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Review

Diatom silica biomineralization: Parallel development of approaches and understanding

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ABSTRACT

Diatom silica cell walls present an intriguing application of biomineralization in a single celled organism. The ability of diatoms to make an enormous variety of silica structures on the nano- to micro-scale is unparalleled in nature. The process is a whole-cell endeavor, involving diverse cellular components that coordinate "bottom up" and "top down" structure formation processes to reproducibly convert genetic information into physical structure. The study of silicification has been similarly all encompassing, involving the application of diverse analytical techniques to examine different aspects of the process. This review highlights the application of different approaches used to study silicification and the insights they have provided, and documents the progress that has been made. The current status offers the possibility of major breakthroughs in our understanding, by enabling a more widespread identification of genes involved, and direct testing of the role these genes play by genetic manipulation.

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1. Introduction

Modern society is reliant on rigid materials, but their use in the tissues of living organisms started long before mankind discovered them. The ability to synthesize rigid, mineralized structures is found across many taxonomic groups and is employed in the creation of bones, teeth and shells or exoskeletons. The process of creating these mineralized structures is called biomineralization; a term which encompasses the creation of multiple types of minerals such as calcium carbonate ($CaCO_3$) and silica (SiO_2). One algal group, diatoms, uses biomineralization to create intricately patterned silica cell walls. Diatoms achieve this through the conversion of soluble silicic acid into amorphous silica, a process called silicification.

Diatoms are a single celled alga found throughout the world's aquatic environments which account for ~20% of annual carbon fixation [1]. Their global success makes them essential to aquatic

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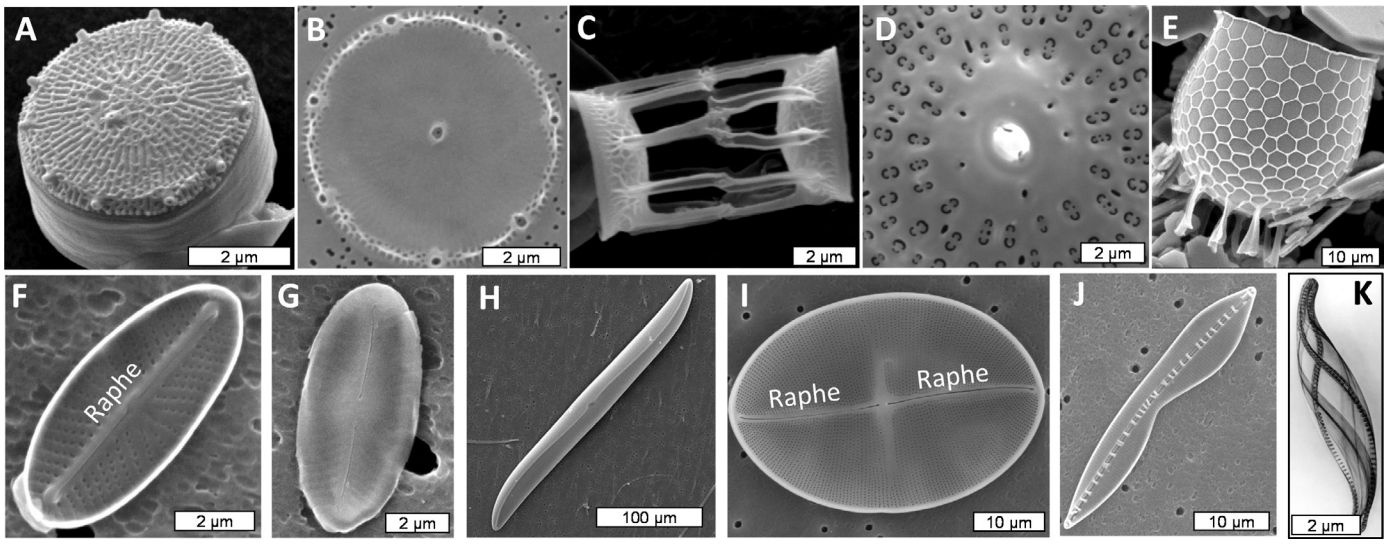

Fig. 1. Diversity of diatom valve structures. (A) *Thalassiosira pseudonana*, (B) *Thalassiosira oceanica*, (C) *Skeletonema costatum*, (D) *Ditylum brightwellii*, (E) *Stephanopyxis turris*, (F) *Navicula pelliculosa* proximal surface, (G) *N. pelliculosa* distal surface, (H) *Gyrosigma balticum*, (I) *Cocconeis sp.*, (J) *Bacilaria paxillifer*, (K) *Cylindrotheca fusiformis*. (A)–(E) are centric species, (F)–(K) are pennate species. The location of the raphe is noted in (F) and (I).

food webs as well as carbon and biogeochemical cycling in the ocean [2]. Diatoms' unique silica cell walls, also called frustules, may have contributed to their ecological success. The rigid structure of the frustule provides mechanical protection [3], shielding the cell from forces in the surrounding environment. The frustule's porous nature allows for the uptake of nutrients from the surrounding medium, and evidence suggests that pore size may play a role in actively facilitating the uptake of differently sized nutrient aggregates [4]. The frustule's three dimensional (3D) physical structures may also play a role in how diatoms physically interact with surfaces in their environment. Cleaned frustules have the ability to adhere to smooth surfaces under high flow pressure depending on their specific structure [5], which may be essential to diatoms that live and reproduce on surfaces. Frustules also alter light coming into the cell in multiple ways [6–8], possibly serving a photo-selective, photo-protective, or light focusing role.

Diatom frustules have enormous morphological diversity (Fig. 1) encompassing multiple scales of features and patterns on their surfaces. Despite this morphological diversity all frustules possess a common structural layout. The frustule is assembled like a Petri dish, with an overlapping top and bottom (Fig. 2). The extreme top and bottom of the frustule are called the valves, while the curved sides are composed of a series of overlapping components called girdle bands. The smaller valve and associated girdle bands, the hypotheca, fit into the larger valve and its associated girdle bands, the epitheca. Girdle bands provide overlap between the two thecae (Fig. 2). This configuration is one commonality between two main classes of diatoms called centrics and pennates (Fig. 2). Centrics are distinguished by having rotational symmetry around a central point of the valve while pennates possess bilateral symmetry [9]. There are further subclasses within centrics and pennates characterized by variations in symmetry and structure. Radial centrics arose first evolutionarily followed by bipolar and multipolar centrics. Centrics were followed by araphid pennates and raphid pennates [10] which are distinguished by their respective lack or possession of a structure called a raphe. The raphe (Figs. 1F, I and 2B) is an elongated slit running the length of the valve through which adhesive mucilage is secreted, enabling the cell to glide across surfaces [9,11]. The wide variety of frustule morphologies and structures demonstrates the flexibility of the silicification process in diatoms.

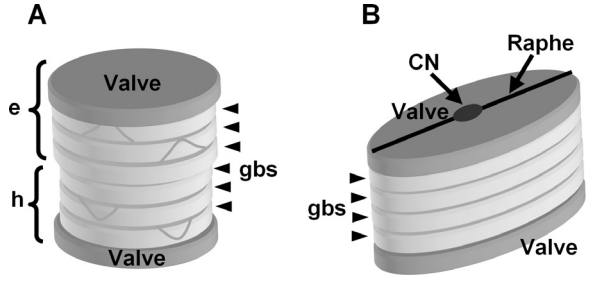

Fig. 2. Schematic diagram of diatom cell wall structure in two major morphological groups. (A) Centric cell walls include an epitheca (e) and hypotheca (h) which overlap each other. The sides of the theca are composed of overlapping girdle bands (gbs) which are attached to the valves and provide the overlap between the two theca. (B) Pennate cell walls are also composed of girdle bands (gbs) and valves but are characterized by an elongated shape and bilateral symmetry relative to centric species. Some pennate species also possess a slit running the length of the valve (the raphe) which originates at the central nodule (CN).

A variety of characteristics make diatoms uniquely suited for the study of silicification, their unicellular nature and intracellular mineralization processes provide a simpler study system than a multicellular organism such as a silicifying sponge. Diatoms can be propagated and manipulated in a controllable manner in the lab, and are amenable to both environmental and genetic manipulation [12–14]. There are advantages to both types of manipulation; environmental manipulation requires no foreknowledge of genes involved, and genetic manipulation allows correlation of genetic information with the design principles involved in structure formation. The flexibility of environmental manipulation has enabled scientists to explore how a suite of factors such as light, heavy metals, and cytoskeletal inhibitors affect cell wall formation [11,15–18]. To date six diatom genome sequences [19–24] and transcriptomes from a large number of species are available [25], creating datasets for exploring the genetic basis of structure formation. Culture manipulations that entrain populations of cells into the same stage of the cell cycle [26] enrich for cells making specific cell wall structures and allow researchers to apply transcriptomics and proteomics to study their formation [27,28]. Genetic information combined with established genetic manipulation tools allow