

Biology of microorganisms

Thomas D. Brock

# $Biology\ of\ microorganisms$

## Biological Science series

William D. McElroy and Carl P. Swanson, editors

THOMAS D. BROCK Biology of microorganisms

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This book has been set in Galaxy, a film version of a contemporary sans-serif typeface, with headings and captions in italic Century Expanded.

This book was designed as a modern textbook for courses in introductory microbiology at the undergraduate level. It should also appeal to anyone interested in obtaining a general knowledge of microbiology and microorganisms. The emphasis throughout is on microorganisms—their functional, ecological, and evolutionary relationships—and on the activities of interest to man that they carry out. Although a considerable amount of material on applied microbiology is presented, it is integrated into chapters on fundamental principles rather than confined to separate chapters. In this way the applications of microbiology illuminate and make the fundamentals more interesting. Eucaryotic microorganisms have been more emphasized than they usually are in microbiology books; instead of being relegated to small isolated chapters, these organisms are discussed wherever relevant, and a special effort has also been made to contrast procaryotic and eucaryotic microorganisms. In addition, separate chapters treat those aspects of eucaryotes which are quite distinct from procaryotes: cell structure, genetics, taxonomy, and life cycles.

Although the book presents the experimental bases for microbiological concepts and facts, material that would be more useful in the laboratory portion of a microbiology course is not given: The aim is not to use space for material that can better be discussed elsewhere.

A special word should be said about the last two chapters, describing the structure, function, and ecology of groups of microorganisms. Although these chapters may be read straight through, another approach is perhaps preferable: to read specific sections in conjunction with earlier chapters. For instance, sections dealing with medically important groups of microorganisms could be read together with Chapter 15 on host-parasite relationships, and sections on autotrophic bacteria could be read with Chapter 6 on the autotrophic way of life.

It is assumed that the reader of this book will have had some acquaintance with general chemistry and general biology as well as at least a superficial acquaintance with some aspects of molecular biology. Although some of this background material is presented in sufficient depth to make the microbial material understandable, the available space has been used as much as possible to discuss microorganisms themselves. There are many good books that clearly and concisely describe the concepts of molecular biology; one who lacks the necessary background should turn to one of these for guidance.

This book could not have been written without the aid of a number of persons. Since no one can be expert on all phases of a subject as large as microbiology, I have welcomed the help of the publishers, who asked a number of specialists to review preliminary versions of various chapters. In order to ensure an objective evaluation, the anonymity of these outside reviewers has been maintained so that I cannot thank them in-

Preface

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dividually; but their assistance has been invaluable, and I hereby thank them collectively.

Illustrative material has been generously provided by many individuals and firms, whose names are cited near the appropriate illustrations; and I am also indebted to those who assisted in the preparation of original drawings or reviewed them. In addition, the courtesy of authors and publishers in allowing me to use previously published figures and tables is gratefully acknowledged. Virtually all the line drawings were prepared especially for this book, and I thank the artist, Russell Peterson, for converting the sketches devised by Louise Brock into final artwork.

The staff at Prentice-Hall, especially John R. Riina and David R. Esner, have provided invaluable aid throughout production, as has the designer, Betty Binns. Competent secretarial and bibliographic assistance has been provided by Linda Detwiler, Mary Swarthout, Nancy Doemel, Sue Bott, Pat Holleman, Bonnie Hodler, and Jane Griffith-Jones. I should also like to express my appreciation to the staff of the Biology Library of Indiana University, without whose cooperation this book could not have been written. Errors and omissions are, of course, my own responsibility, and I should greatly appreciate receiving comments, suggestions, and corrections.

Finally, although it is customary for an author to thank his wife for help and support, these thanks here must go much further: Louise has been involved in a detailed way in the making of this book from its inception and could almost have been included as a coauthor. She has outstandingly handled all the myriad details that must be attended to if such a book as this is to be published, and without her the book might never have been completed.

Thomas D. Brock Bloomington, Indiana, and West Yellowstone, Montana 1 Introduction

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Microbiology is the study of microorganisms, a large and diverse group of free-living forms that exist as single cells or cell clusters. Being free-living, microbial cells are distinct from the cells of animals and plants since the latter are able to live not alone in nature but only in characteristic groups. A single microbial cell is generally able to carry out its life processes of growth, respiration, and reproduction independently of other cells, either of the same kind or of different kinds. Although there are exceptions to this statement, which we will consider later, this definition provides a basis for our introduction to microorganisms.

#### 1.1 Microorganisms as cells

The theory that the cell is the fundamental unit of all living matter is one of the great unifying theories of biology. A single cell is an entity, isolated from other cells by a cell wall or membrane and containing within it a variety of subcellular structures, some of which are found in all cells and some of which are variable in their occurrence. All cells have certain chemical characteristics in common in that they all contain proteins, nucleic acids, lipids, and polysaccharides. Because these chemical components are common throughout the living world, it is thought that all cells have descended from some common ancestor, a primordial cell. Through millions of years of evolution, the tremendous diversity of cell types that exist today have arisen. Cells vary enormously in size, from submicroscopic bacteria too small to be seen even with the light microscope, to the 170- by 135-mm ostrich egg, the largest single cell known. Microbial cells show a narrower but also extensive size range. Some microbial cells are much larger than human cells. The single-celled protozoan Paramecium is 4,800 times the weight of the human red blood cell.

Although each kind of cell has a definite structure and size, cells should not be viewed as unchanging bodies: A cell is a dynamic unit constantly undergoing change and replacing its parts. Even if it is not growing, a cell is continually taking materials from its environment and working them into its own fabric. At the same time, it perpetually discards into its environment cellular materials and waste products. A cell is thus an open system, forever changing yet generally remaining the same.

# one

# Introduction

### 1.2 Microbial diversity

Although microbial cells have much in common, there are in reality two basic plans of cellular architecture, which differ from each other in many

Genus	Species	Common name
Neurospora	crassa	Red bread mold
Neurospora	sitophila	Red bread mold
Neurospora	tetrasperma	Red bread mold

fundamental ways. These two kinds of microbial cells are called procaryotes and eucaryotes. Bacteria and blue-green algae are procaryotes, whereas all other algae, fungi, and protozoa are eucaryotes. The most important difference between procaryotes and eucaryotes is in the structure of the nucleus. The eucaryote has a true nucleus (eu- means "true"; karyo- is the combining form for "nucleus"), a membrane-bound structure within which are the chromosomes that contain the hereditary material. The procarvote, on the other hand, does not have a true nucleus or chromosomes, and its hereditary material is contained in a single naked DNA molecule. There are also many other structural differences between procaryotes and eucaryotes that will be covered in more detail in Chapters 2 and 3. At present it is enough to know that these differences exist and that they are so fundamental as to make us believe they reflect an evolutionary divergence in the early history of life. Since the cells of higher animals and plants are all eucaryotic, it is likely that eucaryotic microorganisms were the forerunners of higher organisms, whereas procaryotes represent a branch that never evolved past the microbial stage.

Because of the diversity of microorganisms, it is useful to give different organisms names, and to do this we must have ways of telling one organism from another. After close study of the structure, composition, and behavior of a microorganism, we can usually recognize a group of characteristics by which it can be distinguished from most other forms. This set of characteristics then becomes the defining attributes of that organism, and a name can be given to it. Microbiologists use the binomial system of nomenclature first developed for plants and animals. The genus is like a surname (for example, Murphy) and includes a number of related organisms, whereas each different type of organism within the genus has a species name, which is like a given name (for example, John). Genus and species names are always used together to describe a specific type of organism, whether it be a single cell or a group of such cells. Thus three specific types of organism go under the common name of "red bread mold" (see the marginal table). Usually the names used come from Latin and Greek and indicate some characteristic of the organism. For instance, Saccharomyces cerevisiae is the species of beer yeast. Yeasts convert sugar into alcohol, and saccharo- means "sugar." A yeast is a fungus, and the combining form -myces derives from the Greek word for fungus. The word cerevisiae derives from the Latin word for "beer." Unfortunately, it is rarely possible to break down the name of a microorganism as easily as in this example, so that even one who knows Latin and Greek would have little success in translating many species names into English. Although we shall try to keep the number of species names to a minimum in this book, the student should be prepared to familiarize himself with at least the most important names (and their spellings!).

In addition to genus and species, higher orders of classification are used. Thus related genera are grouped by their similarities into a family, families into orders, orders into classes, and classes into phyla:

Kingdom Plant
Phylum Eumycophyta
Class Ascomycetaceae
Order Sphaeriales
Family Sordariaceae
Genus Neurospora
Species crassa

Many biologists divide the living world into two groups, plants and animals. Are microorganisms plants or animals? There seems to be no doubt that some microorganisms, such as the chlorophyll-containing algae, are plants, whereas many protozoa seem quite animallike. Yet we run into difficulties in some cases. For instance, the organism Euglena gracilis is a chlorophyll-bearing organism and thus is clearly a plant, yet after certain drug treatments it loses its chloroplasts and never regains them; forever thereafter its offspring live as animals. Although fungi lack chlorophyll, in many ways they are more closely related to the algae than they are to the protozoa. The procaryotic organisms, as a group, are so different from either animals or plants that it would seem foolish to try to place them in one group or the other. One solution proposed by some microbiologists is to collect all microorganisms together in a separate group, the Protista, of equal status with plants and animals. Yet to do this ignores the fact that many algae clearly are more related to plants than they are to animals, and many protozoans have more in common with animals than with plants. Perhaps it would be best if a final judgment were not made at this time; after the reader has become more acquainted with microorganisms, he may make his own decision.

Viruses are not cells. They lack many of the attributes of cells, of which the most important is that they are not dynamic open systems. A single virus particle is a static structure, quite stable and unable to change or replace its parts. Only when it is associated with a cell does a virus acquire some attributes of a living system. Whether or not a virus is to be considered alive will depend on how life itself is defined. We will reserve further discussion of this interesting question until Chapter 10.

#### 1.3 The discovery of microorganisms

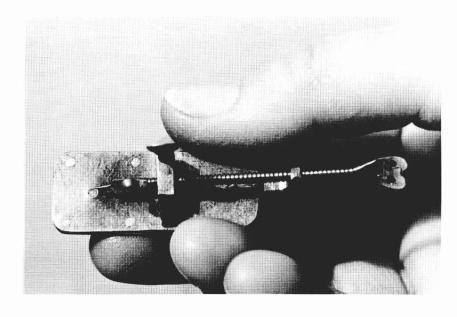
Although the existence of creatures too small to be seen with the eye had long been suspected, their discovery was linked to the invention of the



Figure 1.1 Early drawings by Robert Hooke (1664) of a blue mold growing on the surface of leather: the round structures contain spores of the mold; the lower drawings are of mold growing on the surface of an aging and deteriorating rose leaf. One of the first microscopic descriptions of microorganisms. (From R. Hooke: Micrographia or Some Physiological Descriptions of Minute Bodies Made by Magnifying Glasses with Observations and Inquiries thereupon. London: Royal Society, 1665.)

microscope. Robert Hooke described the fruiting structures of molds in 1664 (Figure 1.1), but the first person to see microorganisms in any detail was the Dutch amateur microscope builder Antonie van Leeuwenhoek, who used simple microscopes of his own construction (Figure 1.2). Leeuwenhoek's microscopes were extremely crude by today's standards, but by careful manipulation and focus he was able to see organisms as small as bacteria. He reported his observations in a series of lively letters to the Royal Society of London, which published them in English translation. Drawings of some of Leeuwenhoek's "wee animalcules" are shown in Figure 1.3. His observations were confirmed by other workers, but progress in understanding the nature of these tiny organisms came slowly. Only in the nineteenth century did improved microscopes become

Figure 1.2 A replica of the kind of microscope used by Leeuwenhoek. The base was a piece of leather, with the lens inserted into the small hole at the left side. The object to be viewed was placed on the small pointed wire attached to the screw, and the object was then moved back and forth by turning the screw. (Replica courtesy of Archives of the American Society for Microbiology.)



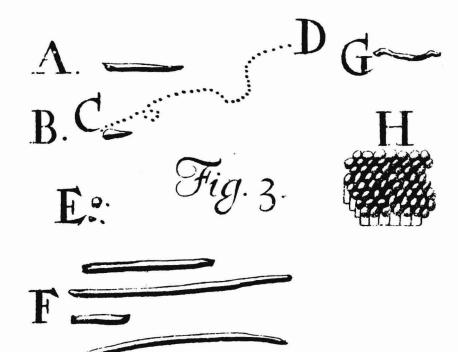


Figure 1.3 Leeuwenhoek's drawings of bacteria, published in 1684. Even from these crude drawings we can recognize several kinds of common bacteria. Bacteria lettered A, C, F, and G are rod-shaped; E, spherical or coccus-shaped bacterium; H, coccus-shaped bacteria in packets. [From "An abstract of a Letter from Mr. Anthony Leevvenhoeck at Delft, dated Sep. 17, 1683," Phil. Trans. Roy. Soc. London 14:568 (1684).]

available, and as a result of the industrial revolution they became more widely distributed. At all stages of its history, the science of microbiology has taken the greatest steps forward when better microscopes have been developed, for these enable scientists to penetrate ever deeper into the mysteries of the cell. Indeed, most of our knowledge of the detailed structure of microbial cells has come only with improvements in electron microscopy in the past ten years! Figure 1.4, which shows the yeast cell as seen with different microscopes, well illustrates this point.

Microbiology as a science did not develop until the latter part of the nineteenth century. This long delay occurred because certain basic techniques for the study of microorganisms needed to be devised. In the nineteenth century investigation of two perplexing questions laid the foundation of microbiological science: (1) Does spontaneous generation occur? (2) What is the nature of contagious disease? Study of these two questions went hand in hand, and sometimes the same people worked on both. By the end of the century both questions were answered, and the science of microbiology was firmly established as a distinct and growing field.

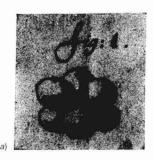
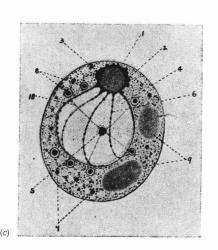
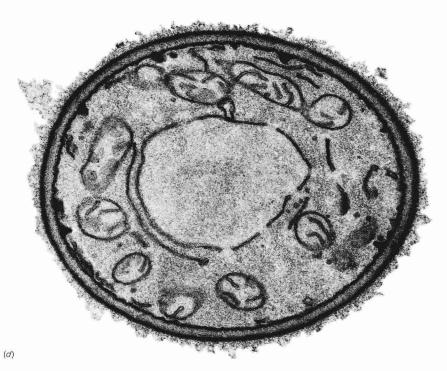


Figure 1.4 The yeast cell as it seemed to different observers. The great increase in our understanding of cell structure came with improvement in our microscopes. (a) Leeuwenhoek's model of yeast, dating from 1680. The six globules represent six separate cells in a cluster. Note the complete absence of any cellular detail. [From Committee of Dutch Scientists (ed.): "A letter of June 14, 1680," in The Collected Letters of Antoni van Leeuwenhoek. Amsterdam: Swets & Zeitlinger, Ltd., 1948.] (b) Pasteur's drawings of yeast, made in 1860, showing the budding process by which yeasts grow. The contrast of the outer cell wall and inner cytoplasm is distinct. The large objects in the cytoplasm are vacuoles. [From L. Pasteur: Ann. Chim. Phys. 58:323 (1860).] (c) drawing of the idea of a yeast cell in 1910. The greater detail inside the cell derives partly from improved microscopy and partly from the use of dyes that increase contrast and stain particular structures. However, some of the labeled structures are probably artifacts. [From H. Wager and A. Peniston: Ann. Bot. 24:45 (1910).] (d) Photograph of a yeast cell as seen with the electron microscope. Only a thin section of the cell can be seen with this microscope. The cell is first treated with chemicals that preserve the structure and stain particular components. [From S. F. Conti and T. D. Brock: J. Bacteriol. 90:524 (1965).]







Introduction

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