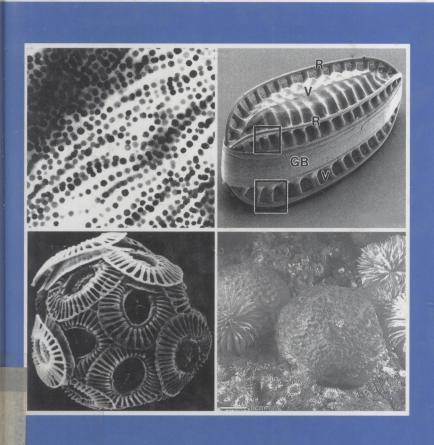


# Biomineralization

From Biology to Biotechnology and Medical Application

Edited by Edmund Baeuerlein



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## Biomineralization

From Biology to Biotechnology and Medical Application

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Weinheim · New York · Chichester Brisbane · Singapore · Toronto

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#### Dedication to

my wife Cornelia for her permanent encouragement and her editorial support

and to

Dieter Oesterhelt the advocate of biotechnology on the occasion of his 60<sup>th</sup> birthday

#### **Preface**

Biomineralization refers to the processes by which organisms precipitate inorganic minerals. This phenomenon is widespread in the biological world, and occurs in bacteria, single-celled protists, plants, invertebrates and vertebrates. Over 60 biominerals are known, the most abundant of which are calcium carbonates, silica and iron oxides. Most biominerals are organized hierarchically and ordered at many length scales, and often have remarkable physical characteristics. The minerals can be deposited intra- or extracellularly and are intimately connected to cellular metabolic processes. Thus biomineralization as a field of scientific study falls within several scientific disciplines, including biochemistry, biology, condensed matter physics, geology, inorganic chemistry, and molecular biology.

This is not a new scientific field; since the 19th century several thousand papers have been published, due largely to potential applications in areas as diverse as medical and dental science, paleontology and paleogeochemistry, materials science and engineering, evolutionary biology and astrobiology. However, the last two decades have seen the development of a new understanding, based partly on new experimental techniques and partly on conceptual advances. This new understanding has been documented in a number of books and symposium volumes covering the period between 1983 and 1991 and including: Biomineralization and Biological Metal Accumulation, edited by P. Westbroek and E. W. de Jong (D. Reidel, Dortdrecht, 1983); On Biomineralization, by H. A. Lowenstam and S. Weiner (Oxford University Press, Oxford, New York, 1989); Biomineralization: Chemical and Biochemical Perspectives, edited by S. Mann, J. Webb and R. J. P. Williams (VCH, Weinheim, 1989); Biomineralization, by K. Simkiss and K. M. Wilbur (Academic Press, New York, 1989); Iron Biominerals, edited by R. B. Frankel and R. P. Blakemore (Plenum, New York, 1991) and Mechanisms and Phylogeny of Mineralization in Biological Systems, edited by S. Suga and H. Nakahara (Springer Verlag, Tokyo,

While many researchers have made important contributions to the field, the modern era arguably began with the publication by Heinz Lowenstam of *Minerals Formed by Organisms* (Science 1981, 211, 1126–1131). In this paper, Lowenstam emphasized the importance of organic macromolecules in biomineralization, and distinguished between biological-controlled and biological-induced biomineralization processes. The theme of organic—inorganic interactions, and concepts such as directed nucleation, molecular recognition, and molecular tectonics were further developed by R. J. P. Williams, Stephen Mann, Stephen Weiner and others. In fact,

the identification of the organic phase and its role in biomineralization in various organisms has been the major theme in biomineralization research over the last two decades. Another important theme, which remains less well developed, is the relationship between biomineralization and metabolism.

The present volume was inspired by a "Workshop on Biomineralization and Nanofabrication", supported by the US Office of Navel Research and organized by one of us (R. B. F). It took place in San Luis Obispo, California, in May, 1996, covered biomineralization phenomena in a number of organisms and looked toward future developments. The other of us (E. B.) was a participant at the workshop and decided to organize the publication of a multi-author volume based on the stimulating presentations. During the planning stage of about three years, progress in the study of proteins involved in biomineralization phenomena by molecular biological methods led to the addition of contributions on silica mineralization in sponges to those on magnetite mineralization in prokaryotes and silica and calcium carbonate mineralization in unicellular eukaryotes. Because biomineralization in unicellular organisms takes place in vesicles, a new membrane biology is developing that may ultimately connect to vesicle-based materials science applications.

The volume begins with a short introduction to biominerals, of which three magnetite, silicic acid and calcium carbonate – are mineralized by organisms described here. The first part, "Prokaryotes", covers biomineralization phenomena on the surfaces of bacteria, as well as the formation of magnetite (Fe<sub>3</sub>O<sub>4</sub>) and greigite (Fe<sub>3</sub>S<sub>4</sub>) nanocrystals in the intracytoplasmatic vesicles (magnetosomes) of magnetotactic bacteria, their role in magnetotaxis, and technical and medical applications of isolated magnetosomes. It also includes in situ identification of magnetotactic bacteria, their phylogenetic relationships, and enzymes and related genes involved in their biomineralization processes. The second part, "Eukaryotes", opens with a unified theory of biomineralization in prokaryotes and eukaryotes from evolutionary and paleontological analysis of the Cambrian explosion 525 Myr ago. This retrospection on the evolution of biomineralization is followed by three complementary chapters on the formation of silica nanostructures in unicellular eukaryotes, the diatoms, and a related chapter on polysiloxane synthesis in a marine sponge. These are followed by a chapter on recent research into the protein components of shell nacre. The volume is completed by two chapters on coccolithophores, unicellular eukaryotes that are covered by mineralized scales of calcium carbonate known as coccoliths. It has been possible to study coccolith mineralization by mutation experiments as well as by isolation of the coccolith vesicles.

June, 2000

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Chapter 13

#### **Abbreviations**

AAS atomic adsorption spectroscopy

ADP adenosine diphosphate

ATCC American Type Culture Collection

ATP adenosine triphosphate ATPase adenosine triphosphatase AFM atomic force microscope

Bfr bacterioferritin

BMP bacterial magnetic particle
CA carbonic anhydrase activity
CCM carbon concentrating mechanism
CDF cation diffusion facilitator
CEA carcino-embryonal-antigen
CM cytoplasmic membrane

CN central nodule
CP chloroplast
CV coccolith vesicle
DEAE diethylaminoethanol
DIC dissolved inorganic carbon

DSi dissolved silicon

DSM Dt. Sammlung für Mikroorganismen EDTA ethylenediaminetetraacetic acid ESI energy spectroscopic imaging

EL extracellular loops
ER endoplasmatic reticulum
FAD flavin adenine dinucleotide

FESEM field emission scanning electron microscopy

FISH fluorescence in situ hybridization

FMN flavin mononucleotide
GA N-acetylglucosamine
GFP green fluorescent protein
GUT grand unified theory

HRTEM high resolution transmission electron microscopy

HPLC high pressure liquid chromatography

ICS intracellular carboxy segment

IgG immunoglobulin G

#### xxii Abbreviations

IL intracellular loops

INS intracellular amino segment

kDa kiloDalton

LPS lipopolysaccharide
MA N-acetyl muramic acid
MM magnetosome membrane

MMP many-celled magnetotactic procaryote

MRI magnetic resonance imaging

MTB magnetotactic bacteria

Myr million years

NAD nicotinamide adenine dinucleotide

NADH nicotinamide adenine dinucleotide, reduced

NADPH nicotinamide adenine dinucleotide phosphate, reduced

NMR nuclear magnetic resonance

OA ornithineamidelipid

OATZ oxic-anoxic transition zone

ORF open reading frame
OM outer membrane
P peptidoglycan layer
PC phosphatidylcholine
PCR polymerase chain reaction
PE phosphatidylethanolamine
PET positron emission tomography

PG phosphatidylglycerol PM plasma membrane R 123 Rhodamine 123

rRNA ribosomal ribonucleic acid SATA succinimidyl-S-acethylthioacetat SAED selected area electron diffraction SCID severe combined immunodeficiency

SD single-magnetic-domain SDS sodium dodecyl sulfate

SDS-PAGE sodium dodecyl sulfate polyacrylamide gel electrophoresis

SDV silica deposition vesicle SEM scanning electron microscopy

SER/THR serine/threonine

SIT silicic acid transporters

STEM scanning transmission electron microscope

STV silicon transport vesicle

TEM transmission electron microscope

TEOS tetraethyleneoxysilane

TMPD tetramethyl-p-phenylenediamine

TPR tetratricopeptide repeat UTP uridine triphosphate

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