Biology of Microorganisms

Fifth Edition

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Cover photo shows an infection thread formed by ***Rhizobium trifolii*** on white clover, ***Trifolium repens***, examined by fluorescence microscopy. A number of bacteria can be seen attached to the root hair. The infection thread consists of a cellulose deposit down which the bacterial cells move to the root.

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Preface

We are pleased to present this fifth edition of *Biology of Microorganisms* to students and instructors of microbiology. Although each edition of this textbook has represented a marked advance over earlier editions, this present edition represents the most complete revision that has ever been accomplished. A quick glance will tell the reader why: The book has been produced for the first time completely in full color. The extensive use of color made it necessary to redesign the whole book. Most of the line drawings are completely new, and even those that were retained from earlier editions have, to a great extent, been fully redrawn. The number of full-color photographs has also been greatly increased. Microbiology is a colorful subject. For the first time in a college textbook, this colorful subject is revealed to the student.

Although the new full-color design is the most obvious change from earlier editions, the content of the book has also been greatly altered. The science of microbiology continues to undergo rapid changes through the impact of new developments in cell and molecular biology, and through major advances in medical and environmental microbiology. The revolution in microbial genetics, first reflected in the previous edition, is now fully presented in the fifth edition. Gene cloning and genetic engineering are having profound impact on the teaching and practice of microbiology. Microbes continue to make important research tools for the study of many fundamental biological processes. Yet microbes are more than research tools—they are of considerable importance and interest in themselves. Therefore, the second major focus of this book is on what microbes are doing in the world at large. 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 biotechnology, food processing, and agriculture arise from applications of microbiological principles. And whole areas, such as virology and immunology, are moving so rapidly that they must be treated in completely new ways. However, the basic approach which has made this book so popular in earlier editions has not been changed.

So many new things have been added to this edition that it is more efficient to list them in outline form. Details can be found in the table of contents and in the chapters themselves.

1. Chapter 1, greatly enlarged in this new edition, is now subtitled "An Overview of Microbiology and Cell Biology." It not only includes a brief, well-illustrated introduction to the nature of microbial life but also an extensive section on microbiological methods, material requested by many instructors.

2. Chapter 2, "Cell Chemistry," is a completely new chapter, added to provide a compact source of information on the important chemicals of living organisms. Chemistry is, to a great extent, the language of biology, and we have felt that by providing this overview early in the book, students will have a convenient reference source for review of the basic chemistry of microbial life.
3. Chapter 3, "Cell Biology," incorporates much of the material found in Chapters 2 and 3 of the previous edition, but greatly enhanced and presented in an integrated fashion. Most of the figures in this chapter are completely new, and have been greatly enhanced by the full-color treatment.
4. Chapter 4, "Nutrition, Metabolism, and Biosynthesis," contains a more compact treatment of microbial metabolism than that found in Chapters 4 and 5 of the previous edition. The present Chapter 4 presents only the key concepts of energetics and heterotrophic metabolism, and the specialized material has been moved to the completely new Chapter 16.
5. Chapter 5, "Macromolecules and Molecular Genetics," is of course almost completely new, reflecting the phenomenal advances that have been made in this field. We have also placed this chapter earlier in the book, reflecting our conviction that genetics is so important and pervasive in modern microbiology that it must be covered as early as possible. Chapter 5 also provides an introduction to the following molecularly oriented chapters.
6. The field of virology has changed so remarkably that the virology chapter in this book has been completely rewritten, and the material on animal viruses greatly expanded. The chapter has been organized in such a way that instructors can choose those kinds of materials that will be most useful for their specific courses.
7. In Chapter 7, "Microbial Genetics," the material on transposons and plasmids has been considerably enhanced, and a whole new section on genetics of yeast has been added, reflecting the current exciting research on these important eucaryotic microorganisms.
8. The chapter "Gene Manipulation and Genetic Engineering," so popular in the previous edition, has been updated and enlarged, and new material on the uses of genetic engineering added.
9. The growth process can be viewed either as a process of macromolecular biosynthesis or as a process with enormous practical implications. Chapter 9, "Growth and Its Control," has been moved so that it comes *after* rather than before the molecular material, thus making it possible to discuss microbial growth in macromolecular terms. But at the same time, the practical material on the *control* of microbial growth has been considerably increased. Because microbial growth in foods is one of the most important practical considerations, a whole new section on *food microbiology* has been added.
10. Continuing with the innovations in this new edition, a whole new chapter, "Microbial Biotechnology," has been added. A number of important industrial microbial processes predate the era of genetic engineering so that this chapter attempts to provide a complete overview of economically important microbial processes. For added student interest, beer- and wine-making are given extensive treatment for the first time in this book (including a brief section on home brewing).
11. Beginning with Chapter 11, a series of chapters, either new or greatly rewritten, provides extensive coverage of the field of medical microbiology and immunology. Chapter 11 begins this part of the book with a presentation of the principles of ***host-parasite relationships***.
12. Probably no field in biology has advanced so rapidly, and has become so important both theoretically and practically, as immunology. "Immunology and Immunity," a chapter so popular in the last edition, has been considerably enhanced and has benefited from extensive new illustrations.
13. Chapter 13, "Clinical and Diagnostic Microbiology", is completely new in this edition. We have been impressed not only by the great sophistication of modern diagnostic methods in microbiology but by the way in which genetics is revolutionizing this field. Building on the genetics background of Chapters 5–9, the present chapter has an extensive treatment of the new ***monoclonal antibody*** and ***nucleic acid probe*** technology for diagnostic microbiology.
14. Continuing the expanded coverage of medical microbiology, Chapter 14, "Epidemiology and Public Health Microbiology," is a brief but almost completely new treatment of this subject.
15. Responding to the requests of many instructors, we have added a separate, rather lengthy, chapter "Major Microbial Diseases." The diseases in this chapter are arranged, as much as is possible, by ***organ systems*** affected or by ***mechanisms of transmission***. As such, this chapter will complement Chapter 19, which provides the conventional taxonomic treatment of pathogens along with the groups of other bacteria.
16. Probably no new chapter has been written so enthusiastically by your two authors as has Chapter

16, "Metabolic Diversity among the Microorganisms." In the previous editions, some of this material was included in the chapter on metabolism or in separate chapters on biosynthesis and autotrophy, but it came too early in the book to warrant the detailed treatment that it deserves. In the present chapter, an integrated picture of metabolic diversity is presented for the first time. Note that this chapter also provides an overview of material needed for the definitive discussion of ecology, evolution, and systematics in the next several chapters.

17. Chapter 17, "Microbial Ecology," while retaining much of the material from the previous edition, has been considerably expanded by the addition of material on ***enrichment culture***, ***measurement of microbial activity in nature***, and ***plant-microbe interactions*** (with emphasis on ***Rhizobium*** and ***Agrobacterium***).

18. Chapter 18, "Molecular Systematics and Microbial Evolution," is completely new and reflects the current excitement in the use of molecular techniques to classify microorganisms. In this chapter, the new classification of microbes which emphasizes the vast differences between ***eubacteria*** and ***archaebacteria*** has been given in considerable detail.

19. Finally, Chapter 19, "The Bacteria," provides that detailed and authoritative reference to procaryotic diversity that instructors have come to expect from this book.

The instructor or student reading the above list of innovations can well imagine why we are so excited and enthusiastic about this new edition of "Biology of Microorganisms." New chapters, extensive revisions, new design, and especially, full-color art! However, this is not the end of the innovations. A whole array of new supplements have been developed by the publisher to make the book more accessible to the student and more useful to the instructor. These supplements include a Study Guide, Test Item File, Computerized Test Item File, Instructor's Manual, and Color Transparencies. In addition, Study Questions have been included at the end of each chapter in the book itself.

This edition has been greatly benefited from the computer-assisted publication skills of Science Tech Publishers, the company responsible for complete editorial and production matters. The use of the computer has made it possible to revise and insert important new information almost up until the end of the book production cycle. The following individuals working at or under the auspices of Science Tech deserve special recognition: Irene Slater for careful keyboarding of a lengthy and extremely complex manuscript; Susan Fariss, Elizabeth McBride, and Kathy Rosner for editorial assistance; Ed Phillips, Lisa Buckley, Cathy Schmaeng, Julie Whitty, Randy Kampen, Lucy Taylor, and Tony Dunn for art; Ruth Siegel for photo research, Barbara Littlewood for the index, and Kathie Brock for consultation. Thomas D. Brock was responsible for the design and for supervision of all editorial, art, typesetting, and production.

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In addition, the Credits section at the end of the book lists the many more who have provided photographs.

The authors would also like to pay special thanks to David Smith of the University of Delaware, a coauthor on the fourth edition, who was unable because of circumstances to participate in the present revision. His advice and consultation during the early planning stages for the present edition were extremely helpful. MTM wishes to thank his wife, Nancy, for her patience and understanding during this very time-consuming revision. TDB wishes to thank MTM for his efforts above and beyond the call of duty, Robert Sickles of Prentice-Hall Editorial for his support in bringing out this innovative edition, and Eleanor Hiatt of Prentice-Hall Production for her careful supervision and unfailing good humor.

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1 Introduction: An Overview of Microbiology and Cell Biology

Microbiology is the study of microorganisms, a large and diverse group of organisms 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 parts of multicellular organisms (Figure 1.1). 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.

What, then, is microbiology all about? We can list several aspects of microbiology here: 1) It is about living cells and how they work. 2) It is about microorganisms, an important class of cells capable of free-living (independent) existence. 3) It is about microbial diversity and evolution, about how different kinds of microbes arise, and why. 4) It is about what microbes do, in the world at large, in human society, in our own bodies, in the bodies of animals and plants. 5) It is about the central role which microbiology plays as a basic biological science and how an understanding of microbiology helps in the understanding of the biology of higher organisms, even including humans.

Why study microbiology? Microbiology, one of the most important of the biological sciences, is studied for two major reasons:

1. As a *basic biological science*, microbiology provides some of the most accessible research tools for probing the nature of life processes. Our most sophisticated understanding of the chemical and physical principles behind living processes has arisen from studies using microorganisms.
2. As an *applied biological science*, microbiology deals with many important practical problems in medicine, agriculture, and industry. Some of the most important diseases of humans, animals, and plants are caused by microorganisms. Microorganisms play major roles in soil fertility and animal production. Many large-scale industrial processes are microbially based, and are now classified under the heading of *biotechnology*.

In this book, both the basic and applied aspects of microbiology are covered in an integrated fashion. We discuss the experimental basis of microbiology, the general principles of cell structure and function, the classification and diversity of microorganisms, biochemical processes in cells, and the genetic basis of microbial growth and evolution. From an applied viewpoint, we discuss disease processes in humans that are caused by microorganisms, the roles of microorganisms in food and agriculture, and industrial (biotechnological) processes employing microorganisms.

The material in this textbook serves as a foundation for advanced work in microbiology. It also serves as a basis for further studies in cell biology.

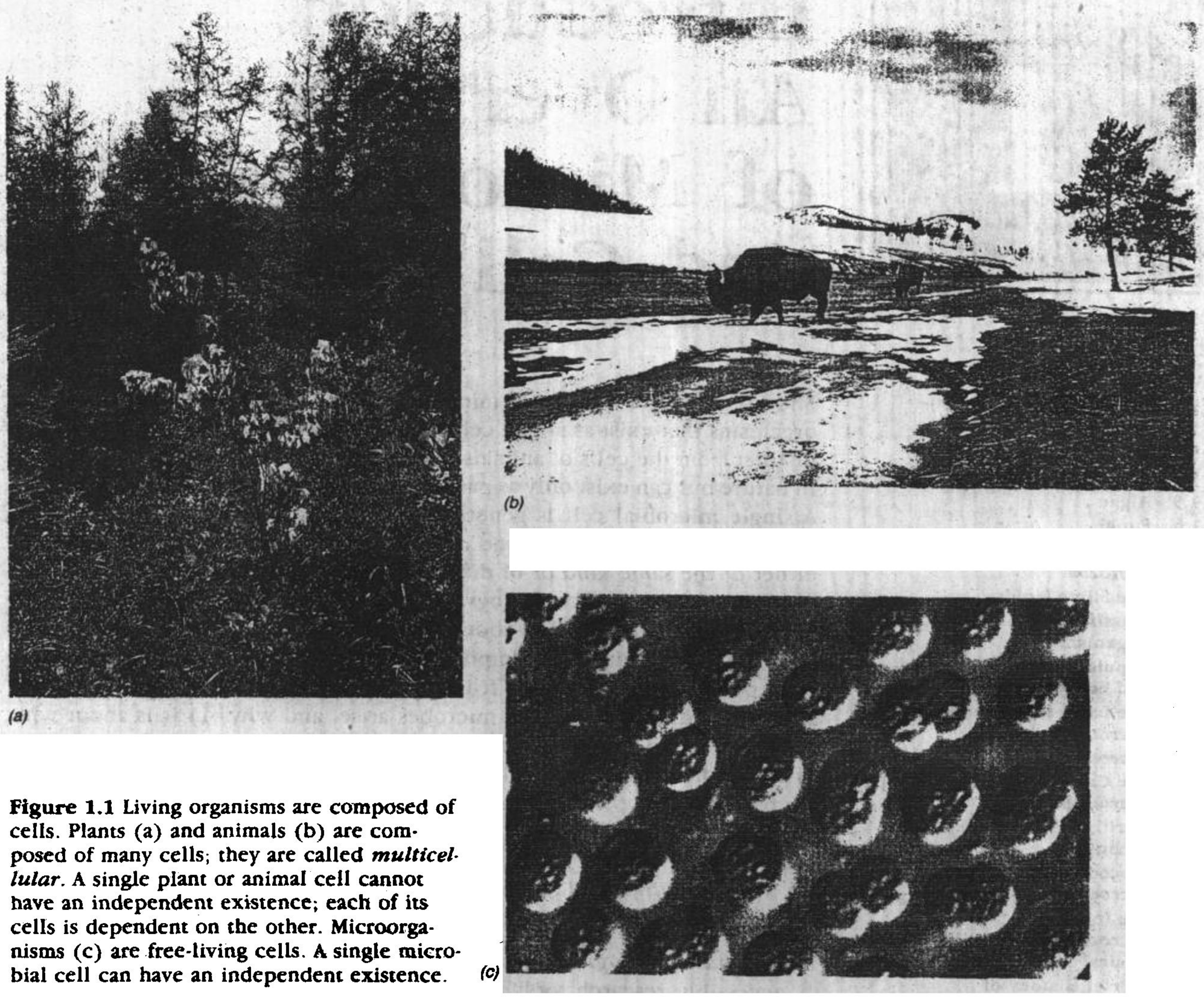

Figure 1.1 Living organisms are composed of cells. Plants (a) and animals (b) are composed of many cells; they are called ***multicellular***. A single plant or animal cell cannot have an independent existence; each of its cells is dependent on the other. Microorganisms (c) are free-living cells. A single microbial cell can have an independent existence.

biochemistry, molecular biology, and genetics. Although a student may begin to study microbiology primarily because of its applied problems, the basic concepts learned will serve as a foundation for advanced study in many areas of contemporary biology. A firm grasp of microbiological principles will also serve as a basis for understanding processes in higher organisms, including humans.

1.1 Microorganisms as Cells

The **cell** is the fundamental unit of all living matter. A single cell is an entity, isolated from other cells by a cell membrane (and perhaps a cell wall) and containing within it a variety of materials and subcellular structures (Figure 1.2). The **cell membrane** is the ***barrier*** which separates the inside of the cell from the outside. Inside the cell membrane are the various structures and chemicals which make it possible for the cell to function. Key structures are the **nucleus** or nuclear region, where the ***information*** needed to make more cells is stored, and the **cytoplasm**, where the ***machinery*** for cell growth and function is present.

All cells contain certain types of chemical components: 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 a single common ancestor, the ***universal ancestor***. Through billions of years of evolution, the tremendous diversity of cell types that exist today has arisen.

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

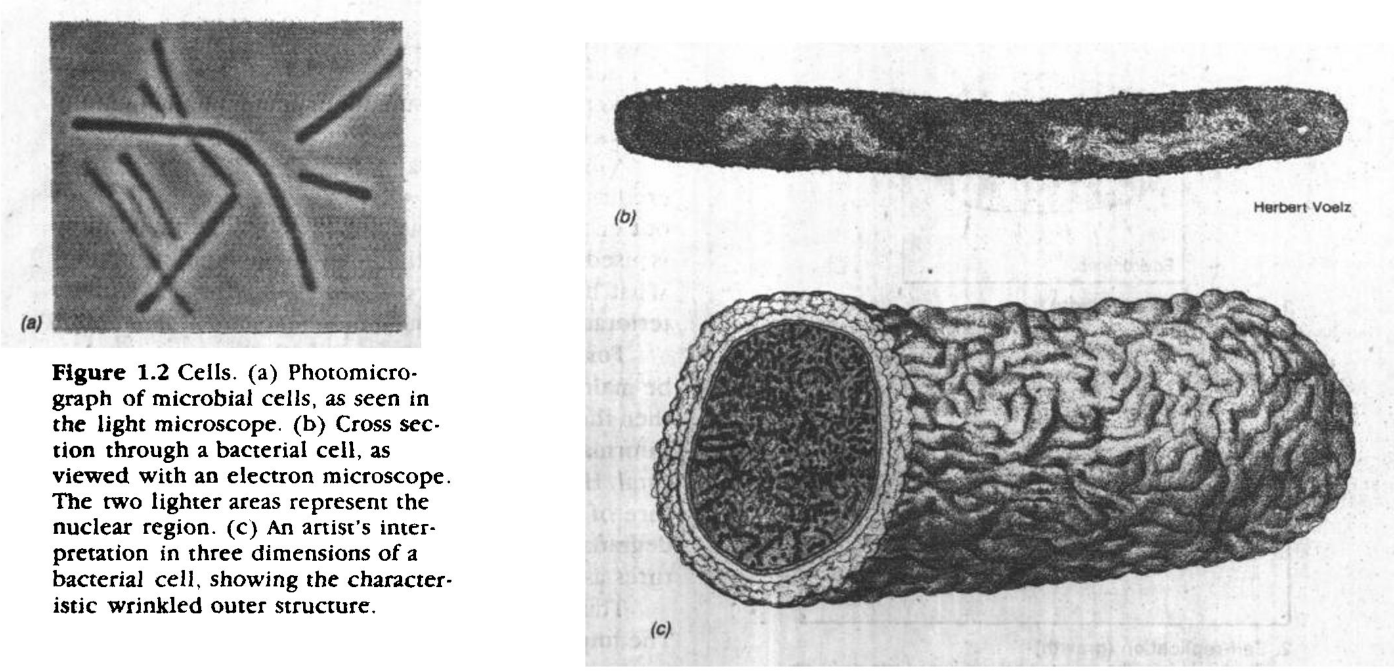

Figure 1.2 Cells. (a) Photomicrograph of microbial cells, as seen in the light microscope. (b) Cross section through a bacterial cell, as viewed with an electron microscope. The two lighter areas represent the nuclear region. (c) An artist's interpretation in three dimensions of a bacterial cell, showing the characteristic wrinkled outer structure.

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.

The hallmarks of a cell A living cell is a complex chemical system. What are the characteristics that set living cells apart from nonliving chemical systems? We list four major characteristics here, discuss them briefly in this chapter, and in more detail in later chapters.

1. **Self-feeding or nutrition**. Cells take up chemicals from the environment, transform these chemicals from one form to another, release energy, and eliminate waste products (Figure 1.3).
2. **Self-replication or growth**. Cells are capable of directing their own synthesis. A cell grows and divides, forming two cells, each nearly identical to the original cell.
3. **Differentiation**. Most kinds of cells also can undergo changes in form or function. When a cell differentiates, certain substances or structures which were not formed previously are now formed, or substances or structures which had been formed previously are no longer formed. Cell differentiation is often a part of the cellular life cycle, in which cells form spores or other structures involved in sexual reproduction, dispersal, or survival of unfavorable conditions.
4. **Chemical signalling**. Another attribute of cells is that they often *interact* or *communicate* with other cells, generally by means of **chemical signals**. Multicellular organisms, such as plants and animals, are composed of many different cell types that have arisen as a result of differentiation from single cells. In multicellular organisms, complex interactions between these different cell types lead to the behavior and function of these cells. One of the striking things about the cells of multicellular organisms is that they are incapable of independent existence in nature, but only exist as part of a whole plant or animal. This interdependence of the cells of higher organisms is one of the hallmarks of multicellular life. Even in the microbial world chemical communication occurs, although it is less highly developed.

The improbable cell A common view of physics is that the universe is moving toward a condition where everything is in great disorder, with molecules and atoms and elementary particles arranged in the most random manner. If the universe is random, life then seems like a miracle, since the living cell is anything but random, being a highly ordered, exceedingly improbable (nonrandom) structure. More careful analysis of life, however, convinces one that there is no divergence between biology and physics. How can this be? First, we note that the idea of randomness implies that the physical system is in *equilibrium* with its surroundings. A living cell, on the other hand, is definitely *not* in equilibrium with its surroundings. We say that the living cell is a *nonequilibrium* system. How is it possible for a cell to

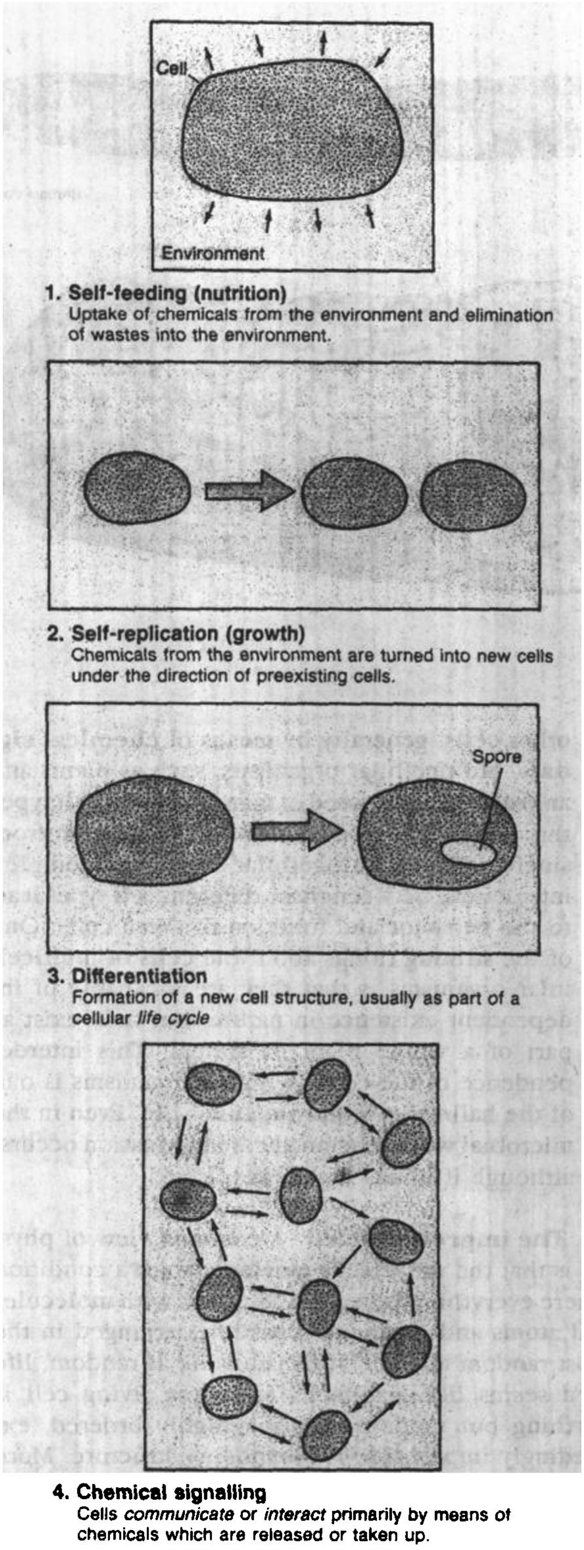

Figure 1.3 The hallmarks of cellular life.

maintain this nonequilibrium condition? A living cell is actually an *open system*, a system in which energy is taken in from the surroundings and used to maintain cell structure.

Viewed in this way, a living cell can be considered as a *chemical system that works*. A cell carries out energy transformations, and some of this energy is used to maintain the structure of the cell itself. What happens if the cell runs out of energy? It deteriorates and eventually dies.

For a cell to function as a cell, its structure must be maintained. If the structure of a cell is destroyed, then the cell usually dies. Biological information, the information needed to produce a new cell, is structural. However, because of the highly improbable nature of a cell, the cell is constantly tending toward degradation, and energy is needed to restore structures as they are being degraded.

Thus, the basis of cell function is cell structure. The importance of structure as a foundation of life is further emphasized when we note that cells are *self-replicating systems*. Cell reproduces cell. Therefore, making a living cell is a matter of making the right structure. This principle, which is the basis of biology, was enunciated many years ago by the famous German cellular pathologist Rudolph Virchow: "Omnis cellula e cellula." *"Every cell from a cell."*

If every cell comes from a preexisting cell, where did the first cell come from? This question is an example of the classic "chicken and egg" conundrum. Which came first, the chicken or the egg? All those trained in genetics know that it must be the egg. In the same way, the first cell must have come from a noncell, something before the cell, a procellular structure. We will discuss the origin of life and the evolution of cells in some detail in Chapter 18.

The nonrandom nature of a living cell is shown most dramatically by an analysis of its chemical composition and a comparison of that chemical composition with the chemical composition of the earth. The average chemical composition of a living cell is quite different from the average chemical composition of the earth. The cell therefore is not a random assortment of chemical elements found on earth (Figure 1.4). This further emphasizes the special or nonrandom nature of a living cell.

However, because a cell is a nonrandom structure it does not necessarily follow that life is a miracle. Life is indeed an improbable phenomenon, and probably arose only once as a result of a series of highly improbable events that occurred on the primitive earth. However, once a cell arose, subsequent events appear highly probable, a result of the inherent chemical reactions which cells are able to carry out.

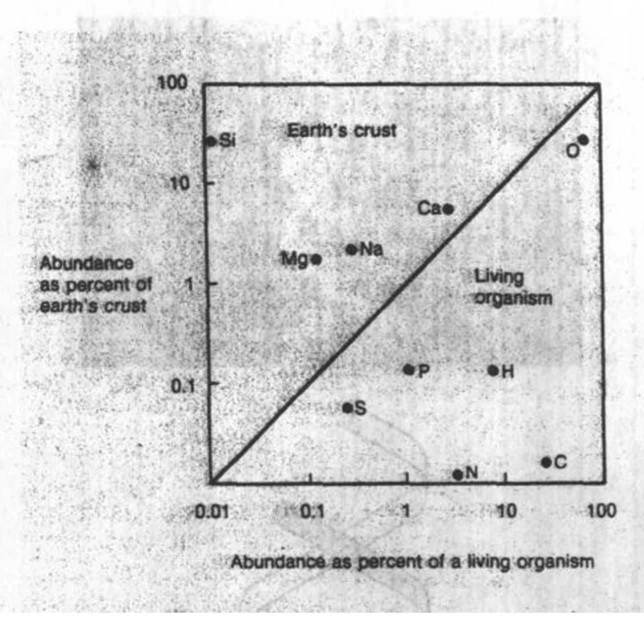

Figure 1.4 Chemical differences between a living organism and the earth. Note that the key elements C, H, O, N, P, and S are much more abundant in living organisms than in nonliving matter. Thus, living organisms *concentrate* these elements from the environment.

Astronomers tell us that there are probably vast numbers of planets in the universe with earth-like conditions on which life might arise or might have arisen. If life is an almost inevitable event when the proper physical and chemical conditions are available, then we can anticipate that there are other planets in the universe with living organisms similar to those found on earth. The precise assemblage of organisms would be different, of course, because so much of evolution depends upon accidents of history, and the time stage and evolution on these other planets would likely be earlier or later than those on earth. But if we were able to sample some of these other planets, it is likely we would not find any surprises.

Two views of a cell Cells can be studied as *machines* which carry out chemical transformations. In this view, the cell is a chemical machine which converts energy from one form to another, breaking molecules down into smaller units, building up larger molecules from smaller ones and carrying out many other kinds of chemical transformations. The term **metabolism** is used to refer to the collective series of chemical processes which occur in living organisms. When we speak of metabolic reactions, we mean *chemical* reactions occurring in living organisms.

Cells can also be studied as *coding devices*, analogous to computers, possessors of information which is either passed on to offspring or is translated. Depending upon our interest, and upon the problem at hand, we may study cells either as chemical machines or as coding devices. In the following we discuss these two attributes briefly.

If a cell is a chemical machine, what are the components which make it function? The components of the cell's chemical machine are **enzymes**, protein molecules capable of catalyzing specific chemical reactions. Whether or not a cell can carry out a particular chemical reaction will depend in the first instance on the presence in the cell of an enzyme that catalyzes the reaction. Specificity of enzymes is frequently very high, so that even very closely related chemical reactions are catalyzed by separate enzymes. The specificity of an enzyme is determined primarily by its structure. Enzymes are proteins. As proteins, enzymes consist of long chains of amino acids (20 different amino acids) which are connected in specific and highly precise ways. It is the amino acid *sequence* of an enzyme that determines its structure as well as its catalytic specificity. Proteins frequently have 100 or more amino acid residues, composed of the 20 types of amino acids. The long chain of amino acids becomes folded into a specific configuration, leading to the formation of various regions or domains which play specific roles in the function of the protein (Figure 1.5). The machine function of a cell (metabolism) is ultimately determined by the amounts and types of the various enzymes of which it is composed.

We now turn to the idea of cells as coding devices. It is when we consider how the amino acid sequence of a protein is determined that we consider cells as coding devices. How is the cell able to arrange amino acids into precise sequences, each leading to the production of a separate kind of protein? To understand this, we must consider the cell as a device for storing information and converting it into the ap-

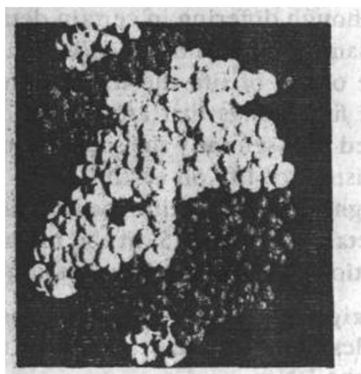

Figure 1.5 The structure of a protein as shown in a computer-generated model. The different domains of the protein are shown in different colors.