

METABOLISM

* * *

Ingrith D. Olsen



Biological Sciences Curriculum Study Book

Pegasus

A DIVISION OF

The Bobbs-Merrill Company, Inc., Publishers

INDIANAPOLIS

NEW YORK

Copyright © 1973 by The Regents of the University of Colorado
Printed in the United States of America

Library of Congress Catalogue Card Number 72-80815

ISBN 0-672-53562-9

ISBN 0-672-63562-3 (pbk)

First Printing

METABOLISM

This book is one of a series, *Pegasus Topics in Biological Science*, prepared under the auspices of the Biological Sciences Curriculum Study.

To Sigurd

Acknowledgments

The evidence, concepts, and problems outlined in this book have originated with a great number of people—biologists, biochemists, and the like. Some are named in the text. Others, while not mentioned in the text, are of equal importance. My own ideas about metabolism have been formulated during related experimentation, reading, and conversation with many people—teachers, students, and other friends. I am grateful to them, and most directly to my colleagues who have taken an active part in the life history of the book. Drs. Robert E. Davies, William Mayer, and Richard Wareham have given sensitive and thorough attention to reviewing the book as a whole. Among associates in the Zoology Department of the University of Washington, Drs. Aubrey Gorbman, William Hahn, and Gordon Orians have made valuable suggestions, and Dr. Richard Cloney supplied the electron micrograph for use in Figure III-3. Dr. A. M. Hemmingsen, Hellerup, Denmark, has given permission to use his graph of metabolic data in Figure VII-2.

Editor's Preface

We *are* what we are made of, not so much flesh and bone, but of myriad chemicals organized, interacting, regulating and regulated. These chemicals of life, precisely controlled, bring a dynamic stability to life: dynamic because their patterns of organization continually change; stable because of the regulated interaction of those changes. This collection of life chemicals is the province of biochemistry; the processes by which these biochemicals interact and change in living systems is metabolism.

Because of the peculiarities of its usually unfamiliar language, the higher level of abstraction and spatial dimensions involved, and the oftentimes complexity of interaction, biochemistry and metabolism are "hard" topics. Ingrith Olsen has skillfully developed the subject of metabolism fully recognizing these pitfalls, while yet avoiding one in the opposite direction, the overly simplis-

tic which leads to the erroneous. Rather than the comprehensive, encyclopedic route, Dr. Olsen has, skillful teacher that she is, selected a few representative molecules as reference points. This greatly facilitates learning much that can be then extended to other molecules. Still, this is not a novel and should not be anticipated in that way. However, it is a dramatic story well told and well worth your attention.

There are other less technical books in this series which build from a treatment of metabolism, notably: LeBaron's *Hormones: A Delicate Balance*, Klemm's *Science, the Brain and Our Future*, Prescott's *Cancer: the Misguided Cell*, Rossmore's *Microbes: Our Unseen Friends* and Weinswig's *Use and Misuse of Drugs Subject to Abuse*. I commend these to you.

Edward J. Kormondy
Olympia, Washington

Contents

	<i>Acknowledgments</i>	<i>vi</i>
	<i>Editor's Preface</i>	<i>vii</i>
	<i>Introduction</i>	<i>1</i>
I	<i>Perspective on Metabolism</i>	<i>6</i>
II	<i>Alanine—A Representative Molecule</i>	<i>17</i>
III	<i>Supplying Energy</i>	<i>26</i>
IV	<i>Problems of Synthesis</i>	<i>53</i>
V	<i>Problems of Excess</i>	<i>76</i>
VI	<i>Metabolism of Inorganic Substances</i>	<i>84</i>
VII	<i>Control of Metabolism</i>	<i>92</i>
VIII	<i>Development of Metabolic Patterns</i>	<i>123</i>
IX	<i>Metabolism and the Environment</i>	<i>138</i>
X	<i>Patterns of Disturbance of Metabolism</i>	<i>159</i>
XI	<i>The Evolution of Metabolic Patterns</i>	<i>173</i>

APPENDIX: <i>Experimental Analysis of</i> <i>Metabolic Pathways</i>	196
<i>A Brief List of Chemical Terms</i>	203
INDEX	207

Introduction

Metabolism is a very general term, signifying the sum of all the chemical reactions which can occur in organisms. It has been partitioned off as the single subject of this book because, at this time in the last third of the twentieth century, it seems quite reasonable to picture living things as elaborate and more or less unstable organizations of chemical constituents, constantly interacting in processes subject to precise control. As parts of the organism break down, they are replaced by new atoms and molecules derived from the external environment. Energy is transformed from stored form and used by the organism in renewing its structure, in growth, in movement, or in any of its many other processes. Chemical breakdown products are formed, and these, as well as heat—waste energy unavailable for direct metabolic use—leave the living organism and enter the external environment. Whereas, in overall perspective, nonliving systems tend always toward disorganization, and increas-

ing randomness, a living system maintains its characteristic organization through complex and precisely controlled energy-requiring processes. Beyond this, organisms reproduce and transfer to their offspring the characteristic patterns and abilities for self-maintenance. Thus, in a universe which generally seems to man to be "running down" in ways summed up by the second law of thermodynamics, living things, by virtue of their metabolism, maintain and even increase their complexity and orderliness.

The above paragraph may seem to fall short of being a general description of real organisms, like palm trees, nematodes, or men. Yet it sketches the concepts which provide a common framework for chemical description of all living forms. With this in mind, this book was planned to serve as an introduction or supplement to detailed study of the physiology and biochemistry of plants or animals. Stress has been placed on the more fundamental and far-reaching aspects of metabolism.

Certain assumptions were made at the outset about the reader. It is likely that your training has included a modern biology course on the secondary or college level. If so, you probably know about most of the basic features of cell structure, important characteristics of enzyme action, the general lines of organization of some multicellular plants or animals, and fundamentals of genetic mechanisms. In addition, you doubtless have some concrete ideas about evolution as the great modifying process in the history of life on earth. With this much background assumed, it is possible to give a consistent account of metabolism in a relatively small book. Yet in the case of one or another of the major biological areas listed, as elsewhere in the book, you may wish to obtain supple-

mentary information on your own. This is the purpose of the annotated bibliographies at the end of this introduction, following each chapter, and in the Appendix.

Like any other writer, I have worked at a disadvantage in writing this book. For of course I could not have detailed information about the background and interests of the reader, and so it is difficult to predict what use the book may prove to have for you. What questions will you ask? How will you react to this or that particular idea? These are things that I would like to know, but cannot. Therefore, much of the effort spent in writing the book was motivated by hope—that it may serve you as an incentive to explore further the vast field of biology as seen from a metabolic viewpoint. After all, perhaps the most important function of any book is to stimulate the reader's personal activity of questioning, of comparison, and, finally, of conceptual synthesis.

References to Introduction

Valuable background information on biological chemistry and physics may be obtained from

- Baker, J. J. W., and G. E. Allen: *Matter, Energy and Life*. 1965. Addison-Wesley, Palo Alto, California.
- Epstein, H. T.: *Elementary Biophysics. Selected Topics*. 1963. Addison-Wesley, Palo Alto, California.
- White, E. H.: *Chemical Background for the Biological Sciences*. 1964. Prentice-Hall, Englewood Cliffs, N.J.

Various phases of cell biology are treated in

- Goldsby, R. A.: *Cells and Energy*. 1967. Macmillan, New York.
- Jensen, W. A.: *The Plant Cell*. 1964. Wadsworth, Belmont, California.
- Kennedy, D. (ed.): *The Living Cell: Readings from Scientific American*. 1965. W. H. Freeman, San Francisco.
- Loewy, A. G., and P. Siekevitz: *Cell Structure and Function*. Second Edition. 1969. Holt, Rinehart and Winston, New York.
- McElroy, W. D.: *Cell Physiology and Biochemistry*. Third Edition. 1971. Prentice-Hall, Englewood Cliffs, N.J.

General introductions to plant and animal physiology on an elementary level may be found in

- Galston, A. W.: *The Life of the Green Plant*. Second Edition. 1964. Prentice-Hall, Englewood Cliffs, N.J.
- Schmidt-Nielsen, K.: *Animal Physiology*. Second Edition. 1964. Prentice-Hall, Englewood Cliffs, N.J.
- Steward, F. C.: *Plants at Work*. 1964. Addison-Wesley, Palo Alto, California.

Several standard biochemistry textbooks will be referred to later in the various chapter reference lists. The reader may find these interesting to consult, although they are large, complex, and so filled with important details as to be somewhat unreadable.

A classic text in the field is

Baldwin, E.: *Dynamic Aspects of Biochemistry*. Fifth Edition. 1967. Cambridge University Press, New York.

Two smaller texts are

Conn, E. E., and P. K. Stumpf: *Outlines of Biochemistry*. Second Edition. 1966. John Wiley, New York.

Rafelson, M. E., and S. B. Binkley: *Basic Biochemistry*. Second Edition. 1968. Macmillan, New York.

I

Perspective on Metabolism

Though metabolism represents the totality of all the chemical reactions which can occur in living organisms, much more is implied by the term than simply a listing of the kinds of interactions that take place among molecules and ions. It is the sum of chemical reactions in context—not merely oxidation of a fat molecule, for instance, but oxidation of fat molecules occurring in particular places within particular cells and organisms. Elements of structure, such as granules, fibers, and membranes, are basic to the ordering of biochemical reactions. Time, environmental conditions, activities and interactions of organisms must be considered. The chemistry of growth and repair, of existence in a steady state, of aging and attack by parasites and predators, of the processes in an organism powering movement, heat production, emission of light—these and all other processes relevant to life are included in the study of metabolism.

This field is so complex, and its understanding so im-