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FRUSTULE FUNCTIONS AND FUNCTIONAL MORPHOLOGY OF *BACILLARIOPHYTA*∗

On the basis of new data on diatom frustule functions, found in the field of nanotechnology, the conclusion was made about a multifunctional role of most frustule structural elements and their taking part in many vital functions of the diatom single-cell organism. The proposal on revision of the morphological terms for the diatom frustule description is put on the modern universal base. The concept on a possible approach to diatom functional morphology and the definitions of *the diatom frustule basic element* (= *db-element*) and *morph of the diatom frustule* (= *df-morph*) for description of fine morphology are suggested. Some structures of frustule as velum, areola, stria are considered in the light of function morphology.

K e y w o r d s : *Bacillariophyta*, diatom frustule, frustule functions, functional morphology, morphological terms, nanotechnology, db-element, df-morph, virga, vimin, velum, areola, stria.

Introduction

The diatom frustule is a unique phenomenon in Nature with the genetic reproduction of the highly organized species-specific inorganic structures which are involved in most vital functions of the enclosed protoplast. These recently discovered diatom cell frustule properties can explain why the presence of the siliceous frustule supplied the advantages in the extremely successful evolution of the *Bacillariophyta* that leads to tremendous species diversity. A complete inventory of the described species, both recent and fossil, is absent and the 40,000 species currently known are only some fraction of the several hundred thousands species estimated to exist. (http://instaar.colorado.edu/~spauldis/ web site of Sarah A. Spaulding). Wide space distribution and considerable quantitative development of the diatoms in geological time have resulted both in significant ecological and biogeochemical roles that at first has been recognized in the research works of akad. V.I. Vernadskiy who called the diatoms

∗ From the Editor:

This paper is placed for publication under the heating of "Discussion". I have sent these ms to four reviewers and received 2 responses that strongly recommended the ms for publications and 2 responses that recommended these ms to be rejected.

I decided to publish this paper anyway. The reader can decide what information is applicable to his/her research. I would be grateful to receive a continuation on the discussion, the pros and cons, of information published here.

as the Earth's siliceous life (Vernadskiy, 1923, 1978). Modern investigations estimate 20-25% of the world net primary production is created by diatoms (Werner, 1977; Treguer et al., 1995), confirm their contribution to global oxygen biosynthesis, siliceous circulation (Streett-Perrott, Barker, 2008), carbon accumulation and its sedimentation on the ocean bottom and also possible linkage of the global cycles of Si and C (Milligan, Morel, 2002).

Three-dimensional hierarchical structure of the diatom frustule, strikingly precisely and rapidly reproduced during bio-mineralization, retains numerous physical-chemical features in micro- nano- scale of size after elimination of the protoplast, that attracts powerful scientific forces from the nanotechnology field in an all-round study of the diatoms. Main directions in diatom research, in particular, diatom biology on the basis of large-scale sequencing programs, diatom cells for biotechnology (the diatoms as transporters of the nutrients from water environment with their low concentrations; cultivation for commercial production of polyunsaturated fatty acids), some aspects of silica biomineralization, properties and application of the diatom shells are represented in brief survey of Lopez et al. (2005).

The different stages of the silica biomineralization from uptake of silica acid from the aquatic environment to silica precipitation into diatom frustule and their possible mechanisms are considered by Grachev with coauthors (2008).

Progress since 2005 in *diatom nanotechnology*, a new interdisciplinary area arisen due to collaborations in biology, biochemistry, biotechnology, physics, chemistry, material science and engineering is discussed and includes 144 literature sources (Gordon et al., 2009).

Contrary to the other groups of unicellular algae which are mostly classified according to their protoplast characters, the taxonomy of the diatoms became satisfactory and generally accepted only when it had been based on the frustule morphology (Schütt, 1896). The following page of *Bacillariophyta* morphology and taxonomy was opened in the next century by electron microscopy that still enriches with new morphological data. *Functional morphology* is a new and promising perspective in all realms concerning *Bacillariophyta* study including diatom taxonomy since it can easy accumulate both previous information on the diatom frustule morphology and the data obtained in diatom nanotechnology. Thus they all together can be involved in diatom morphology and taxonomy in search of the directions reflecting the frustule evolution according to its functional perfection under the environmental variations.

It is also important to emphasize that the taxonomy, in this case, still deals with a *complete organism*, not with genome or its other parts. Moreover, functional morphology of the diatom frustule will contribute to the focus of attention on the diatom single-cell organism as a whole and will lead to understanding of the logic and cause-effect base of the morphological creations.

The aim of the present work is a selection of available information on the diatom frustule functions and a proposal on a possible approach to the diatom functional morphology when all frustule structural elements will be described on the universal basis with recognizing of their functions in diatom unicellular organism.

Results and discussion

Diatom frustule functions

Previous studies of diatoms were mainly concentrated on the description of particular frustule morphological elements that is reflected in proposed terminology for description of the diatom frustule (Anonymous, 1975; Ross et al., 1979; etc.). However the functions of frustule morphological elements were not indicated as soon as most of them were not known. Some kind of paradox consists in that for quite a long time the attention of specialists was concentrated rather on the study of the unique structures of the diatom frustule but not on its most common, universal morphological structures and specially their functions. Some functions of the raphe, fultoportulae and rimoprtulae were considered in a review on frustule morphogenesis (Schmid, 1984). Micromechanical properties of the frustule elements involved in colony formation (Gebeshuber, Crawford, 2006) and in complex linkage of the girdle band in some species of *Cocconeis* sensu lato (De Stefano, De Stefano, 2005) were discussed. However numerous of new discovered functions of the diatom frustule were not yet discussed from biological position. The brief survey both knowing and new diatom frustule functions includes following ones.

1. **Forming function**. The striking diversity of diatoms reflects *a perfect correspondence to endless variety of the environment conditions* – to biotopes. Planktonic diatoms support cell *floating ability* increasing surface area: spines, valve relief etc. Benthic epipelic diatoms possess a *streamline form* that reduces water and substrates resistance when they move. The frustule shape and functional structures of epiphytic diatoms provide *strong attachment to a substrate* even under high flow velocity. This very brief but principal survey does not include tremendous differentiation of environmental conditions that diatoms were able to adapt to and corresponding structural features developed in their frustules. In the papers on nanostructural researches of the diatom frustule the following terms are used: *siliceous skeleton, exoskeleton* that reflect this function of frustule.

2. **Increasing protoplast volume and plasmalemma surface**. Contouring of the inside frustule relief by the plasmalemma results in an increase of its own surface and, thus, provides higher effectiveness of physiological processes connected with membranes, in particularly, nutrient absorption. It can be one of possible mechanism of the well-known adaptation of many diatoms species to oligotrophic environments and their ability to uptake important nutrients such as N, P, Fe, Si from the water with nanomolar-level concentrations. The unicellular water organisms having no solid support tend to form mostly energy-economical spherical or similar body shapes.

3. An effective **mechanical protection** of the protoplast. It is provided by the frustule structure and the biosilica properties. Experimentally established data have shown that frustules both with radial and apical-transapical symmetry withstand high mechanical external pressure on the valve and girdle areas. For instance, *Thalassiosira punctigera* (Castracane) Hasle depending on a cell diameter resists force between 180 up to 260 μN with the cell diameters of 50 μm and 100 μm correspondingly. Mechanical

strength and a cell size are also inversely related between different species. The resisted pressure ranges between 1 and 7 N/mm^2 (equivalent of to 100-700 tonnes/m^2). It was also shown that frustules with apical-transapical symmetry smoothly absorb the stress by the transverse ribs from fragile areas of striae. The modeling of a ribless frustule of *Fragilariopsis kerguelensis* (O'Meara) Hust., has shown that a ribless form requires 60% less force to be broken than a model of one with ribs (Hamm et al., 2003).

4. An effective **biological and chemical protection** of the protoplast. Observation of the morphological features in two radial symmetric diatom species *Coscinodiscus* sp. and *Thalassiosira eccentrica* (Ehrenberg) Cleve by means of scanning electron microscopy and atomic force microscopy has shown that although pore organization in these species is reversed, the size range of the smallest pores in both species is around 40 nm. The conclusion was made about a common frustule function at this pore size excluding viruses or other deleterious particles and the pore size and its organization are optimized for this purpose (Losic et al., 2006). The smallest pores recorded in the frustules with apical-thansapical symmetry have size of 5-10 nm (Mann, 1981).

5. **Selective matters concentration**. Diatom frustules act as particle sorting structures, determining which particles reach the cell membrane and its receptors. Diatom surface micro-topography controls the diffusion and advection of sub-micrometer particles across their surfaces. Particles with no flow localize on the solid areas of diatom frustules and reduce the diffusion compared with those concentrated over the flat glass. Under the flow, particles are deflected from the direction of the flow by up to 170°, with over 60% of particles shifting more than 20° from the direction of the flow. This effect has an important implication for nutrient uptake and fouling of cells by colloids and particulates (Hale, Mitchell, 2001).

6. **Absorption/excretions**. It is obvious that the pore system of diatom frustules provides direct interaction between protoplast and environment for nutrient absorption and excretions of the products of the vital functions, particularly oxygen and carbon produced in photosynthesis (Pickett-Heaps et al., 1990). Fine mechanisms of these processes have not been completely investigated yet. However, there has been discovered a high sensory ability of the diatom frustule structures to different gas species, for instance, NO_2 (Bismuto et al., 2008).

7. An effective **pH buffer**. It appears that the biosilica of diatoms is an effective pH buffer, enabling the enzymatic conversion of bicarbonate into CO_2, which is an important step in inorganic carbon acquisition by these organisms (Milligan, Morel, 2002).

8. **Focusing and filtering light energy** used in photosynthesis. The photonic properties of frustules with radial (*Thalassiosira rotula* Meunier, *Coscinodiscus walesii*) and apical-transapical symmetry (*Cocconeis scutellum* Ehr.) have been studied by Stefano and coauthors (2005, 2007, 2009) and Bismuto and coauthors (2008). The silica skeleton of *C. walesii* is capable of focalizing the incoming light by areolae apertures. The UV (ultraviolent) protection hypothesis for both patterns in frustule symmetry was also experimentally confirmed by scattering (Raven, Waite, 2004). The protection

effectiveness depends mostly on the geometrical arrangement of the frustule pores and its overall thickness and it appears to be more powerful in the diatoms with radial symmetry.

9. **The transistor functions** – nerveless “brain”, a likely computer?

The above discussion on the diatom frustule functions can give the impression that a very limited number of them have been investigated so far. Nevertheless, even this small fraction suggests great perfection of the diatom organism and its frustule. Because the frustule consists of numerous silica parts of micro- nano- scales and both the material and the particle sizes are similar to the ones used in computer techniques, it seems to accomplish similar functions in similar ways – accepting and analyzing information from the outside/inside and making corresponding responses. It may look rather fantastic, but in reality the diatoms are highly intelligent.

Frustule morphology under the light of its function

Despite rapidly accumulating information (according to Grachev) the data on the functions corresponding to fine frustule morphology of the diatoms still remains fragmentary since very few of species have been investigated in that details and certainly a lot of the frustule functions have not yet been discovered. Nevertheless, it is obvious that diatom frustule morphology needs the new terminology including the data on frustule functions. It is incorrect to use for frustule morphological elements the term “*an organelle”* such as in Schmid (1984), or *organelle* (Gebeshuber, Crawford, 2006) since this term is applied for the functional units of the protoplast, an organic living part of cell and involves biochemical mechanisms. The silica frustule after completing of the bio-mineralization became of inorganic component of the diatom cell that has not direct involvolment in cell biochemical exchange of matter. Therefore frustule functional elements need own terminology.

Functional approach implies the study of the separate structures in the organism context, with determination their position and functions in the hierarchies of the whole organism. According to contemporary knowledge any diatom frustule has a principal hierarchical construction with general order: velum – areola – stria – valve – frustule. Functional approach requires a new look at the diatom frustule morphology in order to describe all of its structural units on a systematic basis when their role are defining in the organism life.

It is commonly assumed that regular shape of the diatom frustule, composed from amorphous silica, is formed under structure-directing influence of the templates. Specific biomolecules, *silaffins*, that combine two indispensable functions: 1) capability to induce silica precipitation from precursor compounds and 2) self-assembling into large, structure-directing template aggregates were identified and their physical-chemical studies on a model compound performed (Gröger et al., 2008). The results of an intensive study of the morphogenesis of the diatom frustule and the mechanism of silica precipitation have shown that the supramolecular aggregates are involved in formation of the frustule instead of single SiO_2 molecules (Gröger et al., 2008). Recent studies using high resolution atomic force microscopy, scaning electron microscopy and timelapse light microscopy have revealed a diversity of nano- and meso-scale structures in the diatom frustule, in particular, 50 nm spherical silica particles (cf. colloidl silica) (Gordon, Drum, 1994; Gordon et al., 2009). Thus, a kind of "brick" building of the diatom frustule can be recognized in morphologically homogeneous units.

The available data show that any part of the diatom frustule has special physical-chemical features the effectiveness of which increases with it being included in morphologically more complicated structures. Recently it was proposed to consider the diatom siliceous frustule as genetically reproduced in an hierarchical system of inorganic structures, consisting of basic elements and functional units (= morphs) of different orders that take part in most (all ?) vital functions of diatom single-cell organism (Bukhtiyarova, 2009).

Basic element of the diatom frustule (= db-element) is a morphologically detached, homogeneous frustule element, that possesses special physical-chemical features and provides a primary base for the frustule hierarchical construction. The evolution of the db-elements is subordinated to the functional perfection of the subsequent structures in which they are included. They belong to db-elemets of the diatom frustule as different apertures and cavities in its thickness, regularly repeated and unique silica microelemets.

Morph of the diatom frustule (= df-morph, Greek – *morphe***)** is a compound structural unit of the frustule consisting of db-elements or structural units of the lower orders or both of them, realizing particular functions for diatom single-cell organism and having its own evolution.

We prefer to use the term *morph* instead of *functional structure (unit)* since it refers to morphology taking in consideration the functional aspect and as one word can be used with different necessary epithets.

The *df-morph of the first order* (= *simple df-morph*) consists only of the db-elements. An example of it in the diatom frustule is *velum*.

The *df-morph of subsequent orders* (= *composed df-morph)* includes more than one morph type and can be accompanied by additional db-elements. It corresponds to the second or further frustule hierarchy steps. Areola and stria are characteristic examples of the composed df-morphs.

Within the final structure, i.e. frustule, db-elements and df-morphs are divided into two groups: 1) morphologically similar, consistently repeated, and 2) unique, single ones. Repeated db-elements and df-morphs being considered over vitally important functions of the diatom unicellular organism, increase their effectiveness by redundancy and higher structural organization. In other words, the effectiveness of **n** repeated db-elements or df-morphs is not just equal to their total sum effectiveness, it is of great and fresh (some new) value. Unique morphological structures perform a specialized auxiliary functions.

Because physical-chemical characteristics of any material structure depend on the size of the particles it is compounded from, we suggest to introduce of a size scale in all the definitions of the diatom frustule structures.

The approach to the development of the diatom functional morphology perhaps can be more fruitful in cases where generally accepted classic morphological terms will be conserved and renew their definitions based on the modern knowledge. The work on the renewed definitions of the diatom frustule morphological elements will certainly need the efforts from many specialists in diatom morphology and taxonomy and broad discussion. Here it is suggested new definitions for some common db-elements and df-morphs.

The examples of db-elements

The most important functions of the diatom frustule are belong to the area of the striae. The principle construction of stria includes two siliceous ribs and more thin siliceous area between them perforated by areolae. The term "rib" has unclear sense and often is used in diagnosis for functionally different elements. Therefore we renew the terms "virga" and "vimen" suggested for stria descriptions by E. Cox et R. Ross (1980).

Virga (Lat.) (**Figure**, *1-6*: v – universal repeated siliceous micro db-element in form of a long thickened bar restricting stria area and protecting it from mechanical stress.

Vimine (Lat.) (**Figure**, *2*, *5*: n – universal repeated siliceous nano db-element in form of a plates or short bars between areolae. The type and aggregate of the vimines determines the pattern of the areolar arrangement within the striae.

The examples of df-morphs

Velum is common and probably the most multifunctional df-morph in the diatom frustule. Some part of the pore occlusion types were studied in details by D.G. Mann (1981) who classified raphid diatoms into two main groups: the one that have areolae with velum in the form of *hymen* (= delicate membrane, occupying the whole pore with more or less uniform thickness and perforations) and the other – in the form of *vola* (in simplest type – non-porous flaps of silica attached to the pore wall by a broad base and extending across aperture, leaving only a curved slit by which communication may be effected between outside and the protoplast). The latter has considerably more variability when compared with the former. According to a new information about the functions of the different diatom frustule elements *velum* or *pore occlusion* are the terms mainly corresponding to this df-morph general morphology but almost totally do not reflect its functions.

In our opinion, the term *frustule converter* can be a more precise and clear term because the occlusion of the areola foramen is just one but not the main function of this df-morph. The transformation of the effects of the environmental factors in the suitable for diatom organism (protoplast) manner and values is rather the main function of it (Bukhtiyarova, 2009). For instance, UV (ultraviolent) protection by scattering (Raven, Waite, 2004).

Df-converter (= velum) is a universal regularly repeated nano- (micro-) df-morph of the first order including fine aperture (-s) and siliceous db-element (-s), located within the areola and carrying out the direct exchange functions between protoplast and environment: matters absorption/excretions, light energy focusing and filtering, biological-chemical protecting and others. Df-converter transforms the effects of the environmental factors in the suitable for diatom organism manner and values.

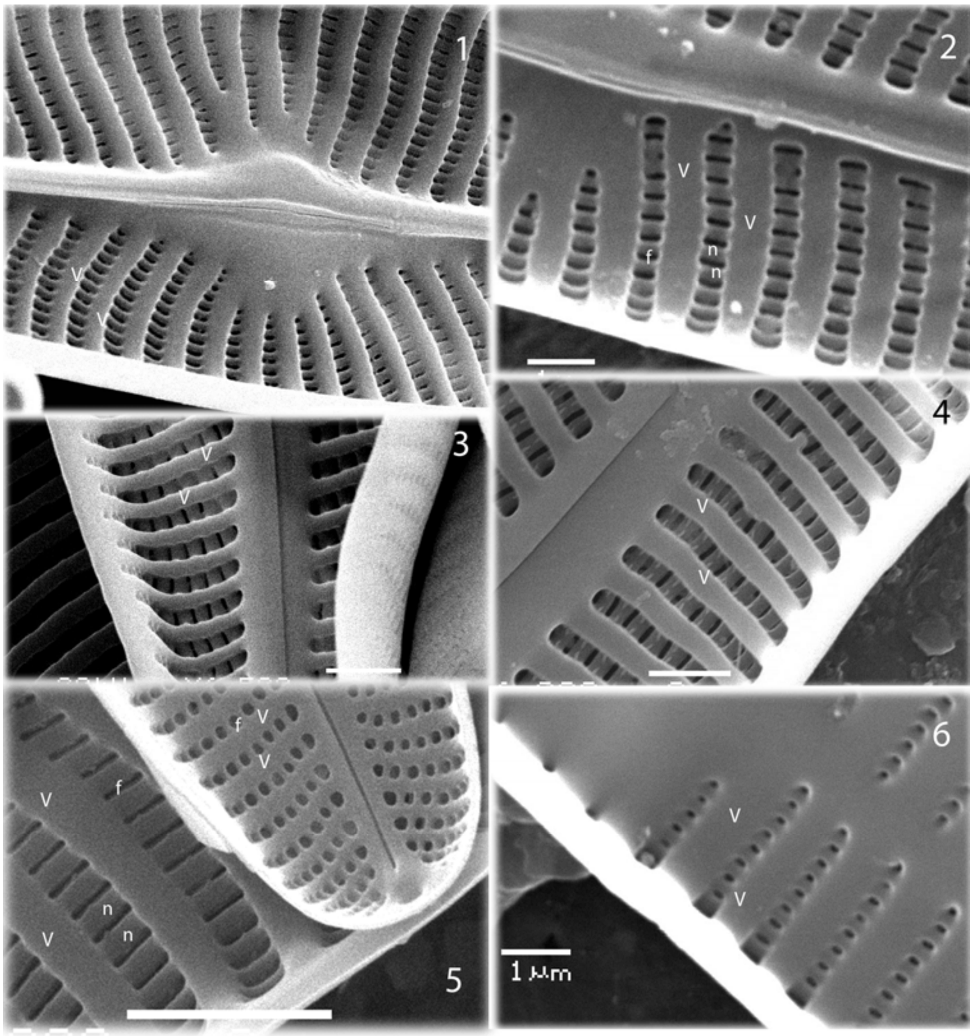

Figure. The examples of db-elements of the diatom frustule: v – virgae, n – vimine, f – foramen of areola. All valve fragments are from inside surface and have destroyed velum, so the areola foramens are visible: *1* – *Navicula* sp.; *2* – *Navicula* sp. 1; *3* – *Cymbella* sp.; *4* – *Cymbella* sp. 1; *5* – *Navicula* sp. 2 – lower valve, *Eolimna* sp. – upper valve; *6* – *Ulnaria* sp. Scale: *1*, *6* – 1 µm; *2-5* – 2 µm

The renewed term of ***areola*** we define as a universal nano- (micro-) df-morph of the second/third order that is constructed from penetrating through the frustule thickness, 1 or 2 df-converters (velum ?) and is organized in regularly repeated groups –

striae. Obviously, the type of velum is the main characteristic of the areola. However, the length of its tube corresponding to the frustule thickness and its inner surface also deals with their functions.

The ***stria*** is a universal repeated micro df-morph of 2-d or 3-d order that includes areolae arrangement within the area restricted by neighboring virgae and provides for interaction of the protoplast with environment through hierarchy system: velum-areolae-stria. The stria has its own evolution that reflects perfection of its functions under particular environmental conditions. There are these following processes discovered in the sria area, stria functions**:** focusing and filtering light energy, selective concentration of the matters on their surface, matters absorption, intensification of physiological processes connected with membranes. It will be possible to discover more stria functions.

Conclusions

After the light and electron microscopy periods functional morphology corresponds to the third stage in the research of diatom morphology that has changed the main accents from WHAT the diatom frustule is to WHY and HOW the diatom frustule was created. Preliminary investigations have shown a *multifunctional role of most frustule structural elements* and their taking part in many vital functions of the diatom single-cell organism. Numerous frustule functions are optimized and synchronized in their morphological hierarchy.

Functional morphology requires the revision of the morphological terms and their definitions for the diatom frustule description and supposes to clarify the *Bacillariophyta* taxonomy.

The diatom functional morphology is an additional cross point in *diatom nanotechnology* for fruitful cooperation.

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ФУНКЦИИ И ФУНКЦИОНАЛЬНАЯ МОРФОЛОГИЯ ПАНЦИРЯ *BACILLARIOPHYTA*

Сделан вывод о полифункциональной роли большинства структурных элементов панциря в жизни клетки диатомовой водоросли на основании данных о функциях панциря диатомовых водорослей, полученных в результате их исследований в области нанотехнологий. Предложена концепция подхода к функциональной морфологии панциря *Bacillariophyta* и ревизии терминологии, используемой при описании его морфологических структур. Сформулированы понятия базисного элемента, *db-элемента* и функциональной единицы, *df-морфы*, панциря диатомовой водоросли. В свете функциональной морфологии рассматриваются некоторые универсальные структуры панциря – вирга, ваймин, велум, ареола, штрих.

К л ю ч е в ы е с л о в а : *Bacillariophyta,* панцирь диатомовой водоросли, функции панциря, функциональная морфология.

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Получена

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