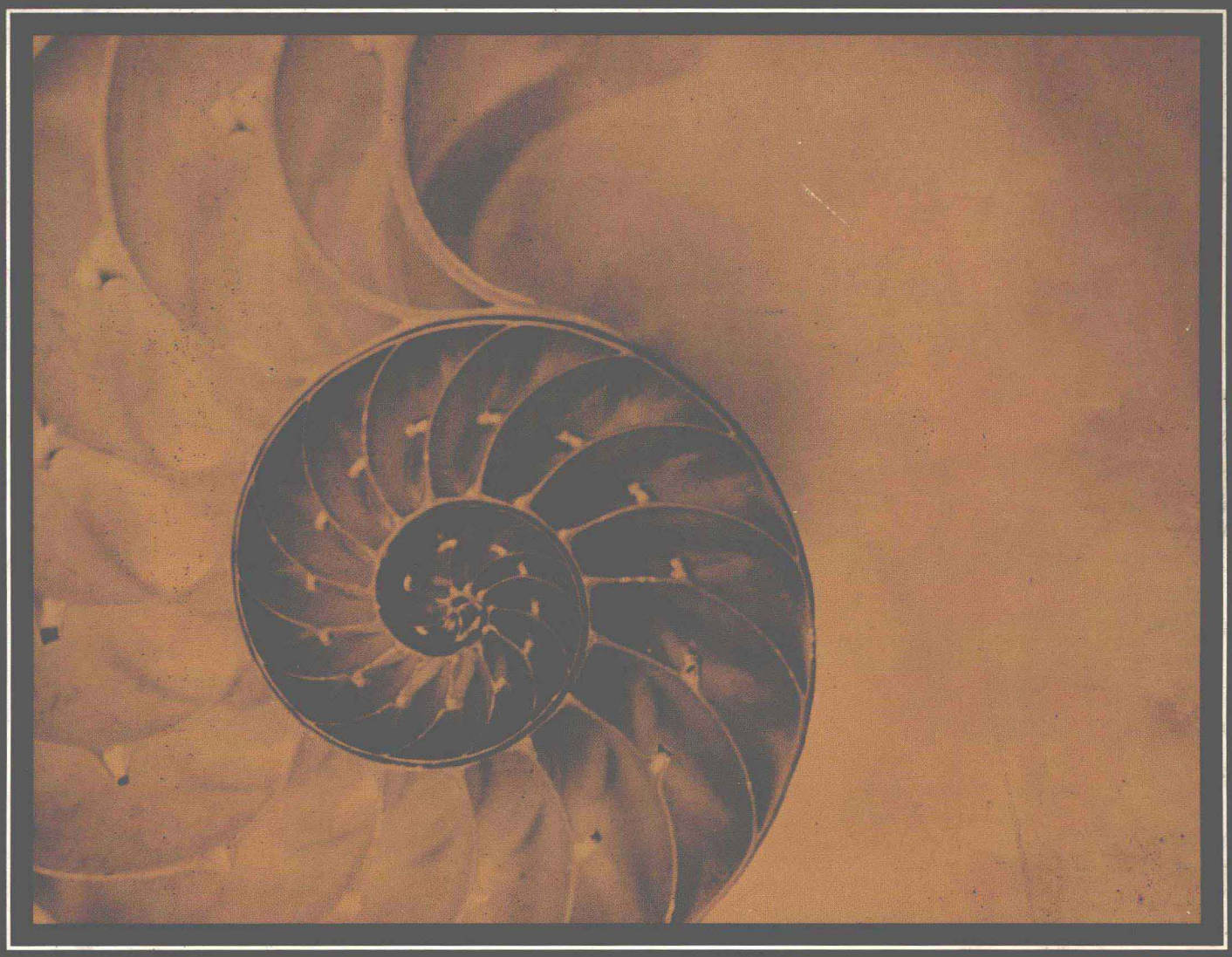

# BIOLOGICAL SCIENCE

FOURTH EDITION

WILLIAM T. KEETON
JAMES L. GOULD

NORTON
INTERNATIONAL STUDENT EDITION

WILLIAM T. KEETON
CORNELL UNIVERSITY

JAMES L. GOULD
PRINCETON UNIVERSITY

WITH CAROL GRANT GOULD

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FOURTH EDITION

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# BIOLOGICAL SCIENCE

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# PREFACE

Few challenges are more exciting and rewarding than teaching introductory biology. A teacher has the responsibility of presenting the essentials of a dynamic and critically relevant discipline to students of widely differing backgrounds and needs, of providing an informed lay understanding for many, and at the same time erecting a secure foundation for more advanced courses for others. Bill Keeton was a pioneer of the integrated approach to teaching introductory biology; his lucid and authoritative text has become the standard against which other books are judged. The success of this exceptional scientist and teacher was based both on his skill at exposition and on his conception of the field, in which he viewed the variety of living things in terms of the similarities and differences in the evolutionary adaptations they have undergone. This perspective led him to treat plants and animals together, comparing and contrasting the problems they face and the solutions that have evolved. For him, biology was never a series of special issues, a litany of social and environmental concerns, or an encyclopedia of premedical facts.

Despite the enduring excellence of *Biological Science*, it is no surprise that six years after the publication of the Third Edition an up-to-date presentation of modern biology is again needed. In preparing this Fourth Edition, we have been very fortunate to have a book of such obvious excellence from which to work.

We had three main objectives in revising: 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; to keep the book manageably brief, which sometimes required the abbreviation or deletion of less essential topics; and to bring the book up to date in both depth and scope, so that it would reflect new discoveries and the shifting emphases in the advanced courses for which it may be the student's primary introduction. In particular, we wished to reinforce the evolutionary theme in all parts of the text, and to provide more intuitive 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 reviewed for accuracy, emphasis, and effectiveness. In the end, every chapter benefited from this process: several were heavily revised and many of the longer chapters were divided into shorter, more manageable ones. Here, in brief, are some of the more important changes:

1. Chapter 1, the introduction, focuses new attention on the historical context in which modern biology developed, the role of intuition in formulating hypotheses, and the distinction between evolution as a process and natural selection as a mechanism.

2. Chapter 2, on simple chemistry, emphasizes the role of electrons in energy storage and release. The presentation of weak bonds—particularly the important concept of electronegativity—provides a groundwork for the later discussion of enzyme function.

3. Chapter 3, on the chemistry of life, now presents a brief, largely intuitive introduction to equilibrium constants that is particularly helpful in understanding how coupled reactions work. There is a new discussion of how the active sites of enzymes function to weaken the appropriate bonds in substrate molecules.

4. In Chapter 4, which focuses on the cell membrane, new descriptions of how the different sorts of microscopes work will enable students to interpret the many EM photographs in the book more easily. A more intuitive presentation of diffusion and osmosis complements the traditional explication. The biggest change has been in the added emphasis on the cell membrane itself, particularly the forces that stabilize it and the way its channels and gates work to regulate the movement of chemicals into and out of the cell. This discussion permits a more molecular presentation of nerve transmission, hormone action, organelle function (including the electron-transport chain), and fluid regulation in later chapters. The description of endocytosis has been enriched by a discussion of coated pits, with the LDL receptor as the primary example.

5. Chapter 5, on the interior of the cell, now presents an updated and expanded discussion of how newly synthesized proteins are labeled, packaged, and shipped by cellular organelles—particularly the ER and the Golgi. There is now explicit treatment of the microtrabecular lattice and a more extensive discussion of the endosymbiotic hypothesis.

6. In Chapter 6, on multicellular organization, the most important change has been the addition of a major discussion of cell-to-cell adhesion, including desmosomes and gap junctions.

7. In Chapters 7 and 8, on energy transformations, respiration is now discussed before photosynthesis; this order has an evolutionary logic, since fermentation probably appeared even before cyclic photosynthesis, but its primary advantage is pedagogical: respiration is easier to understand, and its basic features are virtually identical to those of the more complex chemistry of photosynthesis. It is now possible to teach glycolysis intuitively from a thermodynamic perspective, or as a series of chemical changes. New margin illustrations allow the interested student to follow the molecular alterations of glycolysis step by step, while the text outlines the thermodynamic considerations. The chemiosmotic hypothesis in respiration now receives central attention, and is presented both thermodynamically and anatomically. The treatment of photosynthesis has undergone similar changes, and focuses on its evolution, intuitive thermodynamics, and fascinating anatomy. Of the hundreds of illustrations added or modified to improve the visual presentation of ideas throughout the text, we are particularly pleased with the many new drawings in these two chapters.

8. The chapters on whole-organism physiology (Chapters 9–14) have undergone a number of small but important additions and improvements, most apparent in the new drawings of fluid flow and tissue growth in monocots and dicots, the sections on the evolution and comparative physiology of hearts and circulatory systems, and the treatments of liver and kidney function. As in all the cases in which we have added a molecular emphasis, we believe these details provide a more satisfying, unifying, and comprehensible picture of the life processes they elucidate.

9. The chapters dealing with hormonal control (Chapters 15–17) emphasize the molecular bases of hormone action, second-messenger strategies like that of the calcium-calmodulin system, local chemical mediators and other hormone-like molecules, and the evolution of hormones.

10. The chapters on neurobiology and effectors (Chapters 18–20) have been reorganized and rewritten to reflect a more modern emphasis on molecular mechanisms and the functional issues that relate to sensation and movement. The discussions of interneurons, habituation, and simple circuits use *Aplysia* as their primary example, to complement the extensive treatment of the human CNS. There is new emphasis on how sensory information is processed to extract patterns of shape and movement in the visual world. The discussion of brain evolution has been brought into line with current thinking.

11. Chapter 21, the first of two chapters on behavior, deals with the mechanisms of innate behavior and of learning, and ties these mechanisms to the neurobiology that underlies them; the chapter ends with a discussion of a prime example of the interplay of instinct and learning: bird navigation. Chapter 22 deals with the less mechanistic, more evolutionary aspects of behavior, often called behavioral ecology. Bringing together material formerly divided among several chapters, this discussion treats in one place the concepts of niche and habitat, kin selection and reciprocal altruism, communication, and the social behavior of insects, birds, and mammals (including humans).

12. The genetics and development chapters of Part III required extensive revision to keep pace with the most important new research findings in molecular biology; many more changes have been made in these chapters than can possibly

be mentioned here. Some alterations were strictly pedagogic, such as the reworking of the presentation and accompanying illustrations of mitosis and meiosis in Chapter 23, on cellular reproduction. Also in that chapter, we have added a discussion of the evolution of cell division and sexual recombination, as well as a molecular view of recombination. The genetics chapters (Chapters 24 and 25) have undergone many small changes to improve clarity. They now include new discussions of complementation tests, trihybrid crosses, statistical tests, and the molecular basis of mutation.

13. The chapters on the flow of information in cells (Chapters 26–30) are the most heavily revised in Part III. Our presentation of DNA replication and repair, transcription, messenger RNA "processing" and translation is largely new, and constitutes a modern molecular treatment of these subjects that is eminently suitable for an introductory course. Here, as elsewhere, material most appropriate for majors or advanced students, such as the discussion "Replication of the *E. coli* chromosome," is presented in self-contained boxes that supplement the more general treatment in the text. Extrachromosomal inheritance is now presented in a separate chapter (Chapter 28), which incorporates new or heavily revised discussions of organelle heredity, the mechanisms of viral replication, and recombinant DNA technology. The chapter on the control of gene expression (Chapter 29) is almost entirely new, containing discussions of negative and positive transcriptional control, a revised presentation of the *lac* operon, two boxes on advanced topics ("How control substances bind to DNA" and a particularly well understood example of repression, "The lambda switch"), an exposition of the curious organization of eucaryotic chromosomes, and a modern discussion of cancer and oncogenes. The new chapter on immunology (Chapter 30) features a well-integrated discussion of how B cells and T cells work and interact to produce precisely modulated immune responses. This chapter also includes important discussions of the genetic basis of antibody diversity and of the various mechanisms of genetic variability, including transposition, which may provide the variation necessary for the evolution of novel proteins. Intriguing hypotheses of gene evolution, like that of Gilbert and Blake, are considered.

14. A variety of small improvements have been incorporated into Chapters 31 and 32, on development, but the main revisions are those providing coverage of the mechanistic bases of differentiation and pattern formation. In particular, there is now major treatment of neural development.

15. The first two chapters of Part IV (Chapters 33 and 34) now give more attention than the previous edition to the possible role of chance, and of genetic drift in particular, in evolution. They also provide necessary examples of sympatric speciation and host specificity, and discuss several major controversies among evolutionary biologists; these include the debates over punctuated equilibria and cladistics.

16. The last two chapters of Part IV (Chapters 35 and 36) deal with ecology and biogeography. Many teachers were unhappy with the organization of this material in the Third Edition, with the choice of examples in the sections on ecosystems and community ecology, and with the lack of emphasis on physiological ecology. These criticisms have been taken to heart: the new organization puts material on population size and distribution first in Chapter 35; this is followed by sections on population growth and regulation, and the chapter ends with a discussion of dominance, diversity, stability, and succession. Chapter 36 now begins with a view of the economy of ecosystems—the flow of energy and materials—followed by a new section on the role of the sun in creating worldwide climatic zones. The discussion then focuses on more local factors like mountain ranges, and on the different kinds of biomes. The chapter ends with a consideration of the evolution of biomes and the mechanisms and consequences of species dispersal.

17. The Fourth Edition continues to use Robert H. Whittaker's five-kingdom classification system, modified to accommodate the new findings on Archaebacteria. This system and some alternatives are discussed in Chapter 37, which also includes a modernized account of current ideas about the origin and early evolution of life. In the Third Edition the chapters on classification (now Chapters 38–43) were perhaps the most complete in an introductory book, and they are therefore not much changed, except for Chapter 38, on viruses and Monera, which now includes discussions of viroids, prions, and Archaebacteria. Numerous small changes in the classification of higher animals have been necessary; the sections dealing with the evolution of vertebrates, primates in particular, have also been carefully updated to reflect current thinking.

Throughout the Fourth Edition, our general pedagogical strategy has been to begin a chapter—or, more often, a set of chapters—with an overview of what is to come, thus providing an initial evolutionary or functional outline to help the student place the sections that follow in a useful context. Several new summary diagrams and discussions reflect this approach.

We decided early on to keep the general chapter order of the Third Edition. No single sequence is ideal, and the present one has the advantage of familiarity. We have, however, made every effort to make the parts stand on their own, so that they can be taught in different orders. At Princeton,

for example, we teach Part IV immediately after Part I, followed by Part III, Part V, and then Part II. It is a testament to the flexibility of the Third Edition that we have no difficulty using the book with our idiosyncratic order, and the Fourth Edition should prove even more adaptable. Teachers who wish to keep their presentations of plants and animals separate will find that the new chapter divisions facilitate this approach.

This brief listing of the major changes in the Fourth Edition should not be taken to imply that other parts of the text have escaped careful scrutiny. On the contrary, an intense reevaluation has gone on throughout the book. Despite such exhaustive efforts, there will be parts of the book that do not reflect the most recent advances by the time students use the text. Not only will new developments have occurred in the interim between writing and publication but, lacking a crystal ball, we may have failed to recognize the significance of developments already taking place. For a text author, this is as unfortunate as it is unavoidable, but it is not all bad for students, since it reflects the vitality of the field.

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 Joseph M. Calvo, Cornell; Robert K. Colwell, Berkeley; Peter Grant, Princeton; Andre T. Jagendorf, Cornell; Carol H. McFadden, Cornell; C. O. Patterson, Texas A & M; Thomas Roos, Dartmouth; Daniel I. Rubenstein, Princeton; Peter M. Shugarman, Southern California; Malcolm Steinberg, Princeton; Volker M. Vogt, Cornell; and Timothy C. Williams, Swarthmore College, for help above and beyond the call of duty. Many other important criticisms were provided by Wayne Aspey, Ohio State; Robert A. Bender, Michigan; Anthony Blackler, Cornell; Robert W. Bouma, Cornell; George Bowes, Florida; George Cain, Iowa; W. Zacheus Cande, Berkeley; Steven Jay Gould (no relation), Harvard; Richard Hallberg, Iowa State; Steven Heidemann, Michigan State; Paul Hertz, Barnard; Robert P. Higgins, Smithsonian Institution; William Hodos, Maryland; Anthony R. Kaney, Bryn Mawr College; Joseph Levine, Boston College; William M. Lewis, Colorado; Karel F. Liem, Harvard; Ellis R. Loew, Cornell; Ross J. MacIntyre, Cornell; Peter Marler, Rockefeller; Mitch Masters, Oregon; Kenneth Miller, Brown; John Neess, Wisconsin; Michael Newlon, Iowa; Maggie T. Pennington, College of Charleston; David Pilbeam, Harvard; Patricia J. Pukilla, North Carolina; Robert Savage, Swarthmore College; John A. Schmitt, Ohio State; David Shappirio, Michigan; Steven D. Skopik, Delaware; Eric Skully, Towson State; James Smiley, College of Charleston; Douglas W. Smith, California, San Diego; Daryl Sweeney, Illinois; and Virginia Utermohlen, Cornell. The many new and uniformly excellent pictures and drawings in the Fourth Edition speak more eloquently than can we of the contribution of Ruth Mandel, our photo editor, and of Michael Reingold, the artist. The consistently high quality of the copy was maintained by the unparalleled vigilance and good judgment of Esther Jacobson, with help from Nancy Palmquist. Roy Tedoff and Fred Bidgood made the impossibly complicated task of book production at least seem feasible. Finally, the greatest contribution to both the rigor and the aesthetic appeal of this text was made by our indefatigable editor, James D. Jordan, whose remorseless insistence on clarity of exposition shows on every page. To all of these individuals, our heartfelt thanks.

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

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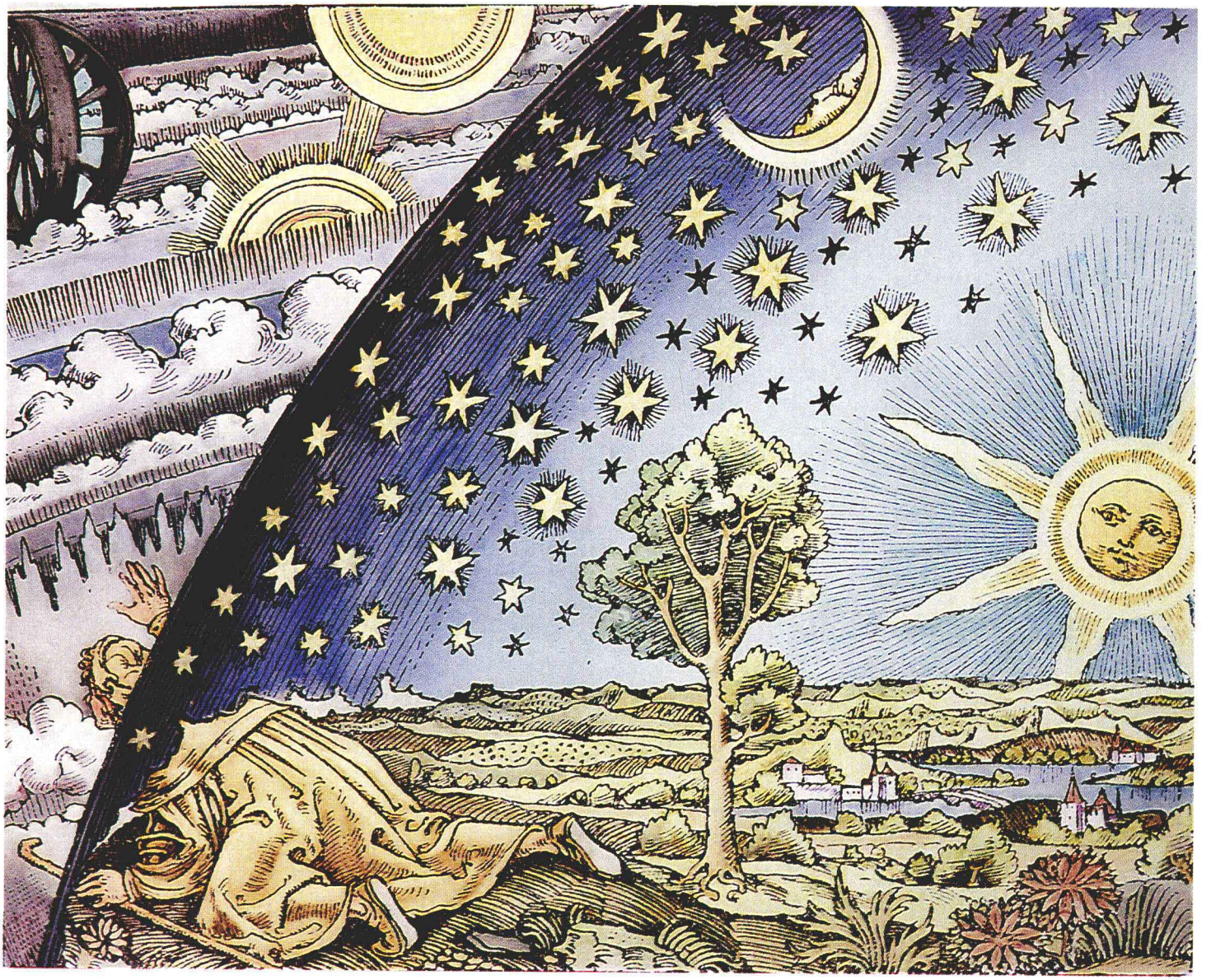

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