservoir (Ito and Takahashi 1982). Later, *S. hamata* was found in North American waters but was initially misidentified as part of the species *S. takahashii* (Nicholls 1981, Figs 40–42). The species *S. grandis*, *S. pectinata*, and *S. genuiformis* are not valid. Specifically, *S. grandis* and *S. pectinata* do not belong to the genus *Spiniferomonas*. K. Nicholls provided micrographs supporting the assertion that described *S. genuiformis* is a growth form of *S. alata*, characterized by curved spines found on individual cells (Nicholls 1989).

In Eastern Siberian reservoirs, the most prevalent species include *S. bourrellyi*, *S. cornuta*, *S. serrata*, and *S. trioralis*, along with the form characteristic of northern Russian reservoirs, *S. trioralis* f. *cuspidata* (Table 1). The high diversity observed in certain reservoirs (Table 2) correlates with sampling frequency. For example, studies were performed over two or three seasons in lakes Labynkyr and Vorota (Bessudova et al. 2019; 2023) and Irkutsk (Bessudova et al. 2023; 2024 in press) and Boguchanskoye Reservoirs (Bessudova and Likhoshway 2017). In other instances, researchers selected periods that coincided with the peak species diversity in the genus, specifically during periods of maximum water warming. For instance, recent studies (Bessudova et al. 2023; 2024 in press) have shown that the highest species diversity occurs in the warmest areas of bays, where water temperatures remain high for longer durations owing to slow water circulation. The elongated spines observed in certain species in these reservoirs may reflect adaptations to cold-water habitats, similar to findings regarding bristle lengths of the genus *Mallomonas* species from the cold-water Lake Baikal (Bessudova et al. 2023).

Studies on species of the genus *Spiniferomonas* are crucial in northern latitudes owing to the sensitivity of these microeukaryotes to variations in species diversity and structure caused by fluctuations in water temperature. Therefore, they should be considered in reservoir monitoring efforts.

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