

Morphological characterization of biominerals from five multicellular marine algae species

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A. M. ZAKHARENKO¹, M. A. NAWAZ^{1*}, V. V. CHAIKA¹,
I. V. ZEMCHENKO¹, T. YU. ORLOVA², A. A. BEGUN²,
R. V. ROMASHKO³, A. N. GALKINA³, A. A. KARABTISOV⁴,
G. CHUNG⁵, K. S. GOLOKHVAST^{1, 6*}

¹ Far Eastern Federal University,
8 Sukhanova St., Vladivostok 690091, Russia
✉ *amjad_ucauos@yahoo.com; rarf@yandex.ru;
chayka.vv@dvfu.ru

² Center for Toxic Algae and Algal Blooms Monitoring
in Coastal Waters,
A.V. Zhirmunsky Institute of Marine Biology,
17 Palchevskogo St., Vladivostok 690041, Russia
✉ torlova06@mail.ru

³ Institute of Automation and Control Processes,
Far Eastern Branch of the Russian Academy of Sciences,
5 Radio St., Vladivostok 690041, Russia
✉ omashko@iacp.dvo.ru

⁴ Far Eastern Geological Institute,
Far Eastern Branch of the Russian Academy of Sciences,
159 Pr. 100-letiya Vladivostoka, Vladivostok 690022, Russia
✉ karabzov@fegi.ru

⁵ Chonnam National University,
Yeosu, 59626, Republic of Korea
✉ chung@chonnam.ac.kr

⁶ N.I. Vavilov All-Russian Institute of Plant Genetic Resources,
42, 44 Bolshaya Morskaya Street,
St. Petersburg 190000, Russia
✉ *droopy@mail.ru

Морфологическая характеристика биоминералов из пяти видов морских водорослей

A. M. ЗАХАРЕНКО¹, М. А. НАВАЗ^{1*}, В. В. ЧАЙКА¹,
И. В. ЗЕМЧЕНКО¹, Т. Ю. ОРЛОВА², А. А. БЕГУН²,
Р. В. РОМАШКО³, А. Н. ГАЛКИНА³, А. А. КАРАБЦОВ⁴,
Г. ЧАНГ⁵, К. С. ГОЛОХВАСТ^{1, 6*}

¹ Дальневосточный федеральный университет,
690091 Россия, г. Владивосток, ул. Суханова, 8
✉ *amjad_ucauos@yahoo.com; rarf@yandex.ru;
chayka.vv@dvfu.ru

² Национальный научный центр морской биологии им. А.В. Жирмунского,
690041 Россия, г. Владивосток, ул. Пальчевского, 17
✉ torlova06@mail.ru

³ Институт автоматики и процессов управления
Дальневосточного отделения Российской академии наук,
690041 Россия, г. Владивосток, ул. Радио, 5
✉ romashko@iacp.dvo.ru

⁴ Дальневосточный геологический институт
Дальневосточного отделения Российской академии наук,
690022 Россия, г. Владивосток,
пр. 100-летия Владивостока, 159
✉ karabzov@fegi.ru

⁵ Национальный университет Чоннам,
59626 Йосу, Республика Корея
✉ chung@chonnam.ac.kr

⁶ Федеральный исследовательский центр
Всероссийский институт генетических ресурсов
растений имени Н.И. Вавилова,
190000 Россия, г. Санкт-Петербург, ул. Б. Морская, 42, 44
✉ *droopy@mail.ru

Silica biominerals are deposited as amorphous solid structures in plant cells and tissues, providing rigidity to different plant parts and assisting in defence. The shape and size of phytoliths are well established and serve as a useful tool in taxonomic analyses. For the first time we extracted and studied silica biominerals of five marine macroalgae, which we observed by light microscopy, scanning electron microscopy, and X-ray diffraction analysis (XRD). More than nine different morphotypes of phytoliths ranging from ≥ 10 to ≥ 350 μm in size were found. Some of them were phytoliths made of silica while others showed characteristics of different minerals of calcium. In our study, the "honeycomb" formations were only recorded in *Laurencia tropica* Yamada and pyramid tabular ones were found only in *Tichocarpus crinitus* (S.G. Gmelin) Ruprecht. The XRD analysis showed that they consisted of virgilite and gypsum substance, respectively. Silica phytoliths are intrinsic parts of the algae and their morphological characterization can provide the basis for palaeo-reconstruction and taxonomic investigation of brown and red algae in palaeontological studies of fossils where all organic matter has decayed.

Key words: biosilica, morphotypes, phytoliths, taxonomic analysis.

Кремниевые биоминералы расположены в виде аморфных структур в клетках и тканях растений, обеспечивая жесткость структуры и защитные функции. Форма и размеры фитолитов хорошо известны и являются полезным инструментом в таксономическом анализе. Впервые мы извлекли и изучили биоминералы кремнезема из пяти морских макроводорослей, которые мы изучили с помощью световой микроскопии, сканирующей электронной микроскопии и рентгеноструктурного анализа (XRD). Было обнаружено более девяти различных морфотипов фитолитов с размерами от ≥ 10 до ≥ 350 микрометров. Часть из этих фитолитов были из оксида кремния, другие из минералов на основе кальция. Гексагональные «сотоподобные» образования были зарегистрированы только у водоросли *Laurencia tropica* Yamada, а фитолиты пирамидальной формы были обнаружены только у красной водоросли *Tichocarpus crinitus* (S.G. Gmelin) Ruprecht. Рентгеноструктурный анализ показал, что они состоят из виргилита и гипса соответственно. Кремниевые фитолиты являются неотъемлемыми частями водорослей, и их морфологическая характеристика может служить основой для палеорекострукции и таксономического исследования бурых и красных водорослей в палеонтологических исследованиях окаменелостей, где вся органическая материя уже разложилась.

Ключевые слова: биргенный кремний, морфотипы, фитолиты, таксономический анализ.

Introduction

Algaculture is the only aquaculture industry involved in plant production, i.e., primary production. Algaculture is focused on marine, estuarine and freshwater algae (Romanenko et al., 2017; Çelekli et al., 2019). There is no doubt that the process of biomineralization inherent to terrestrial plants is also present in algae. Biominerals are ubiquitous in all classical kingdoms of life: in the ocean, in inland waters, and on land. Interestingly, different members of kingdom plantae produce a suite of rigid microscopic biominerals of various compositions i. e., silicon dioxide (silica), calcium carbonate, calcite (calcite coccoliths), and calcium oxalate (cystoliths) with significant quantities of phosphorous, magnesium, aluminium, etc. Biomineralization (silicification and calcification) has arisen very early in plant lineages, i.e., red algae (Florideophyceae), green algae (Ulvophyceae and Charophyceae), brown algae (Phaeophyceae), and Prymnesiophyceae (Raven and Giordano, 2009). Calcium carbonate and/or calcium oxalate accumulates in red and brown algae extracellularly and intracellularly, respectively (Rao et al., 2014). Silica also accumulates in some green and brown algae and is thought to be mainly located on intracellular compartment, i.e., in cell-walls (Parker, 1969). Strictly speaking, phytoliths are amorphous silica deposits, while distinctions for other types of biominerals exist; however, for the purpose of this study, the term “phytolith” will be generalized to all types of observed biominerals in target species. Phytoliths can also be deposited within different intracellular and extracellular structures of plants and, being inorganic matter, they remain as discrete microscopic particles of various shapes and sizes and are, possibly, the most resilient plant fossils (Cuif et al., 2010). Silica provides rigidity to different seaweeds, assists in the protection of reproductive tissues, and aids seaweed growth (Mizuta, Yasui, 2012). Whereas deposited forms of calcium in plants and algae have debateable functions, such as mechanical support, enhancement of photosynthesis by bicarbonate uptake, and it is known that the occurrence of photosynthesis decreases the carbon dioxide production during calcification and affects the net carbon dioxide uptake (Raven and Giordano, 2009).

The utility of phytoliths in fossil and archaeological reconstruction of plant has become a major application (Piperno, 2006; Currie and Perry, 2007). Plant phytoliths are used in taxonomic analyses, paleo-ecological and archaeological studies (Ball et al., 2016; Hodson, 2016; Zurro et al., 2016). Considerable size and structural variation in phytoliths has been reported in many plant species and been used to determine plant species in particular environments or to date fossil samples (Hodson, 2016). Moreover, the shape of individual phytoliths could possibly yield broader group assignment and more precise taxonomic ranking (Song et al., 2016; Zurro et al., 2016). However, phytoliths in seaweed have not been studied extensively, especially their morphology and difference between seaweed and plant phytoliths.

Frequent occurrence of crystalline idioblasts (calcic mineral, crystalline calcium oxalate) in plants confirms that it is the most widespread crystalline biomineralization product in the plant kingdom. These idioblasts are formed of weddellite and whewellite in plants, e.g., cacti (*Carnegiea gigantea* (Engelm.) Britton & Rose), and are converted from weddellite to calcite, which is deposited for longer times and may also serve as carbon sink (Garvie, 2003). Interestingly, phytoliths (especially of calcium nature) can be

cubic, parallelepipedal, tubular oblong, pyramidal, cylindrical polylobate, and of many other defined geometric shapes (Morgan-Edel et al., 2015). While amorphous silica biominerals with unique identifiable characteristics are produced in large quantities in different groups within the plant kingdom and hence, phytolith surface ornamentation, length, thickness, shape, frequency, and geometry are the basic identification characteristics observed using several microscopic techniques, such as light, transmission electron microscopy, scanning electron microscopy (SEM), and X-ray diffraction (XRD) analysis) (Piperno, 2006).

In this study, we used light microscopy, SEM, and XRD for morphological and compositional categorization of phytoliths in three species of red algae (*Mastocarpus stellatus* (Stackhouse) Guiry, *Tichocarpus crinitus* (S.G. Gmelin) Ruprecht, and *Laurencia tropica* Yamada) and two species of brown algae (*Saccharina latissima* (L.) C.E. Lane, C. Mayes, Druehl & G.W. Saunders, *Fucus evanescens* C. Agardh), which are found on the Russian side of the Sea of Japan (Maggs, Stegenga, 1999; Garbary, Tarakhovskaya, 2013). These morphological characterizations will provide the basis for palaeontological studies where the differences in morphology of inorganic remains of algae may prove useful for their taxonomic identification.

Materials and Methods

Extraction of phytoliths

Three species of red algae, *M. stellatus*, *T. crinitus* and *L. tropica*, and two species of brown algae, *S. latissima* and *F. evanescens*, were used in the study. Five specimens of each species were collected at depths of 3–6 m from the Sea of Japan (45°01'21.2"N 136°42'23.3"E); they were identified using monographs, floristic studies, and systematic articles (Saunders, Hommersand, 2004; Zuccarello et al., 2005; Belous et al., 2013). Then algae were placed into plastic containers and stored at –5°C for two days. Phytoliths were extracted using the modified Piperno technique (Piperno, 2006). Approximately 30–50 g of thalli per sample were washed with distilled water twice and burned in covered ceramic-enamelled crucibles in a muffle furnace at +450°C for 4 hrs. The ash was then transferred into glass centrifuge tubes and washed thoroughly with 10 ml of 10% HCl and concentrated nitric acid for 10 minutes, with periodic stirring of the test tube. The samples were then rinsed twice with 10 ml of distilled water and centrifuged for 10 min at 150 g, followed by decanting of water, leaving 0.5 ml mixture in the test tube. A further 200 µl of solution was removed from the test tube bottom with a pipette and the mixture was subjected to microscopy. The remaining solution was used for XRD analysis.

Microscopic investigation

The processed samples were individually placed on a microscope slide. They were examined within one hour on an AxioScope A1 light microscope (Zeiss, Germany) using an AxioCam 3 digital video camera (Zeiss, Germany). The length and width of each particle were measured using the Axio Vision 4.2 program (Zeiss; Oberkochen, Germany). Their morphologies were evaluated by SEM using a Hitachi S-3400N (Hitachi; Tokyo, Japan) with an ultra-dry energy dispersive spectrometer (Thermo Fisher Scientific; Waltham, MA, USA) or with a tabletop SEM TM1000 (Hitachi; Tokyo, Japan). When examined under the S-3400N microscope, the samples were sprayed with platinum; they remained unsprayed when using the TM1000. The definitions of morphotypes as well as the descriptions of phytoliths and

other unidentified mineral particles were carried out according to the International Code for Phytolith Nomenclature 1.0 (Madella et al., 2005).

Mineralogical analysis

Biomineral particles were characterized by XRD analysis. Solutions containing the washed sediments were placed in plastic vials and left to dry completely for 24 hours at ambient temperature; the dry mass was used for mineralogical analysis. The determination of mineral type was carried out using a Maniple Bench Top X-ray Diffraction Analyzer (Riau; Tokyo, Japan), with 30 kV, 15 mA, and monochrome settings.

Results and Discussion

Phytoliths have been recently recognized as proxies to reconstruct ancient environment, flora, and a tool for taxonomy. The low solubility of biominerals makes them a relatively durable component of sedimentary deposits (Schiegl

et al., 2004; Cabanes et al., 2011). The role of calcium and silicon phytoliths in defense against biotic and abiotic stress is well recognized and is progressing with improved understanding of various biochemical pathways (Nawaz et al., 2019). However, this development has been mainly witnessed in land plants. Biomineralization of calcium and silicon compounds in algae has not been explored in detail and description of biominerals in many macroalgae is scarce. More than a dozen types of mineral formations were revealed by light microscopy in the investigated macrophytes. Some of them were phytoliths made of silica, while others showed characteristics of different minerals of calcium (Table 1, Fig. 1).

The distribution and morphologies of biominerals varied among the studied species. The representative samples of biomineral formations found in the five algae studied are shown in Fig. 2. Microscopic examination of algal species (*S. latissima*, *F. evanescens*, *M. stellatus*, *T. crinitus*, and

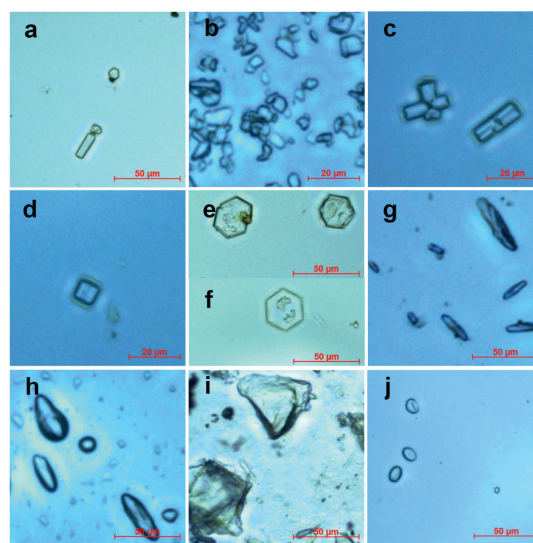


Fig. 1. Morphologies of biominerals in algae:

(a–d) showing hexagonal, rectangular, square tabular and unclassified biominerals in *Mastocarpus stellatus*; (e–h) showing hexagonal, cylindrical/oblong, globular/ovate tabular, and fusiform in *Tichocarpus crinitus*; (i) showing rectangular tabular in *Fucus evanescens*; (j) showing fusiform in *Saccharina latissima* (by: Golohvast et al., 2018)

Рис. 1. Морфология биоминералов в водорослях:

(a–d) показаны шестиугольные, прямоугольные, квадратно-пластинчатые и неклассифицированные биоминералы у *Mastocarpus stellatus*; (e–h) показаны шестиугольные, цилиндрически-продолговатые, округло-овальные, округло-овальные пластинчатые и веретенообразные у *Tichocarpus crinitus*; (i) показаны прямоугольно-пластинчатые у *Fucus evanescens*; (j) показаны веретенообразные у *Saccharina latissima* (по: Голохваст и др., 2018)

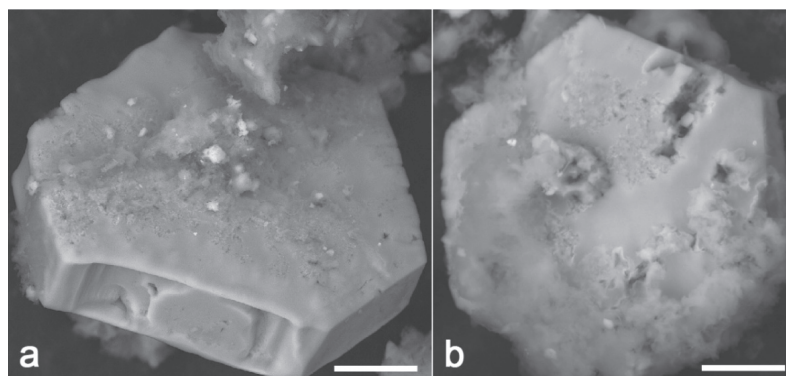


Fig. 2. Hexagonal crystals of an unknown mineral in *Tichocarpus crinitus* preparations observed. Scale bar = 10 µm.

Рис. 2. Шестиугольные кристаллы неизвестного минерала в изученных препаратах *Tichocarpus crinitus*. Шкала = 10 µm.

Table 1. Morphotypes and size of mineral formations (in μm) found in five macrophyte preparations. L = maximum length; W = maximum width

Таблица 1. Морфотипы и размеры минеральных образований (в μm), обнаруженных в пяти макрофитных препаратах. L = максимальная длина; W = максимальная ширина

No.	Morphotype	Material	<i>Mastocarpus stellatus</i>	<i>Tichocarpus crinitus</i>	<i>Laurencia tropica</i>	<i>Fucus evanescens</i>	<i>Saccharina latissima</i>
1	Cylindrical/oblong tabular	silica or unknown		L 10–70	L 25–350		
2	Globular/ovate tabular	silica		L 5–60	L 5–45	L 10–15	
3	Fusiform	silica		W 7–25 L 15–50			L 10–25
4	Hexagonal tabular	unknown	L ~ 10	L 15–25			
5	Pyramidal tabular	silica or unknown		W 10–70 L 25–70			
6	Square tabular	unknown	L ~ 10				
7	Rectangular tabular	unknown	W 8–10 L 12–35		L 30–100	W 100–130 L ~ 50	W 15–20 L 50–60
8	Ovate favose (honeycomb)	silica			W 50–70 L 120–150		
9	Unclassified	silica or unknown	L 25–35	L 15–30	L 10–40	L 10–20	

L. tropica) revealed various structural types of phytoliths (i.e., cylindrical/oblong tabular, globular/ovate tabular, fusiform, hexagonal tabular, pyramid tabular, square tabular, rectangular tabular, and ovate-favose) (Table 1). In our study, the “honeycomb” formations were only recorded in *L. tropica* and pyramid tabular were found only in *T. crinitus* (Table 1). The XRD analysis showed that material consisted of virgilite and gypsum substance. (Fig. 3).

In a previous study, we identified phytoliths in some brown macroalgae, such as *Fucus evanescens*, *Sargassum miyabei* Yendo, *Turbinaria ornata* (Turner) J. Agardh, and *Dictyota dichotoma* (Hudson) J.V. Lamouroux (Golokhvast et al., 2015). This is a first attempt to describe and compare the phytoliths in red and brown macroalgae. Through microscopic examination, the maximum number of morphotypes was observed in *Tichocarpus crinitus* (6) followed by

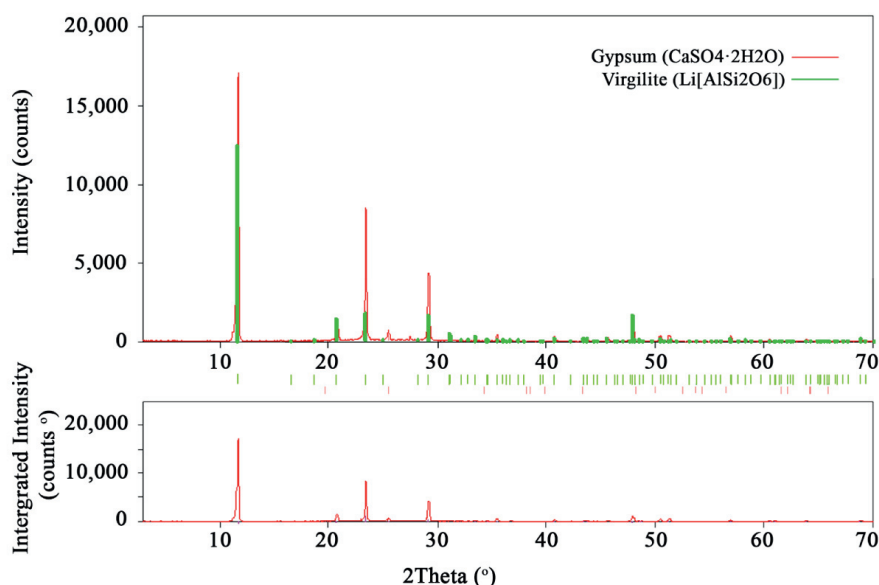


Fig. 3. A typical X-ray diffraction pattern of a mineral sample obtained after drying preparations of the red alga *Mastocarpus stellatus*

Рис. 3. Типичная рентгеновская дифрактометрия образца минерала, полученная после высушивания препаратов красной водоросли *Mastocarpus stellatus*

Laurencia tropica (5), *Mastocarpus stellatus* (4), *Fucus evanescens* (3), and *Saccharina latissima* (2). The hexagonal mineral formation in *Mastocarpus stellatus* and *T. crinitis* is the first finding of this geometrical shape in algae phytoliths. Cylindrical or oblong, pyramidal tabular, square, rectangular tabular crystals described in *Cladophorophyceae* (Leliaert and Coppejans, 2004) were also observed in this study. Cylindrical or oblong tabular forms were not found in either two brown algae. Moreover, these cryptal types also were not observed in *Turbinaria ornata*, *Sargassum miyabei*, or *Dictyota dichotoma* (Golokhvast et al., 2015), which leads to our hypothesis that cylindrical or oblong tabular phytoliths are only contained in red and green seaweeds.

The size ranges of the phytoliths in the algae examined were different from the phytoliths found in plants. In our algae samples they varied from ≥ 10 to ≤ 350 μm , while relatively smaller phytoliths (6.9–25.2 μm) have been reported in grasses (Piperno, 1984). Morphotypes of phytoliths in twelve species of marine angiosperms were also comparatively small (from 9.0 to 92.0 μm), up to 101 μm in *Arthrocnemum indicum* (Willd.) Moq. (Kumari, Kumarasamy, 2014). In our study, the smallest morphotype (square tabular, 10 μm) was found only in *Mastocarpus stellatus* (Table 1). The observation of phytoliths of fixed geometrical shapes, i.e., hexagonal, rectangular and square shapes, in studied macroalgae is of particular interest. Previously it was known that different plant species accumulated similar three dimensional crystals of calcium oxalate and calcite as examined in horsetail and creosote bush (Morgan-Edel et al., 2015). The mineralogical content of these crystals revealed that they are mainly composed of calcium and oxygen with inclusions of Al, S, and Fe (Fig. 3).

In conclusion, phytoliths of a regular hexagonal shape have been discovered for the first time in the red algae. Although limited by small sample size, the results of our study suggest that there are differences in phytoliths between studied seaweed species and higher plants. We recognize that our data have limits to understanding the diversity of phytolith morphology in seaweed and their application in reconstruction of paleo-environments. There is a pressing need of advancing the comparative collection of macroalgae phytolith morphologies.

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ORCID

Zakharenko A.M. <https://orcid.org/0000-0002-9520-8271>
 Nawaz M. A. <https://orcid.org/0000-0001-9901-7555>
 Chaika V.V. <https://orcid.org/0000-0002-7499-8577>
 Zemchenko I.V. <https://orcid.org/0000-0002-1992-8234>
 Orlova T.Yu. <https://orcid.org/0000-0002-6985-5213>
 Begun A.A. <https://orcid.org/0000-0002-8383-796X>
 Romashko R.V. <https://orcid.org/0000-0003-0869-0993>
 Galkina A.N. <https://orcid.org/0000-0002-0489-4342>
 Karabtsov A.A. <https://orcid.org/0000-0001-7022-2942>
 Chung G. <https://orcid.org/0000-0001-8053-689X>
 Golokhvast K.S. <https://orcid.org/0000-0002-4873-2281>