The Enzymes of Biological Membranes SECOND EDITION

Volume 1
Membrane Structure and Dynamics

Anthony N. Martonosi

The Enzymes of Biological Membranes

SECOND EDITION

Volume 1

Membrane Structure and Dynamics

Edited by

Anthony N. Martonosi

State University of New York Syracuse, New York

Library of Congress Cataloging in Publication Data

Main entry under title:

The Enzymes of biological membranes.

Bibliography: v. 1, p.

Includes index.

Contents: v. 1. Membrane structure and dynamics.

1. Membranes (Biology) - Collected works. 2. Enzymes - Collected works. 1. Martonosi, Anthony, 1928-

QH601.E58 1984

574.87/5

84-8423

ISBN 0-306-41451-1 (v. 1)

© 1985 Plenum Press, New York A Division of Plenum Publishing Corporation 233 Spring Street, New York, N.Y. 10013

All rights reserved

No part of this book may be reproduced, stored in a retrieval system, or transmitted in any form or by any means, electronic, mechanical, photocopying, microfilming, recording, or otherwise, without written permission from the Publisher

Printed in the United States of America

Contributors

- Dennis Chapman, Department of Biochemistry and Chemistry, Royal Free Hospital School of Medicine, University of London, London NW3 2PF, England
- Carl M. Cohen, Department of Biomedical Research, St. Elizabeth's Hospital, Boston, Massachusetts; and Departments of Medicine and of Molecular Biology and Microbiology, Tufts University School of Medicine, Boston, Massachusetts
- P. R. Cullis, Department of Biochemistry, University of British Columbia, Vancouver, British Columbia, V6T 1W5, Canada
- Philippe F. Devaux, Institut de Biologie Physico-Chimique, 75005 Paris, France
- Peter B. Garland, Department of Biochemistry, University of Dundee, Dundee DD1 4HN, Scotland, United Kingdom
- M. J. Hope, Department of Biochemistry, University of British Columbia, Vancouver, British Columbia, V6T 1W5, Canada
- Frances Jay, Institute for Cell Biology, Federal Institute of Technology, ETH-Hönggerberg, CH-8093 Zürich, Switzerland
- Pauline Johnson, Department of Biochemistry, University of Dundee, Dundee DD1 4HN, Scotland, United Kingdom
- B. de Kruiff, Department of Molecular Biology, State University of Utrecht, 3584 CH Utrecht, The Netherlands
- Jeff Leaver, Department of Biochemistry and Chemistry, Royal Free Hospital School of Medicine, University of London, London NW3 2PF, England
- Jack A. Lucy, Department of Biochemistry and Chemistry, Royal Free Hospital School of Medicine, University of London, London NW3 2PF, England
- Kurt Mühlethaler, Institute for Cell Biology, Federal Institute of Technology, ETH-Hönggerberg, CH-8093 Zürich, Switzerland
- Camillo Peracchia, Department of Physiology, School of Medicine, University of Rochester, Rochester, New York
- Hans Sigrist, Institute of Biochemistry, University of Berne, CH-3012 Berne, Switzerland
- Deborah K. Smith, Department of Biomedical Research, St. Elizabeth's Hospital, Boston, Massachusetts. Present address: Department of Physiology, Duke University Medical Center, Durham, North Carolina

- T. F. Taraschi, Hahnemann Medical College, Department of Pathology, Philadelphia, Pennsylvania
- David D. Thomas, Department of Biochemistry, University of Minnesota, Medical School, Minneapolis, Minnesota
- Dan W. Urry, Laboratory of Molecular Biophysics, University of Alabama in Birmingham, School of Medicine, Birmingham, Alabama
- C. J. A. Van Echteld, Department of Biochemistry, State University of Utrecht, 3584 CH Utrecht, The Netherlands
- A. J. Verkleij, Department of Molecular Biology, State University of Utrecht, 3584 CH Utrecht, The Netherlands
- Alan S. Waggoner, Center for Fluorescence Research in Biomedical Sciences and Department of Biological Sciences, Carnegie-Mellon University, Pittsburgh, Pennsylvania
- Evangelina E. Yguerabide, Department of Biology, University of California, San Diego, La Jolla, California
- Juan Yguerabide, Department of Biology, University of California, San Diego, La Jolla, California
- Peter Zahler, Institute of Biochemistry, University of Berne, CH-3012 Berne, Switzerland

Preface to the Second Edition

In the first edition of *The Enzymes of Biological Membranes*, published in four volumes in 1976, we collected the mass of widely scattered information on membrane-linked enzymes and metabolic processes up to about 1975. This was a period of transition from the romantic phase of membrane biochemistry, preoccupied with conceptual developments and the general properties of membranes, to an era of mounting interest in the specific properties of membrane-linked enzymes analyzed from the viewpoints of modern enzymology. The level of sophistication in various areas of membrane research varied widely; the structures of cytochrome c and cytochrome c were known to atomic detail, while the majority of membrane-linked enzymes had not even been isolated.

In the intervening eight years our knowledge of membrane-linked enzymes expanded beyond the wildest expectations. The purpose of the second edition of *The Enzymes of Biological Membranes* is to record these developments. The first volume describes the physical and chemical techniques used in the analysis of the structure and dynamics of biological membranes. In the second volume the enzymes and metabolic systems that participate in the biosynthesis of cell and membrane components are discussed. The third and fourth volumes review recent developments in active transport, oxidative phosphorylation and photosynthesis.

The topics of each volume represent a coherent group in an effort to satisfy specialized interests, but this subdivision is to some extent arbitrary. Several subjects of the first edition were omitted either because they were extensively reviewed recently or because there was not sufficient new information to warrant review at this time. New chapters cover areas where major advances have taken place in recent years. As a result, the second edition is a fundamentally new treatise that faithfully and critically reflects the major transformation and progress of membrane biochemistry in the last eight years. For a deeper insight into membrane function, the coverage includes not only well-defined enzymes, but several membrane proteins with noncatalytic functions.

We hope that *The Enzymes of Biological Membranes* will catalyze the search for general principles that may lead to better understanding of the structure and function of membrane proteins. We ask for your comments and criticisms that may help us to achieve this aim.

My warmest thanks to all who contributed to this work.

Anthony N. Martonosi

Syracuse, New York

- Ether-Linked Glycerolipids and Their Bioactive Species: Enzymes and Metabolic Regulation
 Fred Snyder, Ten-ching Lee, and Robert L. Wykle
- Fatty Acid Synthetases of Eukaryotic Cell Salih J. Wakil and James K. Stoops
- 16. Properties and Function of Phosphatidylcholine Transfer Proteins Karel W. A. Wirtz, Tom Teerlink, and Rob Akeroyd
- 17. Carnitine Palmitoyltransferase and Transport of Fatty Acids Charles L. Hoppel and Linda Brady
- Membrane-Bound Enzymes of Cholesterol Biosynthesis: Resolution and Identification of the Components Required for Cholesterol Synthesis from Squalene
 James M. Trzaskos and James L. Gaylor
- 19. Membrane-Bound Enzymes in Plant Sterol Biosynthesis Trevor W. Goodwin, C.B.E., F.R.S.
- 20. Glycosyltransferases Involved in the Biosynthesis of Protein-Bound Oligosaccharides of the Asparagine-N-Acetyl-D-Glucosamine and Serine (Threonine)-N-Acetyl-D-Galactosamine Types
 Harry Schachter, Saroja Narasimhan, Paul Gleeson, George Vella, and Inka Brockhausen

- Biosynthesis of the Bacterial Envelope Polymers Teichoic Acid and Teichuronic Acid
 Ian C. Hancock and James Baddiley
- The Major Outer Membrane Lipoprotein of Escherichia coli: Secretion, Modification and Processing George P. Vlasuk, John Ghrayeb, and Masayori Inouye
- 23. Anchoring and Biosynthesis of a Major Intrinsic Plasma Membrane
 Protein: The Sucrase-Isomaltase Complex of the Small-Intestinal Brush
 Border
 Giorgio Semenza
- 24. Multifunctional Glucose-6-Phosphatase: A Critical Review Robert C. Nordlie and Katherine A. Sukalski
- 25. The Beta Adrenergic Receptor: Elucidation of its Molecular Structure Robert G. L. Shorr, Robert J. Lefkowitz, and Mark G. Caron
- Ionic Channels and Their Metabolic Control
 P. G. Kostyuk

Index

- 27. The Energetics of Active Transport W. D. Stein
- 28. The Na⁺, K⁺-Transporting Adenosine Triphosphatase I. M. Glynn
- The Sarcoplasmic Reticulum Membrane Marek Michalak
- 30. Kinetic Regulation of Catalytic and Transport Activities of Sarcoplasmic Reticulum ATPase Giuseppe Inesi and Leopoldo de Meis
- 31. Calcium-Induced Potassium Transport in Cell Membranes
 B. Sarkadi and G. Gárdos
- 32. Biochemistry of Plasma-Membrane Calcium-Transporting Systems Ernesto Carafoli
- 33. The Calcium Carriers of Mitochondria Martin Crompton
- 34. Intestinal Phosphate Transport
 Meinrad Peterlik
- 35. Ion Transport in Nerve Membrane Lorin J. Mullins

- The Molecular Basis of Neurotransmission: Structure and Function of the Nicotinic Acetylcholine Receptor Robert Anholt, Jon Lindstrom, and Mauricio Montal
- 37. Structural Distinctions among Acetylcholinesterase Forms Terrone L. Rosenberry
- 38. The Gastric H, K-ATPase
 L. D. Faller, A. Smolka, and G. Sachs
- H⁺-Translocating ATPase and Other Membrane Enzymes Involved in the Accumulation and Storage of Biological Amines in Chromaffin Granules
 Sally E. Carty, Robert G. Johnson, and Antonio Scarpa
- 40. Hexose Transport and Its Regulation in Mammalian Cells Jeffrey E. Pessin and Michael P. Czech
- 41. The Bacterial Phosphoenolpyruvate: Sugar Phosphotransferase System Norman D. Meadow, Maria A. Kukuruzinska, and Saul Roseman
- 42. The Maltose–Maltodextrin Transport System of Escherichia coli K-12 Howard A. Shuman
- 43. Bacterial Amino-Acid-Transport Systems
 Robert Landick, Dale L. Oxender, and Giovanna Ferro-Luzzi Ames
- 44. The Iron-Transport Systems of Escherichia coli Volkmar Braun
- 45. Potassium Pathways in Escherichia coli Adam Kepes, Jean Meury, and Aline Robin

Index

- 46. The Enzymes and the Enzyme Complexes of the Mitochondrial Oxidative Phosphorylation System Youssef Hatefi, C. Ian Ragan, and Yves M. Galante
- 47. Proton Diffusion and the Bioenergies of Enzymes in Membranes Robert J. P. Williams
- 48. Relationships between Structure and Function in Cytochrome Oxidase Mårten Wikström, Matti Saraste, and Timo Penttilä
- 49. H⁺-ATPase as an Energy-Converting Enzyme Toshiro Hamamoto and Yasuo Kagawa
- 50. The Proton-Translocating Membrane ATPase (F₁F₀) in Streptococcus faecalis (faecium)
 Adolph Abrams
- 51. Cytochrome b of the Respiratory Chain Henry R. Mahler and Philip S. Perlman
- Cytochrome b₅ and Cytochrome b₅ Reductase from a Chemical and X-Ray Diffraction Viewpoint
 F. Scott Mathews and Edmund W. Czerwinski
- 53. Iron-Sulfur Clusters in Mitochondrial Enzymes
 Thomas P. Singer and Rona R. Ramsay

- 54. The Structure of Mitochondrial Ubiquinol: Cytochrome c Reductase Hanns Weiss, Stephen J. Perkins, and Kevin Leonard
- 55. The Mechanism of the Ubiquinol: Cytochrome c Oxidoreductases of Mitochondria and of Rhodopseudomonas sphaeroides Antony R. Crofts
- 56. Functions of the Subunits and Regulation of Chloroplast Coupling Factor 1 Richard E. McCarty and James V. Moroney
- 57. Biosynthesis of the Yeast Mitochondrial H⁺-ATPase Complex Sangkot Marzuki and Anthony W. Linnane
- 58. Synthesis and Intracellular Transport of Mitochondrial Proteins
 Matthew A. Harmey and Walter Neupert
- Plasma-Membrane Redox Enzymes
 F. L. Crane, H. Löw, and M. G. Clark
- 60. The ADP/ATP Carrier in Mitochondrial Membranes
 Martin Klingenberg
- 61. Bacteriorhodopsin and Rhodopsin: Structure and Function Yuri A. Ovchinnikov and Nazhmutdin G. Abdulaev

Index -

1.	Electr	on Microscopy of Biological Membranes	
	K. Mi	ühlethaler and Frances Jay	
	I. II.	Introduction Methods Used for Studying Biological Membranes in the Electron Microscope A. Sectioning 2 • B. Negative Staining 3 • C. Freeze-Etching and Freeze Fracturing 3 • D. Split Membrane Technique 11 • E. Immunoelectron Microscopy 13 • F. Colloidal Gold Marker 16 • G. Cryoelectron Microscopy 17 • H. Image Processing and Three-Dimensional Structure Determination 19 References	23
2.	Associations of Cytoskeletal Proteins with Plasma Membranes Carl M. Cohen and Deborah K. Smith		
	1.	Introduction	29
	II.	The Components of the Cytoskeleton A. Actin 30 • B. Microtubules 33 • C. Intermediate Filaments 34 • D. The Role of α-Actinin 35	30
	III.	Cytoskeletal Functions	36
	IV.	The Erythrocyte Membrane Skeleton: A Completely Membrane	
		Associated Cytoskeleton A. Composition of the Erythrocyte Membrane Skeleton 38 B. Spectrin 38 C. Actin 39 D. Polypeptides 4.1 and 4.9 39 E. Ankyrin 40 F. Associations between Spectrin, Actin and Band 4.1 41 G. Ultrastructure of the Membrane Skeleton 43	38
â	V.	Cytoskeletal Involvement in Cell–Substratum Associations A. Focal Adhesions 43 • B. The Role of α -Actinin and Vinculin in Focal Adhesions 44 • C. Association of Vinculin with F-Actin 46 • D. Effects of Cell Transformation on Focal Adhesions 46 • E. The Relationship of Focal Adhesions with	43
		the Extracellular Matrix 47 • F. The Formation of Focal Adhesions 50 • G. The Function of Focal Adhesions 51	

	VI.	Cytoskeletal-Membrane Interactions in Microvilli of the Intestinal Brush Border	<i>5</i> 1
	VII.	Membrane-Associated Cytoskeletal Elements and the Control of	51
		Cell Surface Receptor Dynamics	55
		A. Capping 55 • B. Endocytosis 59 • C. Cell Surface Receptor	
	VIII.	Topography and Mobility 61 Summary	64
	1	References	66
? .	Cell (Coupling	
		lo Peracchia	
	1.	Introduction	0.1
	II.	Introduction	81 82
		A. Electrical Coupling 82 • B. Cell-to-Cell Diffusion of	02
		Ions 87 • C. Molecular Probes of Cell-to-Cell Coupling 87	
		D. Metabolic Coupling 88	
	III.	How Molecules Diffuse for Cell-to-Cell	90
		A. Gap Junction Architecture 91 • B. Structure of Cell-to-Cell	
		Channels 96 • C. What Keeps Gap Junction Particles	
	IV.	Aggregated 102 • D. Gap Junction Composition 103 How Cell-to-Cell Diffusion of Molecules is Regulated	106
		A. Uncoupling Agents 107 • B. Is Uncoupling a Graded	100
		Phenomenon? 109 • C. How to Enhance Coupling or Inhibit	
		Uncoupling 109 • D. Change in Junction Structure with	
	7	Uncoupling 109 • E. Hypotheses on Channel Closing Mechanisms 116 • F. Is Calmodulin Involved in the Regulation	
		of Cell-to-Cell Coupling? 116	
		References	121
		F	
	1::11	Deleverable and Manhage Function	
1.		Polymorphism and Membrane Function	Ð
		Kruijff, P. R. Cullis, A. J. Verkleij, M. J. Hope, A. van Echteld, and T. F. Taraschi	
	I.	Introduction	131
	Ш.,	Membrane Lipid Polymorphism: Technical Aspects	132
	III.	Phase Preferences of Membrane Lipids	142
	IV.	The Hexagonal H _{II} Phase	144
	٧.	Modulation of Membrane Lipid Polymorphism A. One Lipid Systems 146 • B. Mixed Lipid Systems 154 • C. Lipid-	145
	VI.	Protein and Lipid-Peptide Interactions 160 "Isotropic" Lipid Structures and Lipid Particles	171
	¥ 1.	isotropic Lipid Structures and Lipid I articles	. / 1

	VII.	The Shape Concept, a Rationale for	
		Lipid Polymorphism	175
	VIII.	Functional Aspects of Lipid Polymorphism	179
		A. Fusion 179 • B. Transport 182 • C. Protein Insertion and	
	IX.	Transport 185	185
	IA.	Lipid Structure in Biological Membranes A. Erythrocyte Membrane 187 • B. Endoplasmic Reticulum	103
		(Microsomes) 188 • C. The Inner Mitochondrial	
		Membrane 189 • D. Bacterial Membranes 191 • E. Rod Outer	
		Segment (ROS) 192 • F. Chloroplast and Prolamellar	
		Body 192 • G. Tight Junction 192	100
	Χ.	Concluding Remarks	193
		References	195
5.	Intrin	sic Protein-Lipid Interactions in Biomembranes	
		eaver and Dennis Chapman	
	Jejj L	200 The Control of th	
	I.	Introduction	205
	II.	Properties of Biomembrane Components A. Lipids 205 • B. Proteins 206	205
	III.	Lipid Composition and Enzyme Activity	207
	IV.	Specificity of Protein-Lipid Interactions	209
	V.	Distribution of Proteins in Membranes	210
	VI.	Perturbation of Lipid Dynamics by Intrinisic Proteins	210
		A. NMR and EPR Spectroscopy 210 • B. Fluorescence	
		Depolarization 212 • C. Range of the Perturbation 215	
	VII.	The Effect of Protein on Lipid Conformation	216
		A. Acyl Chain Region 216 • B. Glycerol Backbone	
		Region 217 • C. Polar Region 217	
	VIII.	The Influence of Lipids on Protein Confermation	217
	IX.	Diffusion of Membrane Components	217
	Χ.	Summary	224
		References	224
	.00		
6.	On the	e Molecular Structure of the Gramicidin Transmembrane Channel	
	Dan V	V. Urry	
			220
	I.	Introduction	229
	**	A. Primary Structure 229	232
	II.	Planar Lipid Bilayer Transport Studies A. Phenomenology of Channel Transport 232 • B. Structural Implications	232

		of the Multiplicity of Single-Channel Conductances 234 • C. Structural Implications of Current/Voltage Curves 235 • D. Structural Deductions from Derivatives and Analogs 240	
	III.	Spectroscopic Characterization of the Lipid Incorporated Channel State	244
		B. Relationship between the Lysolecithin-Gramicidin Heat Incorporated Channel State and the State of Gramicidin in Lipid	
	ı	Vesicles 246 • C. Orientation of Gramicidin Chains in the Lipid Bilayer 248 • D. Determining the Channel Conformation from Ion-Induced Carbonyl Carbon Chemical Shifts 249	
		References	255
7.		entional ESR Spectroscopy of Membrane Proteins: Recent cations	
	Philip	ppe F. Devaux	
	I. II.	Introduction	259
	III.	Non Aggregated Intrinsic Proteins	260
	IV.	Specificity of Lipid-Protein Interactions as Investigated with Spin Labels.	265
		A. 1st Approach: Estimation of the Relative Percentage of Immobilized Component 267 • B. 2nd Approach: Spin—Spin Interaction between Nitroxide Radicals 272	
	V.	Interactions between Extrinsic Proteins and Lipids	275
	VI.	Other Applications of Conventional ESR Spectroscopy to the Investigation of Membrane-Bound Enzymes	276
		References	282
8.		ntion Transfer EPR Studies of Microsecond Rotational Motions in vical Membranes	
	David	D. Thomas	
	I.	Introduction	287