

UDC 582.261.1-14

**THE FINE CELL MORPHOLOGY OF A DIATOM
SKELETONEMA COSTATUM (GREVILLE) CLEVE, 1873
(BACILLARIOPHYTA: THALASSIOSIRALES)
AND ITS ECOLOGICAL SIGNIFICANCE**

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Received 26.05.2025; revised 15.07.2025;
accepted 21.11.2025.

The appearance of thin threads attached to *Skeletonema* spp. cells is a relatively uncommon and poorly understood phenomenon. *Skeletonema costatum* (Greville) Cleve, 1873 forming silicified threads less than 0.2 μm in diameter and up to 50 in length has been studied for the first time in the Black Sea. The effect of various concentrations of silicic acid (DSi) on fine morphology of cells was investigated, and an assumption about the ecological significance of this phenomenon was put forward. As shown, the formation of highly silicified threads requires DSi concentration $> 2 \mu\text{M}$. One of the ecological roles of threads may be the formation of a protective barrier decreasing the grazing of *S. costatum* cells by tintinnids. Another possible ecological role of threads is as follows: they may promote the formation of dying cell aggregates boosting the cell sinking rate. This process is considered to be one of the components of the biological carbon pump in marine ecosystems.

Keywords: silicic acid, ecological significance, morphology, *Skeletonema costatum*, threads

A centric diatom *Skeletonema costatum* (Greville) Cleve, 1873 is a cosmopolitan marine species [Kooistra et al., 2008]. It often dominates the phytoplankton community [Ueno et al., 2023] and can cause red tides [Li et al., 2009; Shen et al., 2012]. In the Black Sea, *S. costatum* is widespread along the coast, especially in bays [Stelmakh et al., 2020; Yasakova et al., 2020]. It grows in mass in March and April (up to 4 million cells·L⁻¹) causing blooms, and disappears in late May [Proshkina-Lavrenko, 1955].

S. costatum belongs to the order Thalassiosirales. Some representatives of this order, for example *Thalassiosira rotula* Meunier [Tran et al., 2023] and *Thalassiosira weissflogii* (Grunow) G. A. Fryxell & Hasle [current accepted name: *Conticribra weissflogii* (Grunow) Stachura-Suchoples & D. M. Williams] [McLachlan et al., 1965; Verity, Villareal, 1986], have slime threads. The slime threads (mucilage, fibrillar appendages) are flexible fibers or threads that extend from the base of a diatom cell and can be seen under a light microscope. These threads are composed of a unique substance: β -chitin [Herth, Barthlott, 1979; McLachlan et al., 1965].

There is little data on threads for the genus *Thalassiosira* Cleve, 1873, and even less on threads for *Skeletonema* Greville, 1865 [Aké Castillo et al., 1995; Castellvi, 1969; Yamada, Takano, 1987]. The first researcher to mention ‘polar fibers’ in *S. costatum* was J. Castellvi [1969]. Polar threads have

a length of approximately 50 μm and a diameter of 0.05 μm . They are inserted exclusively into polar zones of each cell, where the valves and intercellular spines of the silicate frustule can be found. Polar threads are straight, and their number varies between six and eight.

Due to the difficulty in identifying the species, we cannot confidently classify the studied organisms as *S. costatum*. Therefore, when we refer to '*S. costatum*,' we mean a group of closely related species: *S. costatum* sensu lato [Baytut et al., 2013; Kooistra et al., 2008].

For the Black Sea *S. costatum*, the formation of threads has not been previously reported. During our research, we carried out an experiment involving natural phytoplankton. The use of nutrient-rich medium resulted in the formation of polar threads in *S. costatum*. We also examined the effect of different silicic acid concentrations on fine morphology and hypothesized the ecological significance of this phenomenon.

Experiments. Water for the test was sampled in the northeastern Black Sea, in the Blue Bay (Gelendzhik), on 4 October, 2022 (44°34'31"N, 37°58'45"E), from the sea surface (0.5–1.0 m). The samples (total volume of 19 L) were filtered through two layers of nylon gauze (mesh size of 180 μm) to remove mesozooplankton. Nutrient analyses for phosphate, silicic acid, nitrate, nitrite, and ammonia were carried out with a portable spectrophotometer Hach DR 1900 (Hach Lange, the USA) following standard photocolometric methods [Methods of Seawater Analysis, 1999; Modern Methods of Ocean Hydrochemical Investigations, 1992].

The initial concentration of dissolved silicic acid (hereinafter DSi) in the seawater used for the experiment was 4.97 μM . We needed to reduce the DSi content to a value below 1 μM to begin the test. Therefore, we added nitrate (N) and phosphate (P) to the seawater in a ratio of 23.3 : 1 and subjected a 19-L plastic bottle to moderate irradiation in a laboratory setting. After 12 days, DSi concentration dropped below 1 μM . On 14 October, the water was transferred from the initial bottle into 15 plastic containers, 800 mL each; those were placed in orbital shakers PSU-20i (Biosan, Latvia) at a temperature similar to that at the sampling station: (+20 \pm 1) °C. Irradiance was set at 65 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (photosynthetically active radiation) with a light : dark period of 16 h : 8 h. On 17 October, after three days of acclimation, the experiment was started. At the beginning, KNO_3 (N) and Na_2HPO_4 (P) were added into all variants. The starting concentrations were 14 μM for N and 1 μM for P. The N : P ratio was close to the Redfield ratio (16 : 1). After adding silicate, five variants were set with the following DSi content: < 1, 1.5, 2, 3, and 5 μM . There were three replicates of each variant.

Phytoplankton cells were counted on the first and last days. Species were identified in a 0.05-mL Nageotte counting chamber under a light microscope (Micromed, Russia) with a magnification of 200 \times . Taxonomic identification was carried out using the guideline [Identifying Marine Phytoplankton, 1997]. Current names follow AlgaeBase [2026]. Species wet biomass (in $\text{mg}\cdot\text{m}^{-3}$) was calculated from cell abundances and cell volumes estimated using best-fit cell geometries [Hillebrand et al., 1999].

Micrographs of *S. costatum* were taken under a Micromed 3 Alpha microscope equipped with a digital camera Hayear Real 4K UHD 2K 1080P (China). Scanning electron microscopes Vega 3 (Tescan, Czech Republic) and KYKY EM6X00 (KYKY Technology Co., Ltd., China) were used to examine the morphological features of *S. costatum*. Sizes of threads (length and diameter) were measured based on electron microscopy images processed in ImageJ [Schneider et al., 2012].

Fine cell morphology. In scientific literature, there are photos of various *Skeletonema* species with threads [Aké Castillo et al., 1995; Sarno et al., 2007]. Single threads have been identified in two *Skeletonema* species from the Sontecomapan Lagoon in the Gulf of Mexico [Aké Castillo et al., 1995]. These delicate structures can be damaged by acid treatment, which can explain why only a single thread was observed in each cell. Moreover, these structures are hard for electron microscopy to detect due to their small diameter, low optical resolution, or aggressive effect of acids during treatment. In field samples from the Black Sea, *S. costatum* cells with threads have not been observed (Fig. 1a). However, under our experimental conditions, threads were formed (Fig. 1b).

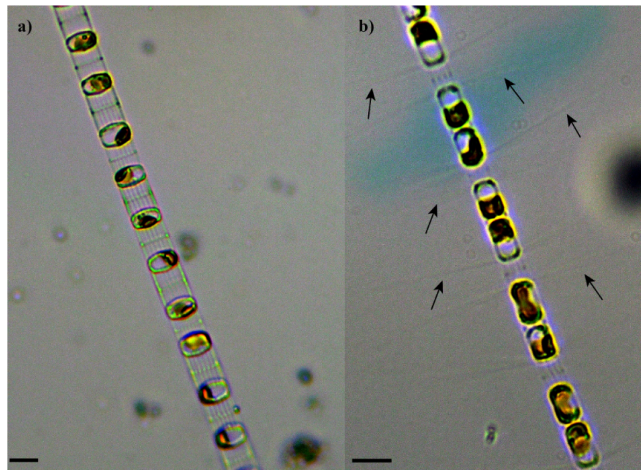


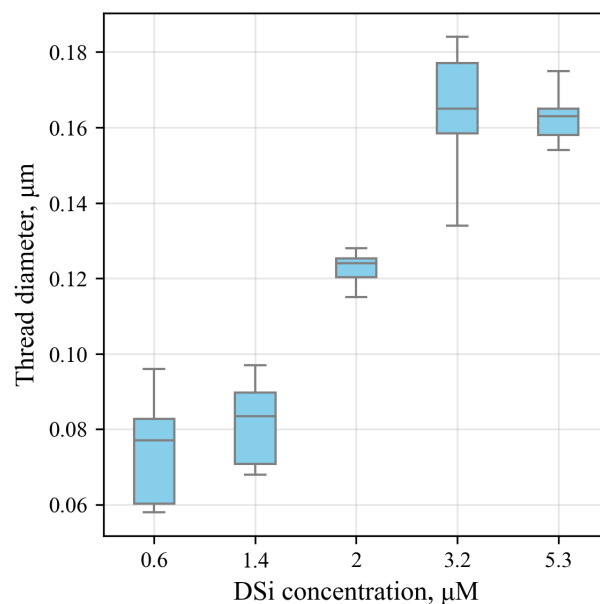
Fig. 1. *Skeletonema costatum* cell colony: a, in a field sample in April 2022 (photo by A. Fedorov); b, in an experiment in October 2022. Threads are arrowed. Scale bars are 10 μm

Рис. 1. Колония клеток *Skeletonema costatum*: а — в месте отбора проб в апреле 2022 г. (фото А. Фёдорова); б — в эксперименте в октябре 2022 г. Нити показаны стрелками. Масштабная линейка — 10 мкм

S. costatum cells averaged 4–10 μm in length and 3–8 μm in diameter. *S. costatum* threads are exceptionally delicate, and in most micrographs, they are broken. Therefore, the entire length was measured in a small number of images. The average length of a thread was $(40.3 \pm 5.3) \mu\text{m}$ (mean value \pm standard deviation) ($n = 7$). In previous studies, threads were approximately 50 μm long [Castellvi, 1969; Yamada, Takano, 1987]. We measured the diameter of threads at various DSi concentrations. The values ranged 0.058 to 0.184 μm (Fig. 2), and increased as the DSi content rose. The most significant boost occurred at DSi of 2 μM and more. It is well known that dissolved silicate is essential for the growth of diatoms. The range of growth-limiting DSi is wide (from ~ 0.5 to 94 μM), with a median of 2.2 μM [Martin-Jézéquel et al., 2000]. According to our experiment, the DSi concentration limiting the growth of *S. costatum* biomass was 0.98 μM (half-saturation constant). At the same time, twice as high DSi was required to produce highly silicified threads. Therefore, we assume that the formation of clearly visible threads can be expected only at a very high DSi content.

Fig. 2. Changes in the diameter of *Skeletonema costatum* threads at different dissolved silicic acid (DSi) content in an experiment. Box plots show minimum and maximum values, the first and third quartiles; the horizontal line inside the rectangle shows the median

Рис. 2. Изменения диаметра нитей *Skeletonema costatum* при разных концентрациях растворённой кремниевой кислоты (DSi) в эксперименте. На коробчатых диаграммах показаны минимальное и максимальное значения, 1-й и 3-й квартили; горизонтальная линия внутри прямоугольника соответствует медиане



Ecological significance. The ecological role of *S. costatum* threads is not clear. However, based on indirect data, it can be the following. During the experiment, we observed active development of a tintinnid *Eutintinnus lusus-undae* (Entz, 1885) (see Supplements 1 and 2: <https://marine-biology.ru/mbj/article/view/517>). The length of its lorica ranged 160 to 400 μm , and the oral diameter was 45 to 55 μm . This tintinnid can be found regularly throughout the Black Sea. It dominates microzooplankton during summer and autumn [Gavrilova, Dovgal, 2019], that is, during the study period. In the experiment, its abundance ranged from 0.4×10^5 to 5×10^5 ind. $\cdot\text{L}^{-1}$.

One possible function of threads could be to form a protective barrier that prevents *S. costatum* cells from grazing by tintinnids. This assumption is confirmed by the fact that the diameter of *S. costatum* with threads exceeds the oral diameter of *E. lusus-undae*. Therefore, threads can at least prevent tintinnids from ingesting these diatoms.

In our test, the direct assessment of the protective function of *S. costatum* threads was impossible due to different abundance of this species: the value varied by more than an order of magnitude in experimental variants. Thus, it was $(0.87 \pm 0.01) \times 10^5$ cells $\cdot\text{L}^{-1}$, when the DSi content was less than 2 μM , and $(27.16 \pm 0.20) \times 10^5$ cells $\cdot\text{L}^{-1}$ in variants with DSi ≥ 2 μM . In nature, there is a positive correlation between the abundance of *S. costatum* and large tintinnids [Biswas et al., 2012; Jyothibabu et al., 2006; Sathish et al., 2024]. Such a relationship suggests that in our experiment, higher abundance of tintinnids could be expected in variants with high abundance of *S. costatum*. However, there were no significant differences between *E. lusus-undae* abundance in variants with the DSi concentration < 2 μM [$(2.17 \pm 0.6) \times 10^5$ ind. $\cdot\text{L}^{-1}$] and the DSi content ≥ 2 μM [$(1.67 \pm 0.3) \times 10^5$ ind. $\cdot\text{L}^{-1}$]. This fact confirms the assumption that tintinnids could not easily graze this diatom species with threads.

Similarly, the growth rate of natural tintinnid populations in the Narragansett Bay significantly lowered during a summer bloom of various *Thalassiosira* cells with thin threads [Verity, 1986; Verity, Villareal, 1986]. Cells of diatoms without these threads were more easily accessible for tintinnids and supported their more intensive growth.

Another possible ecological role of threads is to enhance the ability to consume nutrients from the medium and increase cell buoyancy. This suggestion is based on the fact that threads make the surface of cells larger. In experiments involving *Thalassiosira fluviatilis* Hustedt, threads increased the cell surface area by a factor of 2.8. Cells without threads were found to sink 1.7 times faster than those with threads [Walsby, Xypolyta, 1977]. However, *S. costatum* threads were extremely thin and increased the surface of cells by only 3%, which does not confirm the significance of this factor. The effect of threads on cell buoyancy is quite expected. When diatom cells are lysed, they often aggregate into large flocs, drastically boosting the cell sinking rate [Kiørboe et al., 1994]. Long threads can promote faster aggregation rates, and this is essential for operating a biological carbon pump in marine ecosystems. The formation of threads in *S. costatum* was observed in monocultures or in laboratory experiments where concentrations of mineral elements were high. In nature, this phenomenon can occur under eutrophic conditions, as reported for the Mexican Gulf lagoon [Aké Castillo et al., 1995]. The appearance of cell threads in *Skeletonema* species in nature is a relatively rare phenomenon, and its ecological role is still poorly understood.

This research was carried out within the framework of the state research assignment No. FMWE-2024-0023.

Acknowledgement. We are grateful to Oksana Ocherednik for hydrochemical measurements during the experiments and Alexey Fedorov for his assistance in phytoplankton sampling. We thank Mariia Shulgina for her recommendations and advice on slide preparation for scanning electron microscopy. We sincerely thank Alexander Filippov, Antonina Kremenetskaia, and Zoya Dudnik for their help with scanning electron microscopy.

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**МОРФОЛОГИЯ КЛЕТОК ДИАТОМОВОЙ ВОДОРΟΣЛИ
SKELETONEMA COSTATUM (GREVILLE) CLEVE, 1873
(BACILLARIOPHYTA: THALASSIOSIRALES)
И ЕЁ ЭКОЛОГИЧЕСКОЕ ЗНАЧЕНИЕ**

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Появление тонких нитей у клеток *Skeletonema* spp. является относительно редким и малоизученным феноменом. Впервые в Чёрном море исследована *Skeletonema costatum* (Greville) Cleve, 1873, образующая кремнённые нити диаметром менее 0,2 мкм и длиной до 50 мкм. Проанализировано влияние различных концентраций кремниевой кислоты (DSi) на морфологию клеток, выдвинуто предположение об экологическом значении этого явления. Показано, что для образования сильнокремнённых нитей необходима концентрация DSi выше 2 мкМ. Одним из экологических значений нитей может быть создание защитного барьера, который уменьшает поедание клеток *S. costatum* тинтиннидами. Другое вероятное экологическое значение нитей заключается в том, что они могут способствовать образованию отмирающих клеточных агрегатов, что резко увеличивает скорость погружения клеток. Этот процесс является одним из компонентов работы биологического углеродного насоса в морских экосистемах.

Ключевые слова: кремниевая кислота, экологическое значение, морфология, *Skeletonema costatum*, нити