Thomas D. Brock / David W. Smith / Michael T. Madigan

FOURTH EDITION

BIOLOGY OF MICROORGANISMS

Biology of Microorganisms

Fourth Edition

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Preface

We are pleased to present this fourth edition of *Biology of Microorganisms* to students and instructors of microbiology. Microbiology continues to undergo rapid changes through the impact of new developments in cell, molecular, and environmental microbiology. The revolution in genetics, as witnessed by the development of molecular cloning and genetic engineering techniques, has had profound impact on the teaching and practice of microbiology. Microbes continue to make excellent research tools for the study of many fundamental biological problems. Yet microbes are more than research tools; they are of considerable importance and interest in themselves. Basic research in such areas as ecology and evolution is advancing rapidly because of our increased understanding of fundamental microbial processes. At the same time, practical developments in industrial biotechnology, food processing, and agriculture arise from the application of microbiological principles.

The acceptance of earlier editions of this book has been gratifying. For the fourth edition, co-authors have been added for the first time. Microbiology has been advancing so rapidly that it has become virtually impossible for a single person to write a textbook that is complete, accurate, and up-to-date, and do it within a reasonable length of time. The three authors have worked closely together in the preparation of this edition, each reviewing and correcting the other's material in detail. All of us have had extensive experience teaching university-level courses in which earlier editions have been used, and were intimately familiar with the book.

As before, the book has undergone extensive changes. Also as before, the changes have been evolutionary rather than revolutionary. Naturally, the material on genetics has been extensively reworked. A whole new chapter on genetic engineering has been written, and the rest of the genetics chapters have been extensively revised. Another area that has undergone extensive revision is the chapter dealing with immunology, reflecting the current exciting research in this area. The biochemistry chapters have been modified so as to be more accessible to the beginning student. The bacterial diversity chapter has been carefully revised in line with the many new discoveries that have been made in recent years. Virtually every chapter has seen some changes, and we have taken special care to take all readers' suggestions into consideration.

As in earlier editions, particular care has been taken to keep the length of the book within bounds. We know all too well how easy it would be to simply add new material, but we believe that the ultimate user, the student, should be provided with a textbook, not a tome, and that it is the authors' responsibility to sift through the field and present those ideas and concepts that are most relevant and useful for the contemporary student.

The popular "Bit of History" topics that appeared in the third edition have been retained in the present edition, and several new entries have been added. We are especially pleased that users enjoyed these historical vignettes, which were as much fun to write as they apparently are to read.

The taxonomy of bacteria is undergoing a major revision. The new edition of *Bergey's Manual,* which will be called *Bergey's Manual of Systematic* (rather than *Determinative*) *Bacteriology,* is being published in four volumes, each of which will contain an extensive description of a group of related procaryotic genera. Because this revision is not complete, we present both the current classification of the eighth edition and the general contents of each volume of the new edition in Appendix 4.

We are most grateful to the many reviewers, mostly anonymous, who provided us with frank and constructive criticism. The following reviewers provided detailed comments: Carol Gross, John Martinko, Charles Bensen, Thomas Corner, Walter Konetzka, Jane Phillips, and Robert T. Vinopal. We trust that we have handled all criticisms and corrections properly. All errors of omission or commission are, of course, our own responsibility.

T.D.B.
D.W.S.
M.T.M.

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1 Introduction

Microbiology is the study of microorganisms, a large and diverse group of free-living forms that exist as single cells or cell clusters. Microbial cells are thus distinct from the cells of animals and plants, which are unable to live alone in nature but can exist only as part of multicellular organisms. A single microbial cell is generally able to carry out its life processes of growth, energy generation, and reproduction independently of other cells, either of the same kind or of different kinds. Although there are exceptions, which we shall consider later, this definition provides a basis for our introduction to microorganisms.

1.1 Microorganisms as Cells

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 materials and subcellular structures. All cells 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 has arisen. Cells vary enormously in size, from bacteria too small to be seen 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 being much larger than human cells. The single-celled protozoan *Paramecium* is about 5000 times the weight of the human red blood cell.

Although each kind of cell has a definite structure and size, a cell is a dynamic unit, constantly undergoing change and replacing its parts. Even when 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.

1.2 Microbial Diversity

There are five major groups which are studied by microbiologists: fungi, protozoa, algae, bacteria, and viruses. These five may be divided further: algae, fungi, and protozoa have a form of cellular organization known as **eucaryotic,** the bacteria* are organized in a different way known as **procaryotic,** and viruses are not cells at all. 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-enclosed structure within which are the chromosomes that contain hereditary material. The procaryote, on the other hand, does not have a true nucleus, and its hereditary material is contained in a single naked deoxyribonucleic acid (DNA) molecule. The many other structural differences between procaryotes and eucaryotes will be covered in some 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. Because 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.

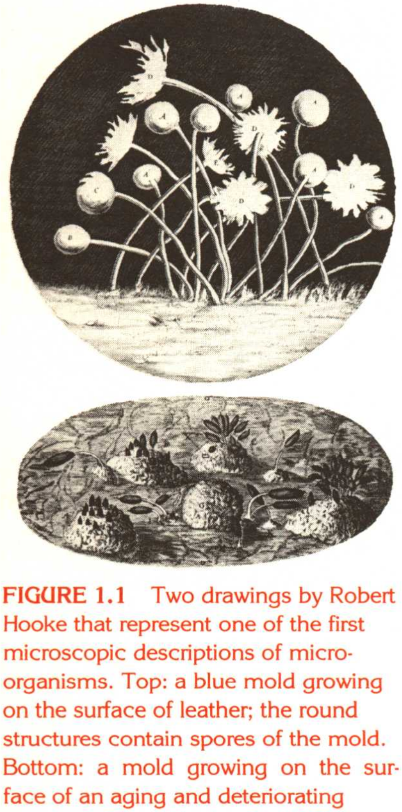

FIGURE 1.1 Two drawings by Robert Hooke that represent one of the first microscopic descriptions of microorganisms. Top: a blue mold growing on the surface of leather; the round structures contain spores of the mold. Bottom: a mold growing on the surface of an aging and deteriorating rose leaf. (From Hooke, R. 1665. Micrographia, or some physiological descriptions of minute bodies made by magnifying glasses, with observations and inquiries thereupon. Royal Society, London.)

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 attributes of a living system. Whether or not a virus is to be considered alive will depend on how life itself is defined. We shall reserve further discussion of this interesting question until Chapter 10.

Microorganisms are so diverse that it is useful to give them names, and to do this we must have ways of telling them apart. After close study of the structure, composition, and behavior of a microorganism, we can usually recognize a group of characteristics unique to a certain organism. Once an organism has been defined by such a set of characteristics, it can be given a name. Microbiologists use the binomial system of nomenclature first developed for plants and animals. The **genus** name is applied to a number of related organisms; each different type of organism within the genus has a **species** name. 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. Usually the names come from Latin and Greek and indicate some characteristic of the organism. For instance, *Saccharomyces*

*This group includes the organisms which were historically called blue-green algae but are now termed **cyanobacteria,** a name which emphasizes their procaryotic form.

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." *Cerevisiae* is Latin for "brewer." However, many organisms are named in whole or in part after the scientists who studied them, so that it is rarely possible to break down the name of a microorganism as easily as we can this one, and 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 to a minimum in this book, students should be prepared to familiarize themselves with at least the most important names (and their spellings!).

Traditionally, the living world has been divided into two kingdoms; plants and animals. Are microorganisms plants or animals? Some microorganisms, such as some of the chlorophyll-containing algae, appear to be plants, whereas many protozoa seem quite animallike. Yet we run into many difficulties. For instance, the organism *Euglena gracilis* is chlorophyll-bearing and may be considered a plant; yet after certain drug treatments it loses its chloroplasts and never regains them; 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 and some scientists classify the procaryotes in a separate kingdom called **Monera.** Some microbiologists propose the formation of a separate kingdom, called **Protista,** to include all eucaryotic microorganisms. Yet such a grouping 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. It is likely that more than three kingdoms exist; some proposals have as many as five. As yet our knowledge of the range of microbial diversity is insufficient to develop a definitive classification.

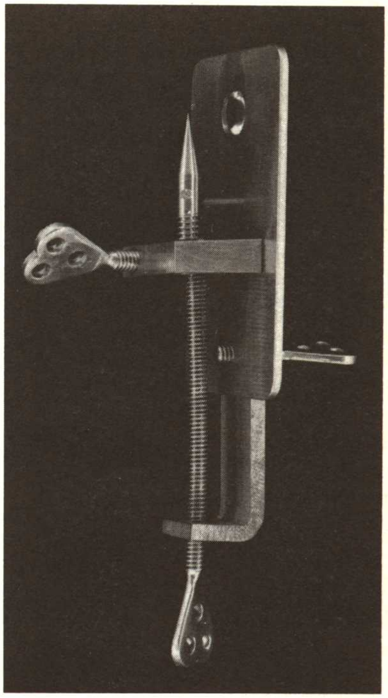

FIGURE 1.2 A replica of the kind of microscope used by Leeuwenhoek. The base was a piece of metal, with the lens inserted into the small hole at the top. The object to be viewed was placed on the small pointed tip at the end of the screw, and was moved back and forth by turning the screws.

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 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 Anton 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 focusing he was able to see organisms as small as bacteria. He reported his observations in a series of 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 available and widely distributed. During its history, the science of