

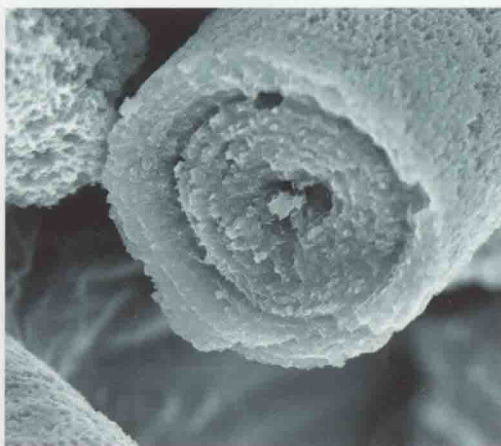
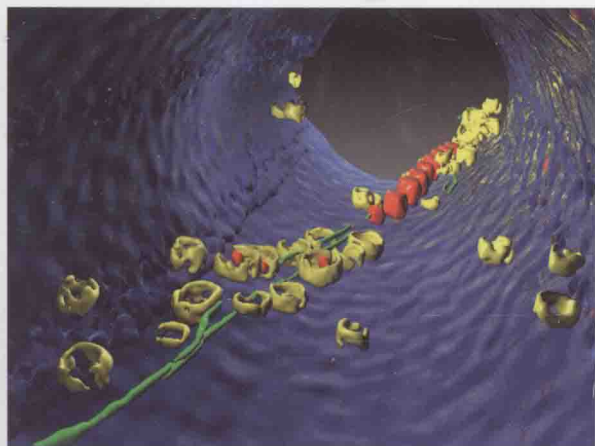
Edited by
Edmund Baeuerlein

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Handbook of Biomineralization

Biological Aspects and Structure Formation

Foreword by Jeremy D. Pickett-Heaps



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Cover Illustration (Top left designed by Jürgen Plitzko)

(Top right, Bottom left and Bottom right designed by Felix Baeuerlein)

Top left: 3-D-visualization of a part of *Magnetospirillum gryphiswaldense* cell with the cytoplasmic membrane (blue), empty vesicles (yellow), growing and mature magnetite crystals (red), and the magnetosome cytoskeletal filament (green). Cryo-electron tomography and visualization by M. Gruska and J. M. Plitzko, MPI Martinsried.
(C. Jogler, D. Schüler, Chap. 9, Fig. 9.4 b modified)

Top right: A skeletal spicule of a sea urchin embryo, isolated, broken, etched and carbon coated, visualized in the SEM by Lindsay Croker.
(F.H. Wilt, C.A. Ettensohn, Chap. 11, Fig. 11.3 modified)

Bottom left: Skeleton of an adult Zebrafish (*Danio rerio*) by Synchrotron Radiation Micro Computer Tomography (SR μ CT)
(F. Neues et al, Chap. 21, Fig. 21.4)

Bottom right: Photograph of the Medusa Periphylla periphylla, remarkable for its statoliths of CaSO₄ hemihydrate in gravity sensing.
(F. Boßelmann, et al, Chap. 15, Fig. 15.1)

Handbook of Biomineralization

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*Edited by
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1807–2007 Knowledge for Generations

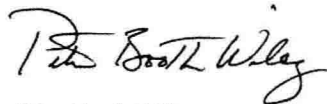
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*This book is dedicated to
my “biomineralization team”
my wife Cornelia, my daughter Henrike, and my son Felix
who accomplished together the pre-editorial management and the cover design
of the three volumes on biomineralization*

and to

*Prof. Dr. Dieter Oesterhelt
who has offered me also, for this new three-volumes edition,
his support*

I am very grateful to all

Foreword: The Enigma of Morphogenesis – A Personal View

When asked to write a foreword to this volume, I decided to share my personal experiences of a frustrating contradiction: how much we now understand about cell structure and function; and how little we know about morphogenesis at the cellular level. My interest in morphogenesis stemmed from looking at cells in a plant root tip. During the 1960s, the electron microscope promised great advances in our ability to relate cell structure and function with the morphogenetic processes that create such cellular organization. Getting off to an encouraging start in graduate research, I discovered the “preprophase band” of microtubules [1] which mass along the cell wall before division in a position that, with uncanny accuracy, predicts the eventual plane of this division. This correlation was most provocative – just the sort that should provide a deeper insight into the mechanisms by which cells control division and morphogenesis. However, after a sobering 40 years of investigation in many laboratories, we still do not know the function or significance of the preprophase band.

I abandoned higher plants in favor of single-celled algae, where the emergence of form is quick, clean, and deceptively simple. Morphogenesis occupies a brief period of the cell cycle, after division; it is precise and predictable in outcome, and without the complexities of cellular interactions. A group of green algae with thousands of different species, the desmids, offered one tractable model system. When these beautifully symmetrical cells divide, they are bisected by the cleavage furrow. They restore their symmetry by each older half-cell generating a new half-cell (“semicell”) that is the mirror image of its parent. This remarkable feat is accomplished in 1 to 4 hours by the osmotically driven enlargement of a wall that starts off as a round balloon. Very soon in expansion, the plasticity of the soft wall becomes subtly altered in a pattern which is precisely programmed in time and space. Thus, the enlarging balloon is magically transformed into a perfect new semicell.

I confidently explored the ultrastructure and cytoskeleton in growing semicells, but eventually had to accept that nothing in their organization indicated how this spatial differentiation is generated. Equally enigmatic were living cells. The cytoplasm in semicells streams vigorously but, as far as I could determine, in an entirely chaotic fashion. Exquisite form emerges from chaos! Again, after some 30

years of effort, we have not the slightest idea how pattern control is brought about by the cell [2].

Among the protists, the diatoms inevitably command the attention of anyone interested in biological form. Their beautifully sculptured cell walls are not only differentiated to an extraordinary degree, but there are also hundreds of thousands of species. Thus, the morphogenetic systems in these cells must satisfy two contradictory demands: first, that they reproduce a given complex shape with absolute, unwavering fidelity; and second, that they be capable of almost infinite variability. And of course, to express form using one of the most refractory materials known, pure silica.

Electron microscopy of these cells was both exciting and mystifying. Morphogenesis in diatoms is obviously completely different to that in desmids. In diatoms, the wall is secreted in discrete segments (the valves and girdle bands), each formed within the special membrane compartment defined by the “silica deposition vesicle” (SDV). This is where the complex chemistry of silica concentration and precipitation takes place – the area of intense research interest, as reflected in this volume, and one for which the details appears increasingly close to resolution. Morphogenesis is brought about by the growing SDV being precisely molded in time and space. The actual molding process turned out to be a surprise, as there is no one or two central systems involved. Instead, an extraordinary range of cytoplasmic organelles (e.g., microtubules, actin filaments, endoplasmic reticulum, mitochondria, vesicles of various types) and cytoplasmic processes (e.g., plasmolysis, protoplast movements and twisting, localized adhesion to the valves, mucilage secretion, interaction of daughter cells) are combined in various combinations by different species to mold the growing SDV [3]. Thus, diatoms to me are the “Maestros of Morphogenesis”, orchestrating complex interactions of many players to remarkable effect. So perhaps it is not surprising that there are hundreds of thousands of different species.

A specific example of this morphogenetic flexibility is seen in the extension of very fine, needle-like spines of silica in four genera: the setae of *Chaetoceros* [4, 5], the labiate process of *Ditylum* [6] and *Rhizosolenia* [7], and the simpler spine of *Proboscia* [8]. Not only do these genera employ different cytoplasmic systems to create and shape the spine, but there are also distinct differences between the two species of *Chaetoceros*. In addition, the labiate process of *Rhizosolenia* adds an extraordinary oscillation of the spine *in vivo* during its extension. So, in this tiny sample of the generation of one small feature, the cytoplasm shows great variation in the morphogenetic systems that it uses. One wonders how many other ways diatoms form spines. Summarizing: it seems that in desmids, no organelles appear correlated with spatial morphogenesis, but diatoms many are. And we have not considered the morphogenetic systems of other unicellular protists, for example, those that make delicately sculptured, species-specific scales and spines from calcium carbonate and silica.

It is axiomatic that the information which controls these morphogenetic processes resides in the cell's genetic system, its DNA. What we entirely lack is any scenario to explain how molecular information in DNA, RNA and proteins, can

be expressed on a vastly greater stage of macromolecular structure with such precision. We seem bound to the old reductionist hope that somehow the answer will drop out if we just get enough information on the bits and pieces involved.

There is little reason for optimism that this will happen, and a metaphor might be useful – one, I believe, originally put forward by E.O. Wilson. Consider an ant. Today, we can study this creature in many ways. We can analyze the structure and behavior of an ant; its anatomy, muscles and sensory abilities; its organs and their function; its biochemistry and genetics; and of course, we can sequence its genome. When we put a million of these ants together, miraculous events transpire. They create social structures and build (for them) enormous, species-specific ant castles. None of the information we collect about our isolated ant provides any indication of these abilities and worse, none has any prospect of so doing. Where does the organizational information reside that confers on them such abilities? The same enigma is surely true of cells. We are swamped by information about cells and their organelles. This information is increasingly reductionistic due to the burgeoning success of molecular biology. Yet none of this information promises any understanding of how, even in principle, information stored in genes can initiate and control processes such as morphogenesis on a vastly greater scale, like the ant and its castle. We appear, yet again, to be confronted with the limits of reductionism because the cell is so much more than the sum of its parts. Where instead to look?

After 40 years' preoccupation with these phenomena, my conclusion is that the morphogenetic properties of the cytoplasm are an expression of its dynamics as much as its constituents. Like the relationship between the ant and the ant-castle, as soon as we stop the dynamics – whether to undertake ultrastructural or molecular analysis – the principles of morphogenesis we seek to investigate are lost to us. We may need entirely new models, approaches and axioms to progress toward understanding one of the most interesting and intractable mysteries of life.

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Cytographics, Online Store
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Preface

Currently, biomineralization is evolving from its heyday of structural research into one of the most exciting fields of molecular biology. In order to bring these new developments to the notice of its chemists and physicists, I had edited two multi-author books on “Biomineralization”, in November 2000 and October 2004. In a competent and detailed review of the second of these books, S. Weiner (*Angew. Chem. Int. Ed.* **2005**, *44*, 4833–4834) noted that he had missed the presence of a general introduction and, in addition to that, a more comprehensive view “... to cover the waterfront of this vast field”.

It was the exemplary intuition of the outstanding publisher, Dr. Gudrun Walter, the Program Director of Wiley-VCH, that encouraged her to outline biomineralization as a fundamental interaction between the organic and inorganic spheres. Consequently, she devised three volumes on biomineralization, covering biomimetic chemistry, materials science, and the life sciences. Moreover, she entrusted me again with this new project which exceeds by far, both in content and extent, the two preceding books.

The first draft three volumes of “Biomineralization” were appended with the subtitle: Biology, Biomimetic and Bio-Inspired-Chemistry, Medicine. In addition, because each volume was planned to consist of 25 to 30 chapters, I invited Prof. Peter Behrens, a well-known expert in biomimetic chemistry and coordinator of the DFG-Priority Program “Principles of Biomineralization”, to co-edit with me the chemistry volume. Prof. Behrens convinced me that biomimetic chemistry is an indispensable approach to study the developments of inorganic/organic hybrids in addition to molecular biology, which, before our co-edition, was in my mind the *only* method. The Spring Meeting 2005 of the Materials Research Society (MRS) was characterized by a broad offer of bio-inspired synthesis and techniques, and this allowed the selection of several new topics. Prof. Matthias Epple, an extraordinary inorganic chemist, whose interests cover the isolation and analysis of biominerals, the synthesis of biomaterials, and the development of new physical methods in materials science and cooperation with medical institutes and clinics, agreed – to my great pleasure – to organize the medical volume essentially by himself.

As all manuscripts for the book arrived at Munich for the pre-editorial management, I had the chance to take a general view of each of the 68 chapters, and this

allowed me to prepare a first draft in Chapter 1 of what might be common in biomineralization reactions but characteristically different from mainstream biochemistry. It is possible that although this draft was too specialized for an introduction, its complexity was simply a reflection of the current state of the art of biomineralization.

January 2007

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