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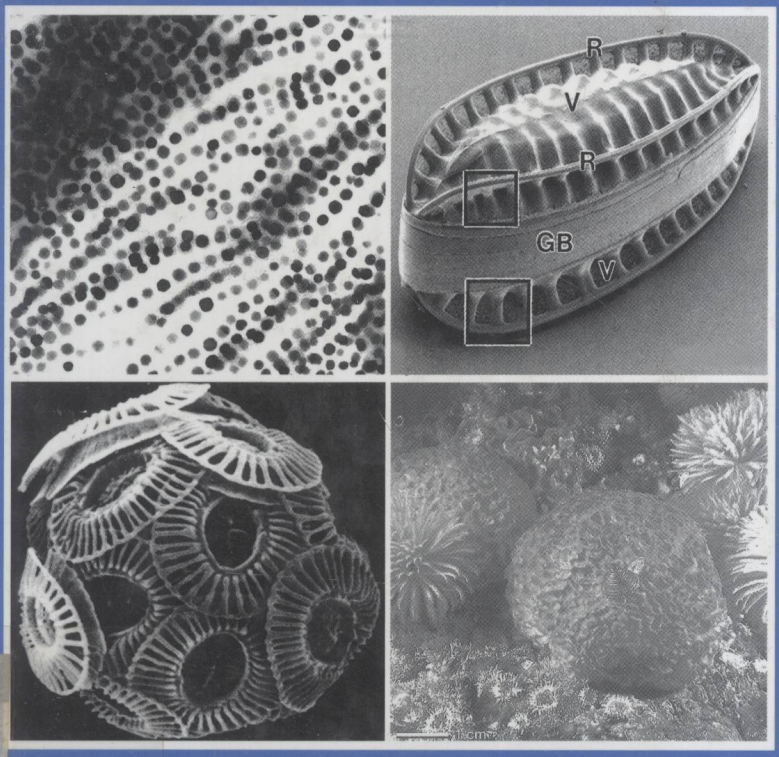
From Biology to Biotechnology and Medical Application

Edited by Edmund Baeuerlein



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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 60th 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, 1991).

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_3O_4) and greigite (Fe_3S_4) 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.

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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

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

Contents