ALGAE — ВОДОРОСЛИ

New observations of *Meringosphaera mediterranea* from Russian Arctic seas, including a review of global distribution

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Abstract. *Meringosphaera mediterranea* is the type species of the genus. The species is widely distributed in the polar, temperate, and tropical marine waters. For many years the systematic position of this species was unclear (the most common opinion was that the species is xanthophyte or chrysophyte alga), and its affiliation to centrohelids was clarified quite recently. In this paper, we report on the finding of *M. mediterranea* in the East Siberian Sea and for the first time in the Laptev Sea and provide a description of this species accompanying by LM and SEM microphotographs. Also, we summarize all available published information on the global distribution of *M. mediterranea*.

Keywords: Haptista, *Meringosphaera*, algae, centrohelid heliozoa, distribution, microscopy, morphology, protists, East Siberian Sea, Laptev Sea, Russia.

Новые исследования *Meringosphaera mediterranea* из арктических морей России, включая данные о глобальном распространении вида

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Резюме. *Meringosphaera mediterranea* — типовой вид рода, широко распространенный в полярных, умеренных и тропических морях. В течение многих лет систематическое положение *M. mediterranea* оставалось неясным (наиболее распространенным мнением было считать этот вид желтозеленой или золотистой водорослью), а принадлежность вида к центрохелидам была показана совсем недавно. В настоящей работе приведены сведения о находке *M. mediterranea* в Восточно-Сибирском море и первой находке вида в море Лаптевых, морфологическое описание и микрофотографии, выполненные с помощью СМ и СЭМ, а также обобщены ранее опубликованные данные о распространении этого нанопланктонного вида в Мировом океане.

Ключевые слова: Haptista, *Meringosphaera*, водоросли, микроскопия, морфология, протисты, распространение, центрохелидные солнечники, Восточно-Сибирское море, море Лаптевых, Россия.

The genus *Meringosphaera* Lohmann includes unicellular species that many researchers have identified as algae. For example, according to AlgaeBase, this genus is placed in Xanthophyceae (Mischococcales, Pleurochloridaceae) and includes 16 formal taxa, of which only 6 species are accepted (Guiry, Guiry, 2021; see also Parke, Dixon, 1964, 1968; Ettl, 1978; Karlson *et al.*, 2020). The genus was described by Lohmann (1903), but lectotypification of this genus with *M. mediterranea* was carried out by Loeblich and Tappan (1963: 193). *Meringosphaera mediterranea* is widely distributed in polar, temperate and tropical marine waters, and is sometimes considered cosmopolitan (e. g., Estep *et al.*, 1984).

For many years the ideas on the taxonomic position of *Meringosphaera* were controversial. Lohmann placed this genus to "Protophyten unsicherer Stellung", i. e., to a group of organisms with an unclear systematic position. He also wrote that the cells contain small green chloroplasts (Lohmann, 1903: 68). Subsequently, different authors placed this genus into a number of algal taxa based on observation of living cells (e.g., chloroplasts), cell covers, presence of carotenoids, storage products, etc. (for more details see Silva, 1979). According to Guiry and Guiry (2021), *Meringosphaera* belongs to the phylum Ochrophyta, class Xanthophyceae. On the other hand, many researchers placed this genus within the class Chrysophyceae (Leadbeater, 1974; Parke, Dixon, 1976; Kristiansen, Sandgren, 1986; etc.). Other authors regarded *Meringosphaera* as a member of the Heliozoa (e.g., Ikävalko, Gradinger, 1997; Ikävalko, 2004) based on a similar type of scales. According to Adl *et al.* (2005, 2019), the genus *Meringosphaera* has uncertain relationships with other eukaryote protists and was listed as *incertae sedis*.

Our interest to *Meringosphaera mediterranea* has arisen due to different reasons. Firstly, despite the fact that this species morphology was studied previously using electron microscopy (both scanning and transmission), some details of its morphology were not properly described. Secondly, despite its wide distribution (the species has been recorded in different regions of the World Ocean), *M. mediterranea* occurs sporadically in samples, which appreciably complicate its study. Thirdly, it is still unknown, if it is possible to cultivate this species?

Thus, the taxonomic position of *Meringosphaera mediterranea* has been uncertain for many years. Keeping in mind the aforementioned, we consider *M. mediterranea* a "mysterious species". Despite that molecular-genetic study of *M. mediterranea* was carried out quite recently (Zlatogursky *et al.*, 2021) and have revealed, that this species is related to centrohelid heliozoa[1] (Haptista), some questions (e.g., about the photosynthetic bodies or plastids, that are in cells of this species) are not resolved and future investigation is necessary.

This paper aims to present a description of *M. mediterranea* from the Russian Arctic seas (the East Siberian Sea and the Laptev Sea) accompanying by LM and SEM mic-

[1] A single original sequence of the 18S rDNA gene was used to resolve the phylogenetic position of the species.

rophotographs and to compare our results with literature data and to summarise and analyze available data on the global distribution of this species.

Material and Methods

Plankton samples were collected within the framework of the integrated environmental monitoring program in the East Siberian Sea and the Laptev Sea. All samples were collected with a bathometer from 3 layers (bottom, intermediate, and surface). Samples from the East Siberian Sea were collected in September 2016, samples from the Laptev Sea were collected in August 2017. We examined 15 samples with a volume of 0.5 l (the East Siberian Sea) and 60 samples with a volume of 3.0 l (the Laptev Sea).

All samples were fixed with formaldehyde (final concentration about 1%). Further, the samples were concentrated by gentle reverse filtration technique with Dacron filters (pore size 2 μm) and analyzed by standard methods (Vinogradov, 1983).

Light microscope (LM) observations were performed with 100 × oil immersion planapochromatic objective with numerical aperture 1.40 at Leica DM2500 microscope equipped with differential interference contrast optics (DIC) and DFC 495 camera. Scanning electron microscope (SEM) observations were performed using a JEOL JSM-6380LA 20kV microscope. For SEM investigation drops of the sample were air-dried on brass stubs and coated with Au-Pd in a Giko IB-3 ion coater.

Samples examined. **East Siberian Sea:** ESS5s (surface), ESS5i (15.5 m depth) — plankton, 73.11°N, 165.56°E; 15 IX 2016; **Laptev Sea:** LS4s — surface, plankton, 76.33°N, 114.9°E; 24 VIII 2017; LS5i — 20.0 m depth, plankton, 76.36°N, 116.1°E; 24 VIII 2017 (Fig. 1). All samples were

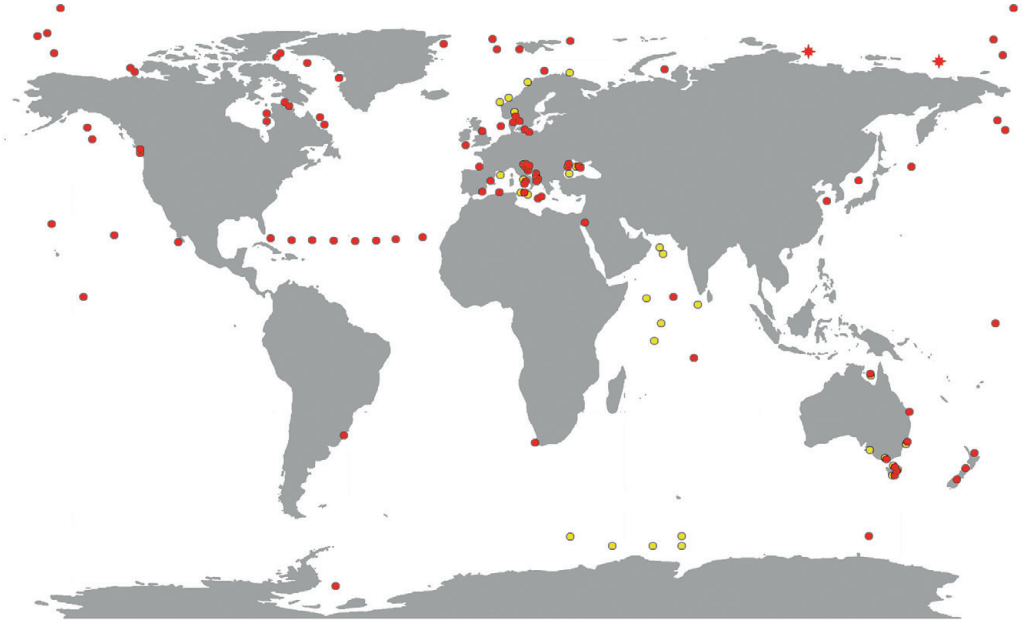

Fig. 1. Global distribution of *Meringosphaera mediterranea*.
Yellow circles — localities according to GBIF (Meringosphaera..., 2019), red circles — localities according to references from Table 1, red stars — localities according to our data.

collected by the first author (A. Georgiev) and deposited in the collection of Mycology and Algology Department, Faculty of Biology, Moscow State University.

Results

Morphology of *Meringosphaera mediterranea*

Meringosphaera mediterranea Lohmann, 1903, Helgoland. Wiss. Meer., Neue Folge 7: 68–69, Taf. 1, Fig. 17, 18. (Plate I)

= *Meringosphaera baltica* Lohmann, 1903, Helgoland. Wiss. Meer., Neue Folge 7: 68–69, Taf. 1, Fig. 19.

Cells solitary, spherical, 6.0–9.5 μm in diam., with numerous plate scales (poorly distinguished with LM), and 16–22 μm long distinctive undulated radiating spine scales (Plate I: 1–4). Two types of scales could be recognized with SEM: plate and spine scales. All plate scales of the same size (2.2–2.6 × 1.2–1.5 μm), with both outer and inner surfaces smooth and plain; each scale elliptic, with a slightly median constriction (Plate I: 5–7); central narrow thickening on the inner surface (Plate I: 5–7). Spine scales 16–22 μm long, 0.33–0.40 μm wide; the shaft of the scale with 6–7 bends. In the external view, the spine scales bases more or less flattened, in the internal view concave; conical regular protuberances (13) present along the edge of each scale base (Plate I: 4–7); each scale base indented (Plate I: 5–7). The spine hollow (Plate I: 5), undulated, tapered with up to 17 irregularly spirally spaced short triangular barbs ("thorns") (0.3–0.4 μm long) directed towards the tip. The first barbs (near the base) longer (0.7–0.9 μm long), regularly located and forming a ring (Plate I: 4–7). As only fixed samples were examined, no chloroplasts and axopodia were visible with LM (Plate I: 1–3).

Habitat. We found this taxon in the East Siberian Sea and the Laptev Sea plankton. The cells of *Meringosphaera mediterranea* occurred sporadically in the studied samples. In the East Siberian Sea *M. mediterranea* was found only in one site with concentration 0.03×10^3 cells l^{-1} (surface) and 0.12×10^3 cells l^{-1} (15.5 m depth). In the Laptev Sea, the species was found in two sites with concentrations of 0.08×10^3 cells l^{-1} (surface) and 0.02×10^3 cells l^{-1} (20.0 m depth).

Global distribution of *Meringosphaera mediterranea*

Since the first description, *Meringosphaera mediterranea* was often recorded in plankton from a range of regions. Here we summarize the available information on the distribution of this species in the World Ocean (in the Arctic, Atlantic, Pacific, Indian and Southern Ocean) (Table 1, Fig. 1).

Plankton of the Russian Arctic seas is poorly studied, and data on the plankton of the East Siberian and the Laptev seas are especially scarce. Noteworthy that *Meringosphaera mediterranea* is reported from the Laptev Sea for the first time.

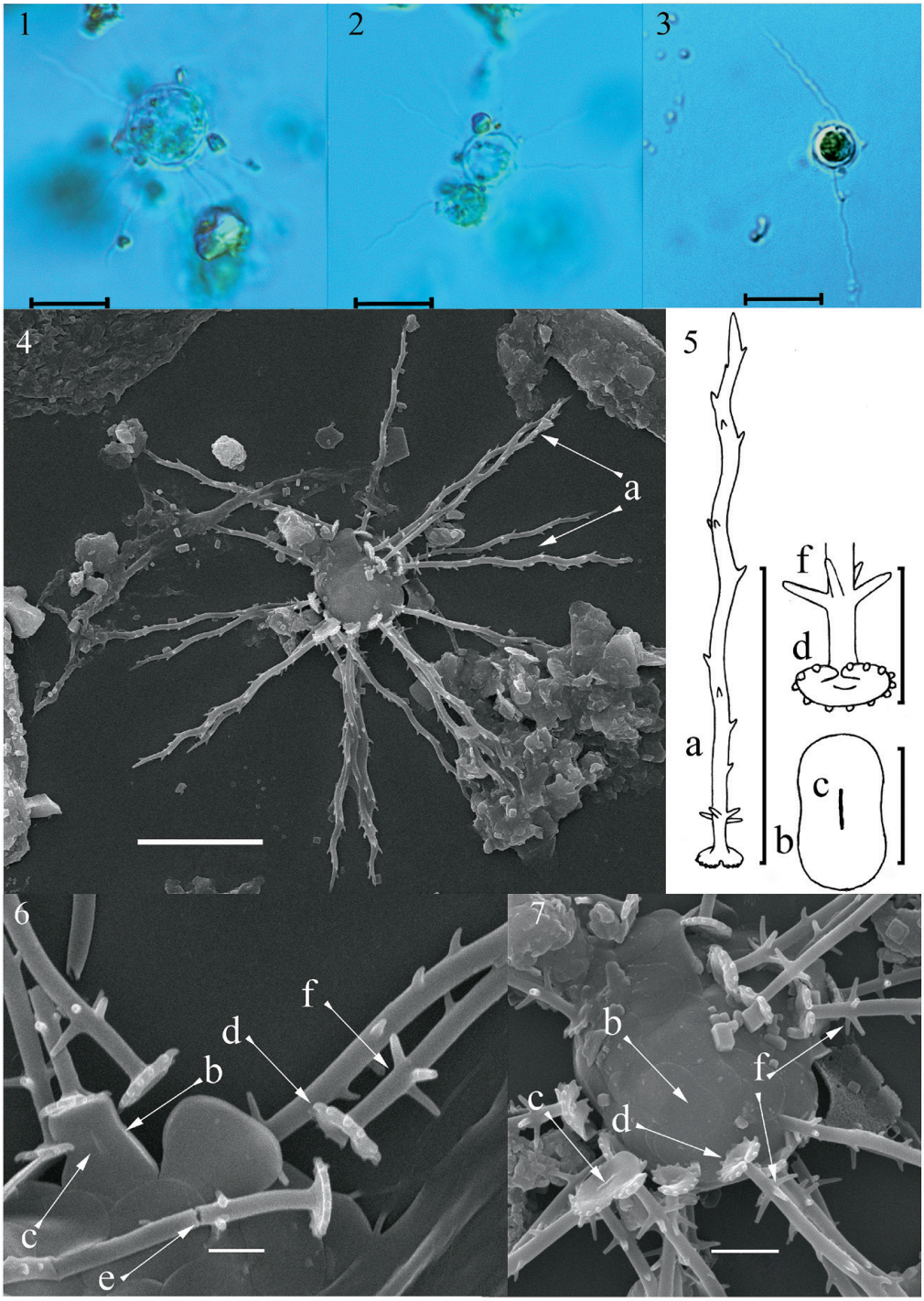

Plate I. 1–7 — *Meringosphaera mediterranea* (1, 2, 4, 6, 7 — sample ESS5i, 3 — sample LS5i).
1–3 — LM; 4, 6, 7 — SEM; 5 — scheme of spine and plate scales.
a — spine scale; b — plate scale; c — inner surface of plate scale with a central narrow thickening;
d — base of spine scale; e — hollow in spine scale; f — regular ring of barbs.
Scale bars: 1–4 —10 μm; 5a — 10 μm; 5b, 5c, 7 — 2 μm; 6 — 1 μm.

Table 1

Distribution of *Meringosphaera mediterranea* in the World Ocean

Ocean	Site[2]	References[3]
Arctic Ocean	Barents Sea	Wulff, 1914
	West Greenland*	Thomsen, 1981
	Hudson Bay and Hudson Strait*	Simard *et al.*, 1996; Harvey *et al.*, 1997
	Polar Sea	Booth, Horner, 1997
	Northern Barents and Greenland Seas and Fram Strait	Okolodkov, 1997
	Kongsfjorden (the Kings Bay, western coast of Spitsbergen)	Hasle, Heimdal, 1998
	Greenland Sea	Ikävalko, Gradinger, 1997; Okolodkov, 2011
	Central Northern Baffin Bay*, West Greenland Current*	Lovejoy *et al.*, 2002
	Canada Basin	Melnikov *et al.*, 2002
	Canadian Beaufort Sea	Różańska *et al.*, 2008
	Kara Sea (Yamal Peninsula coast)	Sukhanova *et al.*, 2011
	Chukchi Sea, Canadian Basin	Joo *et al.*, 2012
	Northern part of the Chukchi Sea	Lee *et al.*, 2015
	Beaufort Sea, northern Baffin Bay*	Blais *et al.*, 2017
	East Siberian Sea	Georgiev, Georgieva, 2017; this study
	Laptev Sea	This study

[2] Some papers do not provide detailed data where the species was recorded.
[3] Records are given in chronological order.

Table 1 (continued)

Ocean	Site	References
Atlantic Ocean	Baltic Sea	Hensen, 1887; Lohmann, 1908
	Mediterranean Sea	Lohmann, 1903, 1908; Sarno *et al.*, 1993; Bouza, Aboal, 2008; Oviedo *et al.*, 2014
	Adriatic Sea	Schiller, 1916 (cit.: Pascher, 1939); Pascher, 1917, 1939; Leadbeater, 1974; Totti *et al.*, 2000; Revelante, 1985 (cit.: Vilicic *et al.*, 2002); Šupraha *et al.*, 2011; Bosak *et al.*, 2012b; Cerino *et al.*, 2012, 2019
	Black Sea	Morozova-Vodyanitskaya, 1954; Ivanov, 1965; Senichkina, 1973; Caraus, 2002; Senicheva, Kostenko, 2004
	Great Britain	Parke, Dixon, 1964, 1976
	Western Mediterranean (the Bay of Algiers)	Leadbeater, 1974
	Denmark	Manton, Leadbeater, 1974
	West Greenland*	Thomsen, 1981
	Weddell Sea**	Buck, Garrison, 1983
	Atlantic Ocean	Estep *et al.*, 1984
	Sea Point, Cape Town	Norris, 1984
	Celtic Sea	Joint, Pomroy, 1986
	Coastal waters of Newfoundland	Urban *et al.*, 1993
	Skagerrak, North Sea	Kuylenstierna, Karlson, 1994
	Hudson Bay and Hudson Strait*	Simard *et al.*, 1996; Harvey *et al.*, 1997
	Central Northern Baffin Bay*, West Greenland Current*	Lovejoy *et al.*, 2002
	Ionian Sea	Malinverno *et al.*, 2003
	Lake Alimini Grande, salt-marsh ecosystem on the Adriatic coast, Southern Italy	Vadrucci *et al.*, 2004
	Danish coast to the North Sea	Škaloud *et al.*, 2006
	Patos Lagoon, Brazil	Bergesch *et al.*, 2008
	Grado-Marano lagoon, Italy (Mediterranean Basin)	Vadrucci *et al.*, 2008
	Tyrrhenian Sea	Zingone *et al.*, 2010
	Northern Baffin Bay*	Blais *et al.*, 2017
	Labrador Sea	Simo-Matchim *et al.*, 2017
	Bay of Biscay	Pinto, 2018
	West Coast of Sweden	Zlatogursky *et al.*, 2021

Table 1 (continued)

Ocean	Site	References
Pacific Ocean	New Zealand	Moestrup, 1979
	Gulf of Alaska	Booth *et al.*, 1982, Martin *et al.*, 1989
	Victorian coastal waters*** (southeastern Australia)	Beech, 1983 (cit.: LeRoi, Hallegraeff, 2006)
	East Australian Current	Hallegraeff, 1983
	Gulf of Carpentaria***	Hallegraeff, Jeffrey, 1984
	Tasman Bay	MacKenzie, Gillespie, 1986
	North Pacific Central Gyre	Hoepffner, Haas, 1990
	Bering Sea	Ventsel, Vasjutina, 1992; Joo *et al.*, 2012
	Canadian fjord, Saanich Inlet	Smith, Hobson, 1994
	Equatorial Pacific Ocean	Vørs *et al.*, 1995; Gorsky *et al.*, 1999
	Sea of Japan	Konovalova, 2003
	Dabob Bay, Washington	Horner *et al.*, 2005
	Western Subarctic Gyre	Komuro *et al.*, 2005
	Western coasts of Baja California, Mexico	Hernández-Becerril *et al.*, 2007
	Tasmanian coastal waters, Australia***	LeRoi, Hallegraeff, 2006
	Yellow Sea	Liu, Chen, 2015
	North Pacific Ocean	Višić, 2018
Indian Ocean	West Indian Ocean	Thorrington-Smith, 1970
	Oceanic part of the Indian Ocean	Norris, 1971 (cit.: Norris, 1984)
	Red Sea, Gulf of Elat (Gulf of Aqaba)	Thomsen, 1978
	Victorian coastal waters*** (southeastern Australia)	Beech, 1983 (cit.: LeRoi, Hallegraeff, 2006)
	Gulf of Carpentaria***	Hallegraeff, Jeffrey, 1984
	Tasmanian coastal waters, Australia***	LeRoi, Hallegraeff, 2006
Southern Ocean	Weddell Sea**	Buck, Garrison, 1983
	South of Australia	Marchant, Scott, 2005

Note: ***** — marked as belonging to the Arctic and the Atlantic Ocean both; ****** — marked as belonging to the Atlantic and the Southern Ocean both; ******* — marked as belonging to the Pacific Ocean and the Indian Ocean both.

Discussion

Analysis of morphological features of *Meringosphaera mediterranea*

Cells of *Meringosphaera mediterranea* have silica scales (Yoshida *et al*., 2006). Previously this species was investigated with a transmission electron microscope (TEM) by Leadbeater (1974), Moestrup (1979), McGrory, Leadbeater (1981), Hallegraeff (1983), Hoepffner, Haas (1990), Preisig (1994), Marchant, Scott (2005), and LeRoi, Hallegraeff (2006). The SEM investigations were performed by Booth *et al*. (1982), Hallegraeff (1983), Norris (1984), Marchant, Scott (2005), Bosak *et al*. (2012a), Liu, Chen (2015), and Zlatogursky *et al*. (2021). Also, few SEM microphotographs of *M. mediterranea* are published in the WorldWeb (Young *et al*., 2017; Karlson *et al*., 2020). Even though many authors studied *M. mediterranea* using electron microscopy, only a few of them provided detailed morphological descriptions of this species.

According to Lohmann (1903), cells of *M. mediterranea* are 6.5 μm in diameter, but other researchers recorded both smaller and larger sizes (Table 2). The smallest cell diameter (3.0 μm) was reported by Thorrington-Smith (1970); the largest one (up to 9.0 μm) — by Pascher (1939), Marchant, Scott (2005), and Zlatogursky *et al*. (2021). In our material cell diameter varied from 6.0 to 9.5 μm.

The spine scale's length in *M. mediterranea* varies considerably (Table 2). The minimal length of spine scales (5 μm) was reported by Thorrington-Smith, but the author noted that "shorter spines (5 μm) present only with long spines (30 μm)" (Thorrington-Smith, 1970: 55). The longest spine scales were reported by Hallegraeff (1983): from 30 to 40 μm. According to Pascher (1939), the spines were up to six times longer than the cell diameter. In our material spine scales 16–22 μm long.

Table 2

Comparison of some morphological features of *Meringosphaera mediterranea*

Cell diameter, μm	Spine scales length, μm	Plate scales size, μm	References
6.0–9.5	16–22	2.2–2.6 × 1.2–1.5	This study
6.5	na	na	Lohmann, 1903
5.0–9.0	up to 6 times longer than cell diameter	na	Pascher, 1939
3.0–6.0	5–30 (usually 10–20)	na	Thorrington-Smith, 1970
na	30–40	0.4 × 0.8	Hallegraeff, 1983
5.0–9.0	13–15	0.4 × 0.8	Marchant, Scott, 2005
5.0	15–20	na	Hoepffner, Haas, 1990
na	14–19	2.5–3.1 × 1.7–1.9	LeRoi, Hallegraeff, 2006
na	10–12	na	Bosak *et al*., 2012a
4.0–9.0	16–25 (a single 31)	1.8–3.2 × 1.4–2.1	Zlatogursky *et al*., 2021

Note: na — not available.

Information on the plate scale size of *Meringosphaera mediterranea* is also scarce (Table 2). In our material, the plate scales had a size more or less similar to that recorded by LeRoi, Hallegraeff (2006), and Zlatogursky *et al.* (2021). On the other hand, Hallegraeff (1983) and Marchant, Scott (2005) reported smaller size plate scales (0.4×0.8 μm), which is several times smaller than was shown for our material and by other authors.

Further we address few questions concerning the morphology of this taxon.

Spine scales. The first is the exact location of the spine scales. Leadbeater (1974) indicated that spine scales are lying on the top of the plate scales, but Booth *et al.* (1982) showed that "flattened base of the spine lay under and was obscured by the scales with the shaft projecting out between the scales" (Booth *et al.*, 1982: 187). On the photo provided by Young *et al.* (2017: File name: JRYSEM-305-020.JPG) the spine scales are clearly lying on the top of the plate scales. We can not make an unambiguous conclusion on the location of the spine scales. Only in one case, we can see that the spine scale appears under the plate scales, but in most cases, the spine scales are visible on the top of the plate scales (Plate 1: 4, 6, 7). In both cases, the arrangement of the spine scales may not correspond to the vital one, such pattern may be a result of an improper fixation. Nevertheless, we can make several assumptions about the formation of both types of scales.

1. Both scales are produced within a silica deposition vesicle (SDV), transported to the cell membrane, and extruded. This way of formation of cell silica structures has been described for many organisms, e.g., chrysophytes and diatoms (Archibald *et al.*, 2017).

2. Apparently, the plate scales form first, and then mature plate scales occupy the correct position on the cell surface; after that, the spine scales are developed and extruded.

3. Probably the spine scale morphogenesis is similar to that in *Mallomonas* when they are being "as flat sheets and then rolled into hollow tubes, which are then hinged to the scales" (Archibald *et al.*, 2017: 345).

We detected some morphological features of *Meringosphaera mediterranea* spine scales, which were not discussed previously. The base of each spine scale has a cut-out (indent), which is clearly seen under SEM (Plate 1: 4–7). It was also visible in the illustrations of Moestrup (1979: Fig. 2), but the author did not describe them in the text. The same morphology of the base spine scales features for specimens that were studied by Zlatogursky *et al.* (2021: Fig. 3c), marked as "notch on the spine scale base". Along the edge of each spine scale base, short conical regular protuberances are presented ("serrated margin" according to Leadbeater (1974)) (Plate 1: 4–7). In our material the same short teeth (protuberances) are present. In Zlatogursky *et al.* (2021: Fig. 3c) multiple short teeth along the margin of the spine scale base are visible (marked as "spikes on the spine scale base"), but they are clearly longer compared to the same structures in our specimens. Notable, each spine scale of our specimens has a "rosette", generated by 4 short barbs which are located near the base (these barbs are arranged in a circle) (Plate 1: 4–7). The same "rosettes" are visible in the illustration of Preisig (1994: Fig. 2).

We point out that some specimens identified as *Meringosphaera mediterranea* by Liu, Chen (2015) and Young *et al.* (2017) have some differences in the morphology of spine scales: the scales shown in SEM photos (Liu, Chen, 2015: Fig. 1d; Young *et al.*, 2017: File name: JRYSEM-317-030.JPG) are obviously more sinuous and have longer protuberances on their bases, than in our material. Such morphological variability probably depends on environmental factors, in particular, with silicon availability. Also, we can assume that is other but similar to *M. mediterranea* species.

Plate scales. We analyzed the morphological features of *Meringosphaera mediterranea* plate scales, which were shown in some TEM studies, and quite recently in SEM. According to Leadbeater's (1974: Pl. 4F) and Moestrup's (1979: Fig. 2) TEM observations, the plate scales had the narrow central ridge (central narrow thickening). Interestingly, that LeRoi and Hallegraeff wrote that "plate scales ... [...] had a narrow raised central thickening (Fig. 3b)" (2006: 219), but this central thickening was not recognizable on the microphotograph. In our SEM study, the ridge was not detected on the outer surface of the plate scales, but it was found on their interior surface (Plate 1: 5–7). Zlatogursky *et al.* (2021: Fig. 3c) also detected short central thickening on the plate scale.

Chloroplasts/photosynthetic bodies. Unfortunately, we were able to study only fixed material and therefore could not distinguish cell's protoplast, including chloroplasts [or "photosynthetic bodies" according to Zlatogursky *et al.* (2021)]. However, some authors noted their presence in this organism cells. For example, Lohmann (1903) wrote about green chloroplasts in cells of *Meringosphaera mediterranea*; Norris (1984: 142) reported "each cell containing several golden-coloured chloroplasts"; this species cells contained 3–6 parietal chloroplasts according to Tomas (1997). According to Zlatogursky *et al.* (2021), all the specimens, which were observed in LM, contain several globular photosynthesizing bodies about 2 μm in diameter and the chlorophyll autofluorescence was clearly visible.

The micromorphological characters are important for evaluation of the status of *Meringosphaera mediterranea* populations from different regions, because some specimens on photos and descriptions, put under this species epithet, have differences. Also, the study of living cells and/or electron microscopic and molecular investigation will help to understand the nature of photosynthetic bodies.

Distribution of *Meringosphaera mediterranea*

We analyzed 80 papers referred to *Meringosphaera mediterranea*, from the first findings in the Baltic Sea and the Mediterranean Sea to modern ones. The species was recorded in more than 80 locations in different parts of the World Ocean (Table 1). The analysis of this information is complicated because the authors generally did not provide geographical coordinates and/or quantitative species characteristics (e.g., species abundance) and provided only some general lists of taxa found during their often large-scale surveys (e.g., Buck, Garrison, 1983; Okolodkov, 1997; Lovejoy *et al.*, 2002; Komuro *et al.*, 2005; Bouza, Aboal, 2008; Blais *et al.*, 2017). In some papers, the species lists were

presented for certain regions (e.g., Parke, Dixon, 1964, 1976; Ivanov, 1965; Caraus, 2002; Marchant, Scott, 2005), but without geographical coordinates and quantitative indicators too. It should be noted that data on *M. mediterranea* abundance were represented only in 17 (out of 80 analyzed) publications. However, even scant information is important for understanding the global distribution of this species.

The Arctic Ocean. Records of *Meringosphaera mediterranea* in the Arctic seas were present in 17 publications. The highest abundance of *M. mediterranea* in the Arctic seas was reported for the Chukchi Sea and the Canadian Basin in July–September 2008 (5.47×10^3 and 8.40×10^3 cells l^{-1}, respectively) (Joo *et al.*, 2012). In Hudson Bay and Hudson Strait *M. mediterranea* was recorded as abundant species with a maximum of 2.40×10^3 cells l^{-1} (Harvey *et al.*, 1997). Simard *et al.* (1996) reported 4.00×10^3 cells l^{-1} for the same localities. For the Arctic seas (Barents, White, Kara, Laptev, East Siberian, and Chukchi), including sea costs of Russia, *M. mediterranea* remains unnoticed only in the White Sea. In the Kara Sea, the abundance of *M. mediterranea* was 0.80×10^3 cells l^{-1} (Sukhanova *et al.*, 2011). In this study, we present data on *M. mediterranea* in the East Siberian Sea and the Laptev Sea. In the East Siberian Sea, the abundance was 0.03×10^3 cells l^{-1} (surface) and 0.12×10^3 cells l^{-1} (15.5 m depth). In the Laptev Sea, this species was recorded for the first time and was found in 2 sites with an abundance of 0.08×10^3 cells l^{-1} (surface) and 0.02×10^3 cells l^{-1} (20.0 m depth). These values are significantly lower than analogous ones for the seas of Canada. In the Arctic region, *M. mediterranea* was noted not only in the water column but also in sub-ice assemblages, melt pools, multi-year and first-year ice (Booth, Horner, 1997; Okolodkov, 1997; Melnikov *et al.*, 2002; Lee *et al.*, 2015).

The Atlantic Ocean. Records of *Meringosphaera mediterranea* in the Atlantic Ocean were present in 44 publications, with 19 papers concerned the Mediterranean Sea. Moreover, basically, these investigations are either devoted to the morphological data on the species, or this species is represented in the check-list among other species of the region. Information about *M. mediterranea* abundance is given only by Šupraha *et al.* (2011) for the Adriatic Sea (1.40×10^3 cells l^{-1}). We decided to analyze the seasonality of *M. mediterranea* in the Mediterranean Sea, however, it is rather difficult to conclude the occurrence of this species. In general, *M. mediterranea* was recorded in different seasons, for example, in the autumn-winter period (Lohmann, 1903; Malinverno *et al.*, 2003), in August–September (Leadbeater, 1974), and April (Oviedo *et al.*, 2014). However, it is impossible to conclude in which season this species dominates, since the publications provided some summarized data on certain periods (a year or several years), without qualifying reference in which season the species was recorded (Sarno *et al.*, 1993; Totti *et al.*, 2000; Vadrucci *et al.*, 2004; Bouza, Aboal, 2008; Bosak *et al.*, 2012b; Cerino *et al.*, 2012). In general, for the Atlantic Ocean maximal abundances of *M. mediterranea* were recorded in the Black Sea (60.00×10^3 cells l^{-1}) (Morozova-Vodyanitskaya, 1954), the Celtic Sea (58.70×10^3 cells l^{-1}) (Joint, Pomroy, 1986), and the Baltic Sea (20.00×10^3 cells l^{-1}) (Lohmann, 1908). In the North Sea, *M. mediterranea* was occasionally recorded in summer and autumn 1991 (Kuylenstierna, Karlson, 1994). Estep *et al.*

(1984) found *M. mediterranea* at different depths (1, 10, 35, and 65 m) at 8 (out of 10) stations along the latitude of 24°30'N from south of Canary Islands to South Florida in August–September 1981. In general, we can conclude, that in the Atlantic Ocean *M. mediterranea* occurs quite often in the plankton in different seasons.

The Pacific Ocean. Records of *Meringosphaera mediterranea* in the Pacific Ocean are represented in 20 publications. Most records are from the coastal regions of North America, Australia, and New Zealand. Thus, in the surface samples from the Gulf of Alaska (Booth *et al*., 1982) in May and June 1978 the maximum abundance of *M. mediterranea* was 80.00×10^3 cells l^{-1}. For the Bering Sea, the maximum abundance of this species was 5.27×10^3 cells l^{-1} (Joo *et al*., 2012). For North-West Shelf (Australia) *M. mediterranea* was listed among dominants and subdominants, however, abundance was not given (Hallegraeff, Jeffrey, 1984). For Tasman Bay, the abundance of *M. mediterranea* in the spring was 3.60×10^3 cells l^{-1} (MacKenzie, Gillespie, 1986). In addition, *M. mediterranea* was recorded in the Tasmanian and Australian coastal waters (LeRoi, Hallegraeff, 2006). For the Western coasts of Baja California (Mexico) this species was listed as "very common", but without data on abundance (Hernández-Becerril *et al*., 2007).

The Indian Ocean. For the Indian Ocean, there were 6 publications in which *Meringosphaera mediterranea* was recorded. In the West Indian Ocean *M. mediterranea* "was one of the most common and abundant species, occurring at every station and in abundance greater than 50 cells l^{-1} at every station except five" (Thorrington-Smith, 1970: 55); the maximum abundance was 1.90×10^3 cells l^{-1}.

The Southern Ocean. For the Southern Ocean, a single collapsed specimen of *Meringosphaera mediterranea* was found in the Weddell Sea ice-edge region during the Austral summer of 1980 (Buck, Garrison, 1983). *Meringosphaera mediterranea* is recorded in the list of Antarctic protists (Marchant, Scott, 2005), but without data on the region, geographic coordinates, and species abundance.

A convenient tool for analyzing the species distribution is the databases (DBs) where each find is supplied with geographical coordinates. The main sources for DBs are unpublished results of various expeditions and voyages, research works, and results of the analysis of the collections. Thus, the DB GBIF[4] (Meringosphaera..., 2019) contains 332 georeferenced records of *Meringosphaera mediterranea* from 34 occurrence datasets. Summarizing the data, it can be noted that the largest number of *M. mediterranea* records (178) is confined to the Mediterranean Sea, predominantly (173) produced by long-term plankton studies at the fixed coastal station in the Gulf of Naples (Italy). For the Black Sea 54 records of *M. mediterranea* in various parts of the basin are present; for the coastal waters of Australia and Tasmania — 55 records; for the coastal waters of Norway and Sweden — 32. There are 11 records of *M. mediterranea* from the Indian Ocean made on the basis of 6 different surveys (Meringosphaera..., 2019).

Comparing the published sources on the distribution of *Meringosphaera mediterranea* (Table 1) and the GBIF data (Meringosphaera..., 2019) it can be noted that

[4] Global Biodiversity Information Facility.

they complement each other. For example, data from Table 1 indicate the occurrence of this species in the Mediterranean and the Black seas, in the coastal waters of Australia and Norway, however, data on plankton species presented in the GBIF (Meringosphaera..., 2019) allow expanding and clarifying the distribution of *M. mediterranea* in these water areas. In addition, for some areas (the coastal waters of Antarctic and Indian oceans, the coastal waters of Norway) represented in the GBIF (Meringosphaera..., 2019) we did not find data in the analyzed literature. On the other hand, an analysis of published sources made it possible to point out numerous records of this species in the Arctic, Atlantic, and Pacific oceans that were not reflected in the GBIF. In our opinion, such data sources combining is necessary for revealing of the species distribution range. Therefore, the distribution map for *M. mediterranea* in the World Ocean (Fig. 1) was based both on published (Table 1) and the GBIF (Meringosphaera..., 2019)[5] data. The map of *M. mediterranea* occurrence in the World Ocean is presented by Zlatogursky *et al.* (2021), but our map (Fig. 1) shows findings of this species, which are absent in Zlatogursky *et al.* (2021). In particular, we marked *M. mediterranea* in the seas of Japan and Okhotsk, in different Arctic seas (the Norwegian, Barents, Kara, Chukchi, and Beaufort seas), which are not given by Zlatogursky *et al.* (2021). Also, *M. mediterranea* was repeatedly indicated by different authors for the Black Sea (Table 1) and data on its numerous findings in the Black Sea are also given in the GBIF (Meringosphaera ..., 2019). In addition, Zlatogursky *et al.* (2021) indicate that *M. mediterranea* inhabits at the salinity of 32 to 41 ppt and never occurs at salinity below 28 ppt. However, the average salinity of the Black Sea is significantly lower than the average oceanic salinity and amounts to 17.5 to 19 ppt (surface water) and 22 ppt (deep water) (Sorokin, 2002). Therefore, probably, *M. mediterranea* is able to inhabit a wider salinity range, which is important for understanding the ecology of the species.

Thereby we can conclude that *Meringosphaera mediterranea* is widespread and occurs in all oceans, both in coastal and in open waters, at different depths and in different seasons. In general, most researchers point to sporadic findings and low abundance of the species in samples [the maximum abundance of *M. mediterranea* was detected in the Gulf of Alaska (see Booth *et al.*, 1982)]. Probably due to *M. mediterranea* small size, it is often overlooked in the plankton samples. Analysis of the *Meringosphaera* sequence metabarcoding dataset shown its global distribution with maximum relative abundances in surface waters (Zlatogursky *et al.*, 2021).

Thus, we believe that the data on the global distribution of *Meringosphaera mediterranea* summarized in this work, as well as the analysis of its morphology are important for further studies. With a high probability, there exist other species closely related to *M. mediterranea*. For this reason, subsequent morphological and molecular studies of different *Meringosphaera*-like morphotypes are necessary.

[5] Fig. 1 shows only those GBIF records (Meringosphaera..., 2019) that are not mentioned in published sources (Table 1).

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