KEETON/GOULD

BIOLOGICAL SCIENCE

5TH EDITION

WILLIAM T. KEETON

JAMES L. GOULD

WITH CAROL GRANT GOULD

BIOLOGICAL SCIENCE

FIFTH EDITION

W • W • NORTON & COMPANY • NEW YORK • LONDON

PRINTED IN THE UNITED STATES OF AMERICA

This book is composed in Aster. Composition by New England Typographic Service, Inc. Manufacturing by R. R. Donnelley & Sons, Company. Book design by Antonina Krass.

FIFTH EDITION

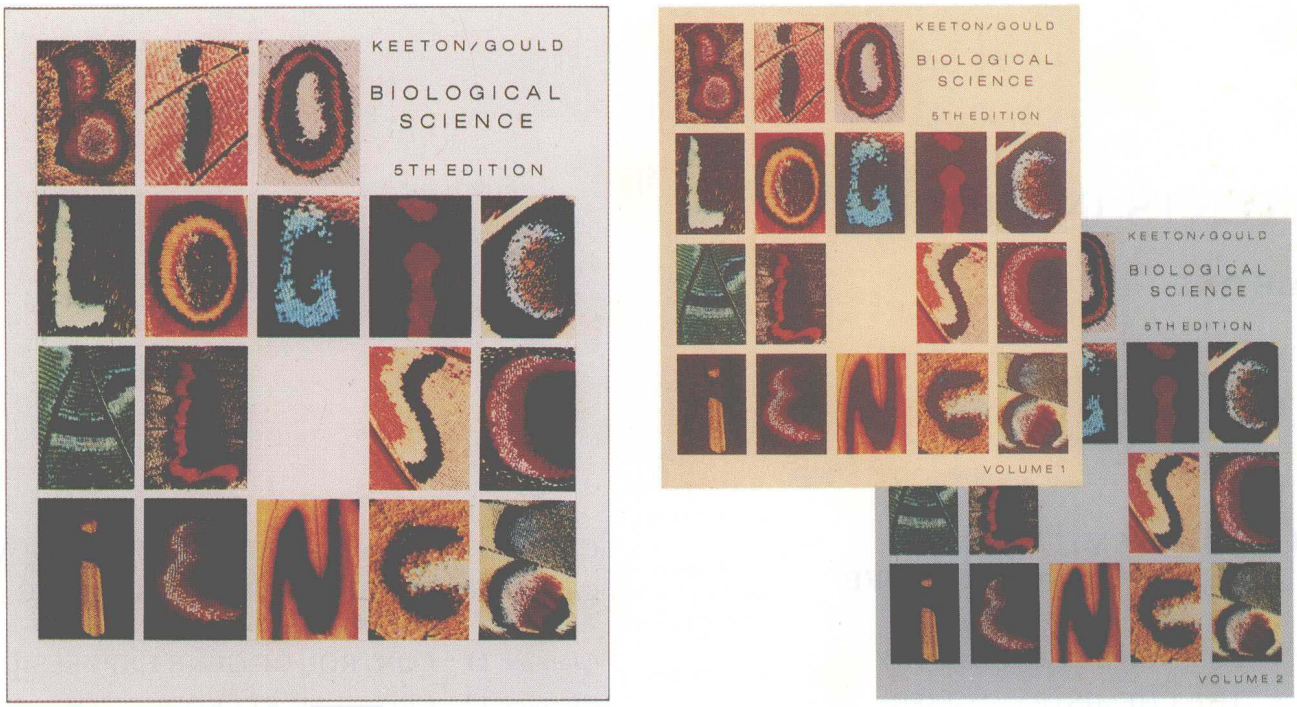
Library of Congress Cataloging-in-Publication Data

Keeton, William T.
Biological science/William T. Keeton, James L. Gould, with Carol Grant Gould. —5th ed.
p. cm.
ISBN 0-393-96223-7
1. Biology. I. Gould, James L., 1945- . II. Gould, Carol Grant. III. Title.
QH308.2.K44 1993
574—dc20 92-19326
ISBN 0-393-96223-7 (cl)
ISBN 0-393-96224-5 (V. I pa)
ISBN 0-393-96225-3 (V. II pa)

W. W. Norton & Company, Inc., 500 Fifth Avenue, New York, N.Y. 10110
W. W. Norton & Company Ltd., 10 Coptic Street, London WC1A 1PU

2 3 4 5 6 7 8 9 0

ABOUT THE COVER



IN ONE VOLUME OR TWO

The colorful letters on the cover, spelling the title of this book, are enlarged photographs of patterns found on the wings of butterflies and moths. They were photographed from all over the world by Kjell B. Sandved of the Smithsonian Institution's National Museum of Natural History in Washington, D.C.

Butterfly-wing patterns may discourage predators and identify potential mates; their developmental histories are under intense scrutiny. As a striking example of the diversity of forms in just one group of species, they demonstrate the vast richness of the variation on which evolution acts, a central theme of modern biology.

PREFACE

When Bill Keeton's first edition of *Biological Science* appeared in 1967, it started a revolution so complete that we now take his vision for granted. Instead of separate introductory courses (and texts) in microbiology, botany, and zoology, Bill saw that all of biology could (and should) be united. Today it seems obvious that the cells and molecules of plants, animals, and unicellular organisms are very similar—indeed, so nearly identical in most respects that the differences are full of evolutionary significance. Today we begin with the assumption that natural selection operates on organisms of all three groups in similar ways, and that studying the interactions of different groups with one another is essential to any real understanding of ecology. Moreover, as Bill showed most convincingly from the outset, the basic physiological challenges faced by animals, plants, and microorganisms—gas exchange, nutrient procurement, internal circulation, coordination of function, and so on—can be best understood by juxtaposition and contrast. For him, and now for nearly everyone, biology is a unified subject. It is this view of biological science that is his enduring legacy to us all, and the guiding principle upon which this book continues to be based.

We had three main objectives in preparing the Fifth Edition: (1) to bring the book up to date in both depth and scope, so that it continues to reflect new discoveries and to anticipate shifting emphases in the advanced courses for which it may be the student's only preparation; (2) to continue to improve the clarity of the presentation wherever possible, adding more intuitive explanations and more functional examples, and thus making even the most complex subject matter accessible to a wider range of students; (3) to keep the book manageably brief, which sometimes required the abbreviation or deletion of less important topics. Above all, we wanted to reinforce the evolutionary theme in all parts of the text, and to provide more satisfactory molecular explanations of the mechanisms of biology in all chapters. From our own experience and the comments of other teachers of introductory biology, it was clear that the content of every chapter had to be scrutinized once again for accuracy, emphasis, and effectiveness. In the end, every chapter benefited from this process.

CHANGES IN ORGANIZATION

Several major changes in the new edition will be immediately apparent. The sequence of chapters originally laid out by Bill Keeton alternated cellular and organismal topics, so that each semester of his course had some of each. More and more, however, the two semesters of introductory biology are taught by different instructors (often from different departments); one contingent usually focuses on cellular and molecular topics, often from an evolutionary perspective, while the other deals principally with evolution, diversity,

physiology, and ecology. It is a continuing tribute to the quality and flexibility of Bill's writing that many schools have taught from *Biological Science* in this order even though the book had a different sequence. Although the order of chapters now follows (roughly) a more common levels-of-organization approach, we have taken special care that the new edition still works with Bill's original order of teaching, and that it continues to provide the coherence of presentation and development that is essential for mastering biological principles.

The reorganization of the book has several advantages. Part II, THE PERPETUATION OF LIFE (formerly Part III), now follows THE CHEMICAL AND CELLULAR BASIS OF LIFE, Part I. Within Part II the order of chapters has been rearranged to allow the student to move directly from the subcellular emphasis of Part I into the molecular basis of information flow. To accomplish this logical transition, we have postponed the material on cell division and classical genetics: cell division now immediately precedes embryology and development, and inheritance comes at the end, leading directly into the discussion of the genetic basis of evolution in Part III, EVOLUTIONARY BIOLOGY. Part III now ends with a section on phylogeny, which lays the groundwork for Part IV, THE GENESIS AND DIVERSITY OF ORGANISMS. The chronicle of diversity in Part IV in turn provides the background for the comparative physiology of organisms in Part V, THE BIOLOGY OF ORGANISMS. And Part V culminates in the study of the mechanisms and evolution of behavior, which leads naturally into ECOLOGY, Part VI.

Some teachers will be pleased to find that we have restored the Selected Readings to the ends of chapters in the Fifth Edition, and that we have added Concepts for Review and Study Questions at the ends of chapters. We have not followed what we feel is the ineffectual practice of including multiple-choice questions at the ends of chapters, but have instead focused on questions that encourage students to review the basic concepts and big ideas, and that provoke thought about the material. These questions are a helpful complement to the more thorough and disciplined study regime provided by Carol H. McFadden's excellent *Study Guide*.

Other obvious changes include the availability of the book in a more portable two-volume format in addition to the conventional single-volume version, and the inclusion of many new four-color illustrations throughout the text. Users of the previous edition will see immediately that we have added many new photographs and line drawings to this edition to summarize, dramatize, and reinforce points made in the text. We have avoided the all-too-common shortcut of developing illustrations independently of the text. Readers of *Biological Science* have come to expect an unfailing harmony of text and illustration, and we have worked hard to make sure that difficult concepts are reinforced visually, and that all terms and ideas presented in illustrations are fully documented in the text.

A GUIDE TO SPECIFIC CHANGES

In the interest of brevity we list only major changes in this edition. The *Instructor's Manual* provides a more thorough description of the revisions and their rationale.

Chapter 1 (Introduction) has added new topics in modern biology, forecasting new material in each of the six parts.

PART I: THE CHEMICAL AND CELLULAR BASIS OF LIFE

Chapter 2 (Some Simple Chemistry) further explains the polarity of water molecules with a discussion of how soaps and detergents work.

Chapter 3 (The Chemistry of Life) introduces "designer" enzymes and new information on the chemical composition of the cell.

Chapter 4 (At the Boundary of the Cell) has new material on clathrin and the formation of vesicles.

Chapter 5 (Inside the Cell) has more information on the mailing-label strategy of targeting proteins, and more about peroxisomes, microfilaments, microtubules, intermediate filaments, mechanisms of cell movement (including cilia and flagella, previously in the muscle chapter), and the intracellular transport of organelles and vesicles, especially the roles of kinesin and dynamin.

Chapter 6 (Energy Tranformations: Respiration) places added emphasis on the role of electronegativity of oxygen versus other atoms, and has a clearer and simpler summary diagram for the anatomy of respiration.

Chapter 7 (Energy Transformation: Photosynthesis) now explores the physiological ecology of granal versus stromal thylakoids, and also contains a new *Exploring Further* section on the structure of the photosynthetic reaction center.

PART II: THE PERPETUATION OF LIFE

Chapter 8 (The Structure and Replication of DNA) now includes a discussion of the replication of DNA in organelles.

Chapter 9 (Transcription and Translation) includes new material on how transcription is terminated, the mechanism of

exon splicing, the process of translation, and how ribosomes bind to the endoplasmic reticulum.

Chapter 10 (Mobile Genes and Genetic Engineering) is new. It deals with mechanisms of genetic mobility including transduction, transformation, plasmids, lytic versus lysogenic viruses, retroviruses, and transposons. It also explores the evolutionary significance and interrelationships for these processes or entities, and the practical use of each for genetic engineering. There are also new discussions of the polymerase chain reaction and gene therapy.

Chapter 11 (Control of Gene Expression) contains new material on the structure of DNA-binding proteins, the structure and function of the CAP-activator system, transcription factors, inducers, and enhancers. New sections have also been added on telomeres, genetic imprinting, alternative splicing, translation inhibitors (including anti-sense RNA), and mRNA and protein-digesting enzymes that control molecular lifespans. There is now a discussion of mutations of control versus structural regions and an expanded section on cancer, including the mechanisms of metastasis, oncogene formation, and oncogene operation.

Chapter 12 (Cellular Reproduction) has new sections on cyclins and control of the cell cycle, the evolutionary logic of meiosis, the timing of meiosis in plants, and the investment in diploid and haploid phases in the life history of a species.

Chapter 13 (The Course of Animal Development) no longer incorporates a discussion of plant development, which has been integrated into a later chapter on plant hormones. This change more fully recognizes that development patterns in plants are fundamentally different from those in animals. In plants, since rigid cell walls make most morphogenesis impossible, differential growth is critical; there is no need for many different organs since plants are autotrophic, and growth continues in select tissues throughout the life of the plant rather than being turned off, as in animals. These important developmental strategies are compared and contrasted in their respective chapters.

Chapter 14 (Mechanisms of Animal Development) more clearly distinguishes induction and differentiation, and provides a fuller discussion of the role of CAMs in cell migration and morphogenesis, forecasting their role in immunology. There is now a discussion of somites and the strategy of iteration of subunits in bilaterally symmetric animals, a treatment of morphogen action and pattern formation in *Drosophila*, including homeotic genes and homeobox sequences, and a description of the likely role of retinoic acid in vertebrate development.

Chapter 15 (Immunology) was largely rewritten and reillustrated to update and simplify the treatment. Most of the material on gene evolution is now incorporated in subsequent evolution chapters in the context of how new alleles arise; this chapter retains a discussion of hypermutation and the hypothesis that immune-system molecules evolved from CAMs. New material has been added on the lymphatic system, and the structure, life history, and effects of the AIDS virus.

Chapter 16 (Inheritance) now covers both Mendelian and non-Mendelian patterns of inheritance in one chapter. This combined treatment eases the transition from the preceding molecular discussions to the sections on the allelic distributions in populations that follow in Chapter 17.

PART III: EVOLUTIONARY BIOLOGY

Chapter 17 (Variation, Selection, and Adaptation) incorporates new material on the genetic bases of variation, frequency-dependent selection, and sexual selection. An *Exploring Further* section questions the evolutionary value of sexual reproduction and introduces the gene-repair, red-queen, and tangled-bank hypotheses.

Chapter 18 (Speciation and Phylogeny) has more on punctuated equilibrium, the Burgess shale fauna, the relationship between development and evolutionary change, the quantification of relatedness in different classification schemes, cladistics, and molecular taxonomy.

PART IV: THE GENESIS AND DIVERSITY OF ORGANISMS

Chapter 19 (The Origin of Life) has a new section on the possible role of comets and asteroids in contributing water, organic molecules, and other conditions favorable for life to the earth, together with a discussion of ribozymes as possibly the first enzymes and information-storage molecules. Material on the endosymbiotic hypothesis has been updated, and there is now an improved discussion of the ambiguities inherent in kingdom classifications. The kingdom-classification scheme adopted for the Fifth Edition has been thoroughly modernized, based on the latest and most reliable sequence comparisons.

Chapter 20 (Viruses and Bacteria) has more on viroids, prions, and aquatic viruses; it also has a more ecological, functional, and evolutionary treatment of bacteria. Along with a modern, sequence-based phylogeny of bacteria, it

presents an explicit comparison of Gram-positive and Gram-negative cell walls, more on mycoplasmas and myxobacteria, and a more comprehensive treatment of archaebacteria.

Chapter 21 (Archaezoans and Protists) covers organisms of both groups together, omitting the chlorophyll *c* algae (now in Chapter 22) and some single-celled groups that belong with the fungi. The new sequence-based phylogeny is correlated with the latest ultrastructural findings.

Chapter 22 (Chromistans and Plants) encompasses both Chromista and Plantae; it includes a new functional/evolutionary comparison of the algae and higher plants, a discussion of sexual selection in plants, and a summary of plant tissues.

Chapter 23 (Fungi) has an overview of fungal niches, including the one occupied by the pneumonia-causing species that kills many AIDS patients.

Chapter 24 (Invertebrate Animals) places greater emphasis on the progression of developmental patterns and the many parallels with plant evolution, specifically in regard to surface-to-volume ratios and the transition from water to land.

Chapter 25 (Chordate Animals) includes an overview of animal tissues, as well as more on mass extinctions and the use of sequence analysis to trace human evolution.

PART V: THE BIOLOGY OF ORGANISMS

Chapter 26 (Nutrient Procurement and Processing by Plants and Other Autotrophs) has an expanded explanation of water movement, recast in terms of water potential (to allow for the effects of turgor pressure). There is also more on nitrogen fixation.

Chapter 27 (Nutrient Procurement and Processing by Animals and Other Heterotrophs) now mentions avian fermentors, compares the waste-disposal problem in plants with that in animals, and has a new section on plant poisons.

Chapter 28 (Gas Exchange) has an expanded discussion of the control of stomatal opening and closing, and the implications for water use by plants. There is also a new section on water conservation by animals during breathing, with particular reference to the role of countercurrent exchange in water recovery.

Chapter 29 (Internal Transport in Unicellular Organisms and Plants) now discusses plant circulation in terms of water potential, to allow for consideration of temperature gradients, as opposed to just osmotic gradients. There is also a comprehensive presentation of the TATC (transpiration-adhesion-tension-cohesion) theory, as well as new sections on the water cycle in plants and adaptations for water conservation.

Chapter 30 (Internal Transport in Animals) has a major new section on temperature regulation, including the costs and benefits of homeothermy, fevers, and temporal heterothermy. A revised discussion of heat conservation and cooling focuses on the role of countercurrent exchange. Also included are a discussion of the evolution of hemoglobin, an examination of O_2-CO_2 exchange in corpuscles, and an overview of the many functions of the circulatory system, by way of introduction to the next few chapters.

Chapter 31 (Regulation of Body Fluids) has a revised description of kidney function.

Chapter 32 (Development and Chemical Control in Plants) now includes discussions of flower development and homeobox control. There is also more on root growth, tropisms, spacing, and root-to-shoot ratios, as well as an expanded section on photoperiodism and flowering.

Chapter 33 (Chemical Control in Animals) includes a new discussion of atrial natriuretic factor (ANF), nitric oxide, somatostatin, and the hormonal regulation of blood composition and volume. There is also an updated discussion of insulin and diabetes, an explanation of the G-protein transduction system, and more on the evolution of hormones.

Chapter 34 (Hormones and Vertebrate Reproduction) has a description of how the abortion-inducing drug RU 486 works.

Chapter 35 (Nervous Control) discusses the role of chloride channels in cystic fibrosis and of nitric oxide as a transmitter. A shortened discussion of presynaptic phenomena (habituation, sensitization, and conditioning) is now incorporated into the text rather than being set off in a box.

Chapter 36 (Sensory Reception and Processing) has a discussion of the recent discovery of olfactory-receptor genes and an updated description of the molecular basis of visual and auditory transduction. There is also a new discussion of frequency-tuning within the ear and lateral line organs. The discussion of visual processing has been brought up to date and related to effects of neural anomalies, including the possible biological cause of dyslexia.

Chapter 37 (Muscles) now takes into account the use of hydrostatic movement by vertebrates.

Chapter 38 (Animal Behavior) combines and shortens what

had been two chapters, with some behavioral topics moved to more appropriate places in Parts III and VI. There is also a new section on risks and deception, and the discussion of programmed learning has been expanded.

PART VI: ECOLOGY

Chapter 39 (Ecology of Populations and Communities) incorporates completely rewritten sections on population regulation and different forms of density-dependent limitation. The definition of a niche has been revised, and a new section has been added on social organization, including a discussion of the costs and benefits of sociality, the mechanisms of resource control, and the nature and role of altruism. The discussion of human ecology is now here, and the projections of human population growth have been updated.

Chapter 40 (Ecosystems and Biogeography) includes a revised discussion of trophic levels and food webs. The costs and benefits of livestock ranching are also considered, and there is more about human effects on the cycling of materials, including the probable roles of CO_2, methane, and pollution in altering climate. This theme is complemented by an enlarged discussion of the fluorocarbons in ozone destruction and an updated discussion of the chemical basis of plant loss to acid rain and ozone. The section on island biogeography has been updated.

ESSENCE OF BIOLOGY: HYPERCARD AND WINDOWS™ SUPPLEMENT

This edition of *Biological Science* is accompanied by two new supplements: a HyperCard review and a Windows™ review, developed in collaboration with Grant F. Gould. Suitable for use with Apple Macintosh and DOS 386 computers, respectively, these reviews consist of "stacks" of "cards" summarizing each part, chapter by chapter, together with a set of multiple-choice questions for each chapter, as well as a glossary. Each review card provides a succinct discussion of a concept and allows direct access to the review questions, the glossary, and a table of contents. Most cards include illustrations, some of which are animated to help demonstrate dynamic processes. The first use of any term in the glossary is in boldface, and clicking a mouse-driven cursor on it takes the student directly to its definition. The definitions themselves incorporate cross references to other glossary terms, so that clicking on a boldfaced word in a definition takes the user to that card. The review questions include responses to each choice that explain why the answer selected is correct or incorrect. Other useful features will become clear as the student explores this novel interactive learning aid. We wish to thank the students in the introductory biology course at Princeton for serving as guinea pigs for the preliminary version of the review and for providing valuable feedback; Jessica Avery at W.W. Norton suggested many thoughtful improvements.

ACKNOWLEDGMENTS

A revision of this magnitude of a book with such high standards to maintain would have been impossible without the help of many reviewers. In particular, we would like to thank Wayne M. Becker, University of Wisconsin; Robert A. Bender, University of Michigan; Dennis Bogyo, Valdosta State College; Carole Brown, Wake Forest University; Christine L. Case, Skyline College; Thomas Cavalier-Smith, University of British Columbia; Anne M. Cusic, University of Alabama; Peter J. Davies, Cornell University; Michael Foote, Wake Forest University; Joseph Frankel, University of Iowa; Florence Gleason, University of Minnesota; Lane Graham, University of Manitoba; Barbara Hilyer, University of Alabama; Carl Hopkins, Cornell University; John B. Jenkins, Swarthmore College; Dan Jones, University of Alabama; Alan R. Kabat, Harvard University; Glenn Klassen, University of Manitoba; Ken Marion, University of Alabama; Robert M. May, Oxford University ; Scott Orcutt, University of Akron; Maggie T. Pennington, College of Charleston; Wiltraud Pfeiffer, University of California, Davis; Thomas L. Poulson, University of Illinois; Thomas B. Roos, Dartmouth College; Steve Strand, University of California, Los Angeles; W. Edward Sullivan, Princeton University; Heinz Valtin, Dartmouth Medical School; Joseph W. Vanable, Purdue University; Liz Van Volkenburgh, University of Washington, Charles F. Westoff, Princeton University, and D. Reid Wiseman, College of Charleston.

The many new and uniformly excellent pictures and drawings in the Fifth Edition speak more eloquently than we can of the contributions of Ruth Mandel, our photo editor, and of Michael Reingold and Michael Goodman, the artists. Clark Carroll and John McAusland helped in the preparation of the artwork. The copy editing was expertly handled by Emily Arulpragasam, while Lee Marcott, as project editor, managed somehow to coordinate everything and keep everyone on track. The greatest contribution to both the rigor and the aesthetic appeal of the text was made by our tireless editors, James D. Jordan and Joseph Wisnovsky. To all of these individuals, our heartfelt thanks.

J.L.G.
C.G.G.

Princeton, New Jersey
March 1992

CONTENTS IN BRIEF

VOLUME ONE

VOLUME TWO

CONTENTS