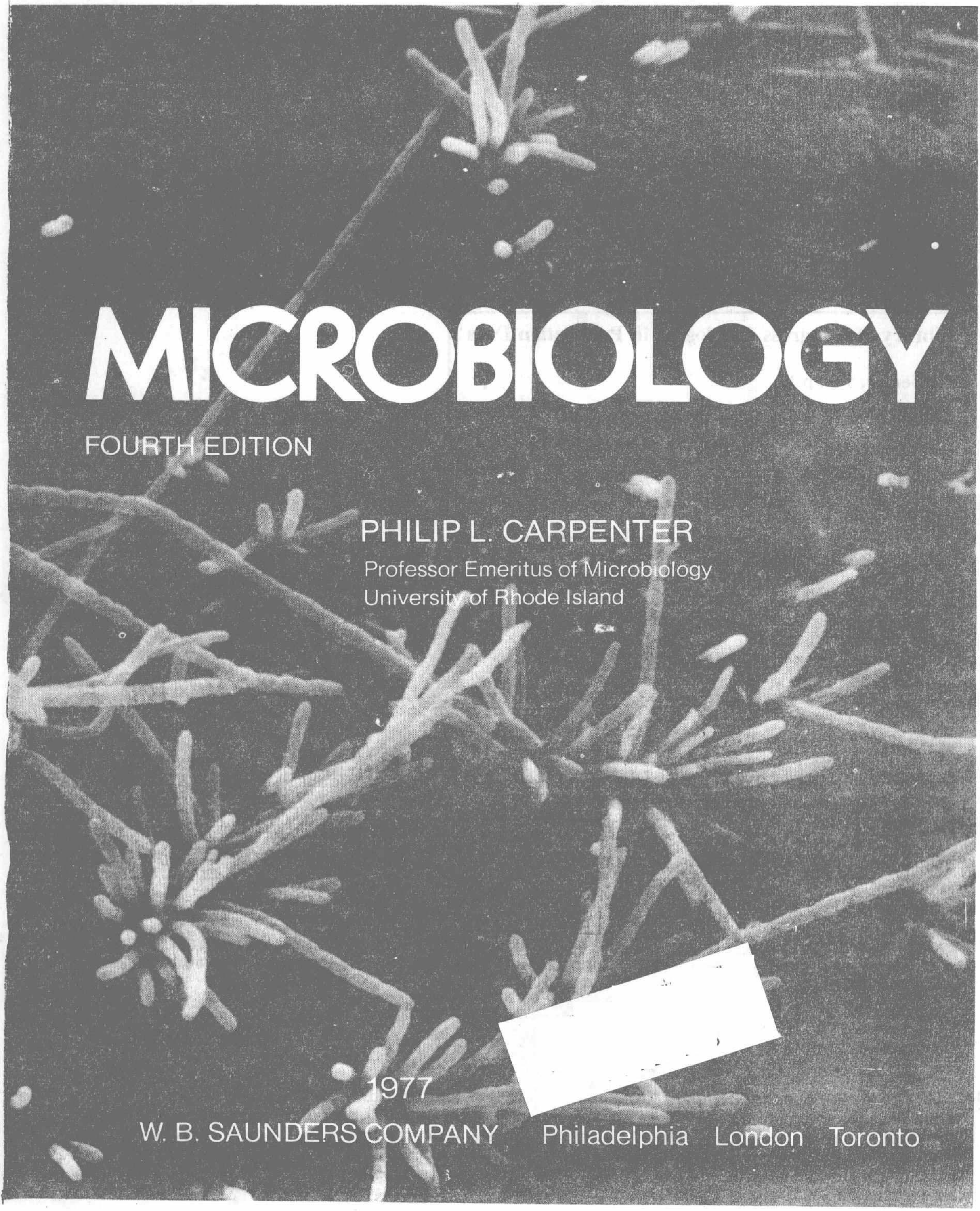
MICROBIOLOGY

FOURTH EDITION

PHILIP L. CARPENTER



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Cover and title page illustration is a scanning electron micrograph of microcolonies of *Leucothrix mucor* on the carapace of a lobster larva. Courtesy John Sieburth, from *Microbial Seascapes*, Baltimore, University Park Press, 1975.

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PREFACE

The ecologic problems arising from pollution of the environment by wastes of all kinds—detergents, insecticides, hydrocarbons, hot water, and radioactive materials—make it imperative that intelligent citizens have a background in the basic sciences. Inasmuch as biologic forms, from viruses through the most highly evolved plants and animals, are constructed of chemical elements that obey the laws of chemistry and physics, it is necessary to be grounded in these physical sciences before anything more than a superficial, descriptive acquaintance with living organisms can be achieved. The student will therefore profit most from his course in microbiology if he has some knowledge of biology and chemistry, preferably including organic chemistry; otherwise the instructor should review basic principles so that the student will not be "lost" in the areas of microbial physiology and genetics.

Like its predecessors, the fourth edition of *Microbiology* is intended for the student who is being introduced to the field. This may be his only course in microbiology, or he may later take advanced, specialized courses. His primary interest may be in any of the various branches of microbiology; or he may be interested in general biology, molecular biology, medicine, nursing, pharmacy, medical technology, agriculture, home economics, secondary education, or liberal arts.

The organization of the fourth edition is essentially the same as that of the third edition. The chapter on systematic bacteriology has been completely rewritten in accordance with the eighth edition of *Bergey's Manual of Determinative Bacteriology,* and its suggested nomenclature has been followed throughout the text. The chapter on bacterial metabolism has been restructured, and the chapters on bacterial genetics and immunity have been up-dated.

I am indebted to Dr. Norris P. Wood and Dr. Paul S. Cohen of the University of Rhode Island for assistance in revision of the chapters on bacterial metabolism and bacterial genetics. The many suggestions that have been offered, either directly or through the staff of the W. B. Saunders Company, have been very useful and are greatly appreciated. My special thanks go to Mr. Richard Lampert, formerly Biology Editor of the W. B. Saunders Company, for his suggestions and help. Numerous individuals and companies have kindly provided illustrative material, as noted in the figure legends. Special thanks are due to Dr. John McN. Sieburth, Professor of Oceanography and Microbiology at the University of Rhode Island, for the use of several scanning electron micrographs, notably the photograph of *Leucothrix* on the cover and title page.

It is a particular pleasure to acknowledge the important role of my wife, Helen E. Carpenter, who endures calmly the long and antisocial silences of continuous preoccupation and then patiently finds her way through interlineated rough draft and garbled dictation and transcribes it accurately into legible manuscript.

PHILIP L. CARPENTER

WAKEFIELD, RHODE ISLAND

A LETTER TO STUDENTS

Before you read the first chapter, I would like to welcome you to a new field of study and to wish you pleasure and profit from it. I would also like to give you a bird's-eye view of what is ahead and offer a few suggestions that may help you get the most from your study.

Microbiology is not just a book or a course in college. It is the study of small organisms, which have many of the same attributes as higher forms of life. By observing test tube experiments with microorganisms we can learn many things about how other organisms function.

Glance through the Table of Contents. You will notice that this book is divided into five sections. The first section introduces you to the study of microorganisms—what they are, how they were studied in the early days of microbiology, and how they are studied now.

The second section deals with the biology of the more primitive microorganisms, particularly the bacteria—what they look like and how they are grouped, how they secure energy and building materials, how they make cellular components, how they grow and die, and how their growth and death can be controlled.

In the third section you will become acquainted (or reacquainted) with other microorganisms, the higher protists: protozoa, algae, molds, and yeasts. Most of these are larger than bacteria, and although some consist of multicellular aggregates visible with the naked eye, single cells usually suffice to reproduce the entire organism. Many are handled and cultivated in the same way as bacteria.

The fourth section introduces you to the study of diseases caused by microorganisms. First, it is necessary to know what kinds of microorganisms are normally associated with the body and how other organisms produce disease. Then, since the body is not entirely passive in this situation, you should know how it resists infection. Finally, you will learn about some pathogenic agents that are usually transmitted by the four principal routes: personal contact, water and food, direct inoculation, and air.

By this time you may imagine harmful microbes at every turn, so we close with a section that includes some of the useful aspects of microbiology: the roles of microorganisms in soil and water, in dairy products and other foods, and in industry.

When you study, get an overall picture of the subject first by skimming the subheadings within each chapter. Write a *brief* topic outline of a chapter or subject. Don't memorize a lot of details first; they never make sense by themselves, but if you know the general outline, the details fit into place without much conscious effort. Learning details without knowing how they are connected with one another is like looking at a large portrait only a few inches away; all you see is an eye or a foot, and your impression of the picture is distorted and incomplete until you back away and look at it as a whole.

Many of your fellow students approach microbiology with dread, expecting to be required to memorize long lists of names and other terms that seem to mean nothing. Naturally, there are unfamiliar terms in any new subject, but, as you read, hear, *and use* them, they soon become familiar. Moreover, the words do mean something, as you can learn with only a little trouble. Usually the first Index reference to a new word contains a definition, description, or derivation. If it does not, look the word up in a standard dictionary or in a medical dictionary. Note that the Glossary, immediately following the last chapter, defines many new words and gives Latin and Greek derivations. The end papers inside the front and back covers also contain much useful information: methods of forming Latin plurals with examples from microbiology, metric measures used in science and soon to be in general daily use, and prefixes and suffixes employed in microbiology (with their aid you can often translate an unfamiliar word).

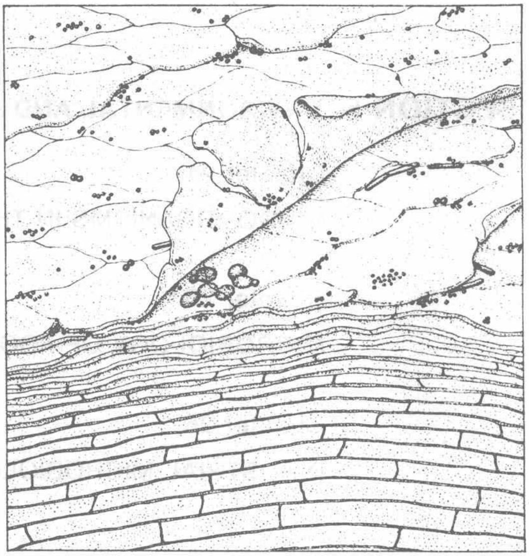
At the end of each chapter is a list of suggestions for supplementary readings, in which further information can be found. Many of these are books, and since no page citations are indicated, you will have to use the index to find the topic you wish. If you are interested in still further information, the results of current research are found in many periodicals. The *Journal of General Microbiology,* for example, is a British publication with excellent papers on the biologic activities of the various microorganisms. Its closest American counterpart is the *Journal of Bacteriology,* published by the American Society for Microbiology. Other publications of the Society include the *Journal of Virology,* the *Journal of Clinical Microbiology,* and *Infection and Immunity,* whose titles are self-explanatory, and *Applied and Environmental Microbiology,* which contains papers on antibiotics, fermentations, enzymes, and the microbiology of manufactured products and of the environment. Papers surveying recent work on a topic are found in *Bacteriological Reviews*. The *Journal of Infectious Diseases* contains articles on the causes, pathogenesis, host response, and laboratory diagnosis of diseases caused by microorganisms.

PHILIP L. CARPENTER

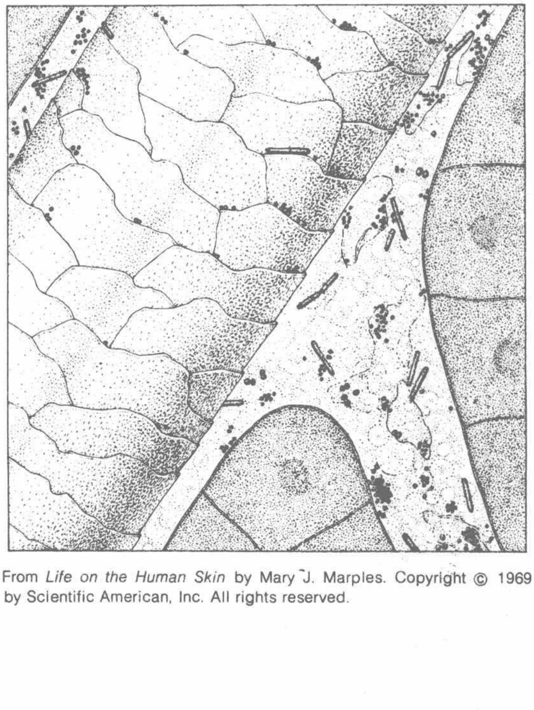
WAKEFIELD, RHODE ISLAND

CONTENTS

SECTION ONE



MICROORGANISMS AND THEIR STUDY



THE WORLD OF MICROORGANISMS 1

Bacteria, yeasts, molds, algae, protozoa, and viruses constitute a seemingly heterogeneous group of biologic entities, but they resemble one another in their small size and relative simplicity of structure and organization, and hence are called microorganisms or, as some authorities prefer, *protists* (Greek: *protista,* the very first). Study of them constitutes the science of microbiology.

Many microorganisms are unicellular, some consist of loose aggregates of independent cells, showing little if any specialization of function, and some form long filaments containing several potentially independent vital units or protoplasts within a single cell wall (e.g., *coenocytic* molds and algae). Structural simplicity does not, however, necessarily imply physiologic simplicity. Microorganisms perform the same fundamental activities within their single cells as "higher" organisms do within their many-celled structures: utilization of food and energy, formation of new protoplasm, reproduction. It is important to remember that microorganisms are essentially the same biologically as other organisms.

Their small size makes it difficult to study the anatomy of individual cells, but the homogeneity of a population of microorganisms often permits an experimenter to investigate a particular phenomenon or chemical reaction (e.g., the metabolism of an amino acid) free from some of the complications introduced by the multicellularity of larger organisms. It is for this reason that microorganisms are especially useful tools in the study of genetics, cell physiology, and other aspects of molecular biology. Moreover, the spectrum of forms comprising the microbial world includes those on the border line between obviously living organisms and obviously nonliving matter. Study of these forms provides insight into the fundamental nature of life.

CHARACTERISTICS OF LIVING SYSTEMS

After 1664, when Hooke observed that plants are composed of many smaller individual structures, it became recognized that the cell is the basic unit of life, whether plant or animal. Exactly what this basic unit comprises is largely a matter of definition. At the level of the higher plant or animal there is no disagreement: the cell is a discrete unit with common structural and chemical properties. It is bounded by a wall or membrane, which encloses cytoplasm containing proteins, deoxyribonucleic acid, and ribonucleic acid as necessary constituents. It has certain chemical activities known collectively as metabolism: the synthetic processes by which all its constituents are made from available ingredients and the transformations that convert energy from external sources into energy-rich bonds. Reproduction of the cell takes place by division, following orderly increases in the amount of its chemical components.

At the level of the smallest microorganisms there has been some difference of opinion as to what constitutes a cell or even a living organism. Viruses consist of protein and deoxyribonucleic *or* ribonucleic acid, and in some cases (e.g., the myxoviruses) are bounded by a membrane, but they lack the ability to perform metabolic activities or to replicate outside the proper environment (i.e., a host cell). They are, in fact, replicated only from and in the form of their genetic material; protein may be synthesized simultaneously but separately, and the two components are assembled at a later stage.

Bacteria are approximately the same size as the substructures or *organelles* of the cells of higher plants or animals that carry out various metabolic and reproductive activities, and electron microscopy reveals hardly any organelle in the bacterial cell that is structurally identical with a similar functional unit in the cells of larger organisms. Some authors therefore consider that bacteria are closer to the viruses than they are to "cells." However, bacteria possess both kinds of nucleic acid (DNA and RNA); all their components increase and the cells divide by a process of fission; and they possess many enzymes, some of which are active in converting the energy of foodstuffs into the high-energy chemical bonds essential for biologic syntheses.

The definition of life is essentially a philosophic matter that cannot be settled by argument, although discussion serves the useful purpose of focusing attention on the complexity of the problem. Without entering the realm of controversy we can note that every biologic form contains protein and deoxyribonucleic acid or ribonucleic acid. Protein serves protective and catalytic functions, and in the latter role participates in energy transformation and transfer. Nucleic acids include the genetic material wherein is stored the information necessary to determine the chemical and physical behavior of the system. These ingredients and activities seem to constitute the irreducible minimum consistent with life.

MICROBIAL CELL TYPES: PROCARYOTIC AND EUCARYOTIC

Microbial cells are of two distinct types. The least developed type consists of the bacteria and blue-green algae and is designated *procaryotic* (Greek: *pro,* before, primordial, + *karyon,* nucleus). The more highly evolved cell type, *eucaryotic,* is found in all other biologic forms: higher algae, protozoa, fungi, as well as higher plants and animals.

Procaryotic and eucaryotic cells differ in many important respects. Procaryotic cell walls are rigid and serve to maintain the structural integrity of the cells. They consist of repeating units of mucopeptide in a three-dimensional array (Fig. 1–1). Within the cell wall is a plasma membrane surrounding the protoplasm, which contains the chromatin body or nucleus, ribosomes, chlorophyll-containing membranes or chromatophores (in photosynthetic species), and occasional granules, oil droplets, and vacuoles. One or more flagella are found on some procaryotic cells.

The procaryotic nucleus consists of a single, closed loop of naked DNA that is not bounded by a membrane. Nuclear division is accomplished by replication and splitting of the DNA, and several nuclear divisions may occur before the cell divides, with the result that multinucleate cells are found in rapidly growing cultures.

The cytoplasm of procaryotic cells is packed with ribosomes, which have a characteristic fine structure (Fig. 1–2). They are nearly spherical, hollow, and often arranged in rodlets; their function is to synthesize protein.

Photosynthesis in procaryotic cells takes place in cytoplasmic bodies that differ from the chloroplasts of eucaryotic cells. In blue-green algae, these consist of leaflike lamellar plates or *thylakoids,* distributed throughout the cytoplasm (Fig. 1–3). The chromatophores of photosynthetic bacteria vary from one species to another. They can be viewed as parts of the cytoplasmic membrane, modified in various specific ways. In some species they consist of invaginations of the cytoplasmic membrane, extending inward in the form of connected vesicles and bulged tubules, and comprise 40 to 50 per cent of the cytoplasm (Fig. 1–4). Some species have a system of parallel tubes and others

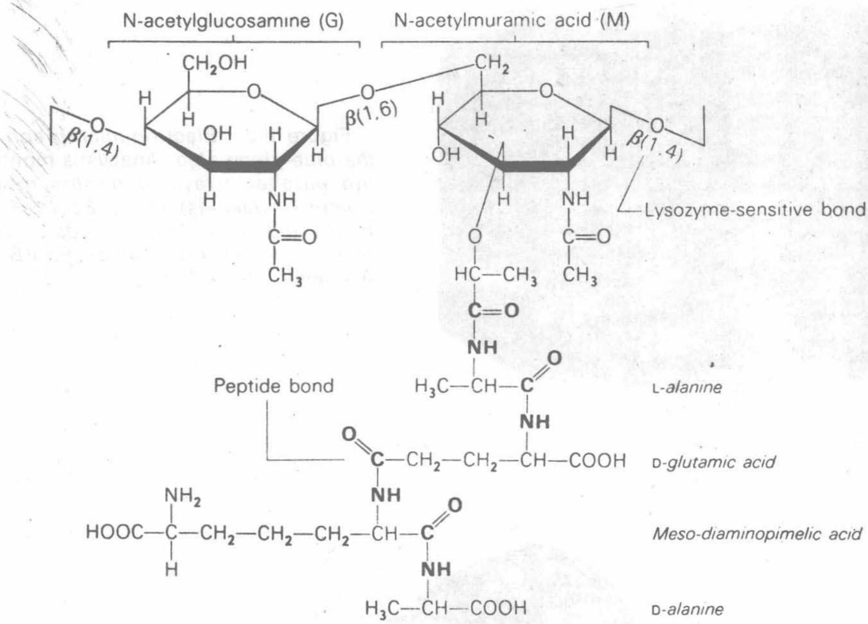


Figure 1–1. *The repeating units that comprise the cell wall mucopeptide of a procaryotic organism,* Escherichia coli. *N-acetylglucosamine* (G) *and N-acetylmuramic acid* (M) *alternate in chains, which are cross-linked by peptide bonds (shown in boldface). (From Brock: Biology of Microorganisms. Englewood Cliffs, N.J., Prentice-Hall, Inc., 1970.)*

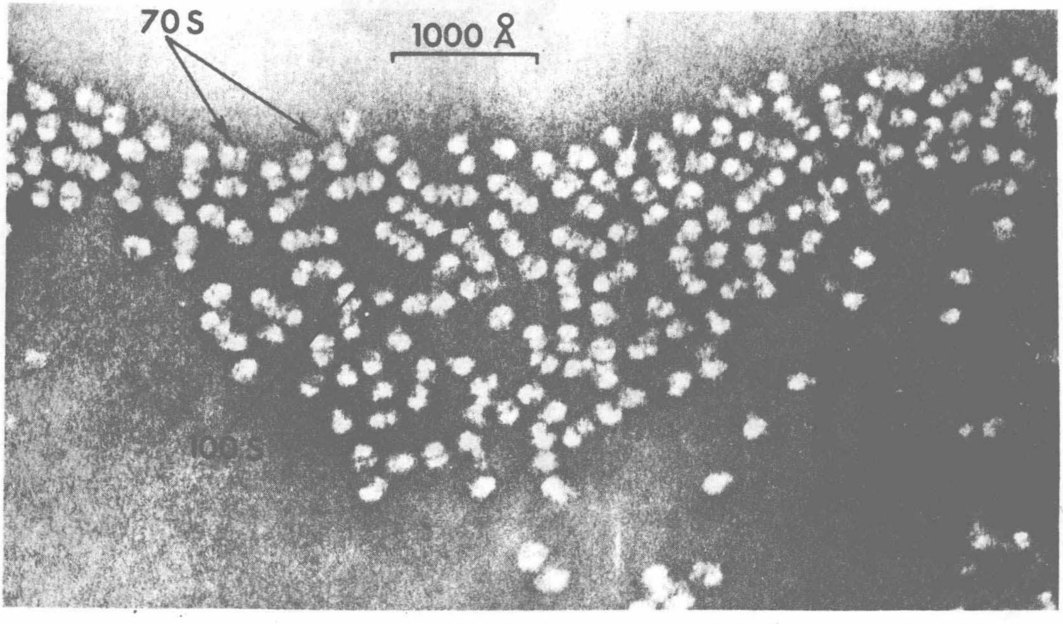


Figure 1–2. *Electron micrograph of microsomal particles (ribosomes) of* E. coli *negatively stained with phosphotungstic acid. This is a mixture of two kinds of particles: (70S) monomers, containing two unequal subunits, and (100S) dimers, composed of two monomers joined at their smaller subunits (200,000X). (From Huxley and Zubay, J. Molec. Biol., 2:14, 1960.)*

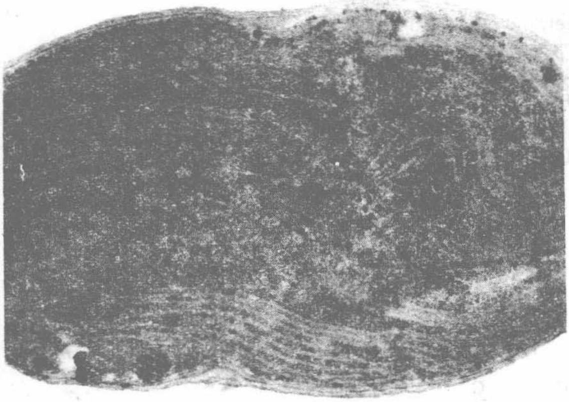


Figure 1–3. *Electron micrograph of a cell of the blue-green alga,* Anacystis montana, *showing parallel arrays of photosynthetic membranes (thylakoids). (From Echlin, P., in Gibbs, B. M., and D. A. Shapton (eds.): Identification Methods for Microbiologists, Part B. New York, Academic Press, 1968.)*

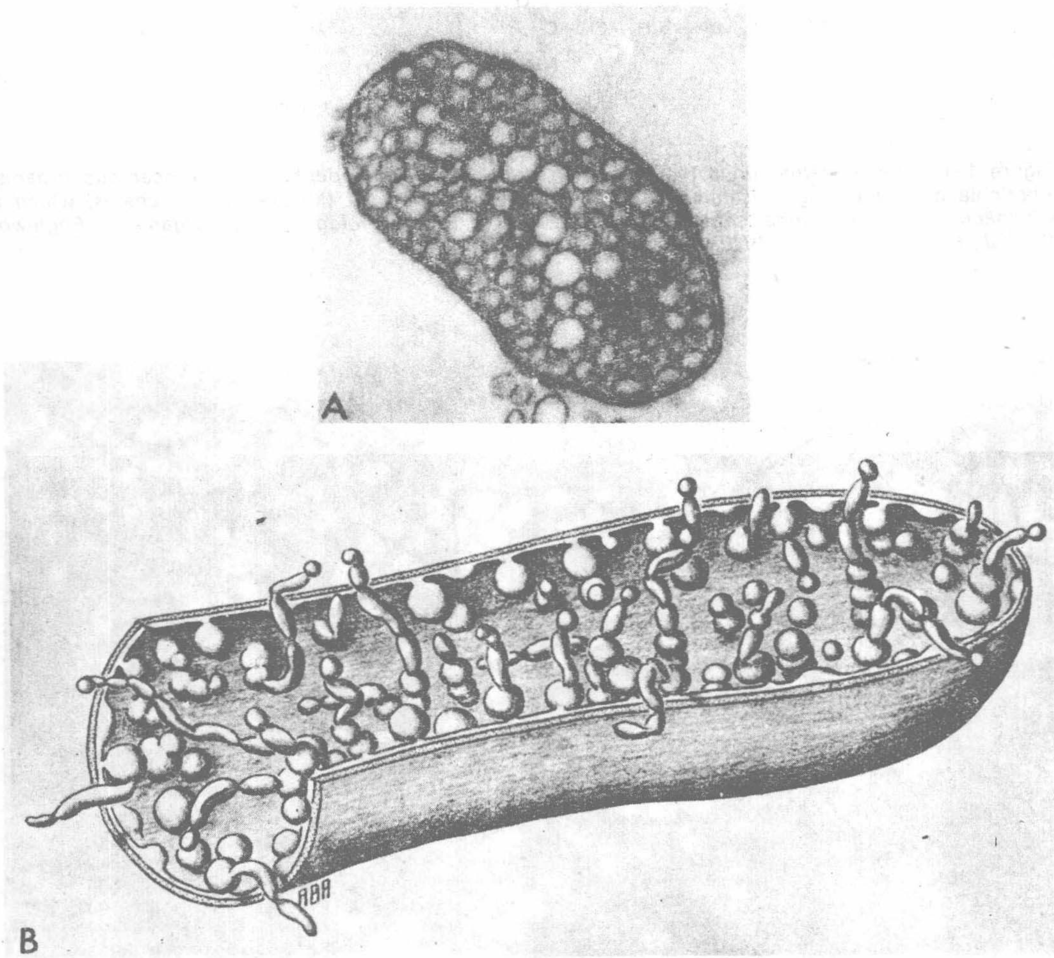


Figure 1–4. A, *Electron micrograph of section of* Rhodospirillum rubrum, *a photosynthetic bacterium, showing vesicular chromatophores (40,000X).* B, *Artist's reconstruction of the three-dimensional appearance of the chromatophore membrane system of* R. rubrum. *(From Holt, S. C., and A. G. Marr, J. Bacteriol., 89:1402–1412, 1965.)*

have an irregular network of branched and bulged tubes. In still others there is a lamellar membrane system, resembling that of the blue-green algae, near the periphery of the cytoplasm and sometimes associated with vesicles. The photosynthetic apparatus in procaryotes is comparatively simple. Since this apparatus is connected with the cytoplasmic membrane, the integrity of the membrane is essential for the photosynthetic process.

Respiratory activities in procaryotes are performed by enzymes associated with the plasma membrane and possibly with the mesosomes, which are bounded by a membrane that seems to be continuous with the plasma membrane.

A flagellum of a procaryotic microorganism consists of a fibril composed of three subfibrils, twisted about each other in a helix like a triple-threaded screw (see Figure 5–19).

Whereas the procaryotic cell is comparatively undifferentiated and possesses few membranous structures except the plasma membrane, photosynthetic thylakoids, and possibly the mesosomes, eucaryotic cells contain many subcellular structures or organelles and are strikingly membranous in nature. The eucaryotic nucleus is enclosed in a membrane and it consists of DNA molecules that comprise the chromosomes, of which there are always more than one per nucleus. The DNA in a eucaryotic nucleus is joined to basic proteins called histones, whereas DNA of procaryotes is not. This is a distinctive difference between the two types of cells. Sexual reproduction is characteristic of most eucaryotes, and in the process of meiosis reassortment of the entire chromosome takes place. Procaryotic cells display only fragmentary evidence of a sexual type of reproduction. Meiosis does not occur, and usually only portions of the genetic information are transferred.

The membranous nature of the eucaryotic cell is illustrated by the electron micrograph of a pancreatic cell shown in Figure 1–5. Most of the cytoplasm is filled with a network of membranes, the *endoplasmic reticulum*, which is the site of much enzymatic activity. The granular endoplasmic reticulum is active in protein synthesis.

Respiration in eucaryotic cells is performed in the mitochondria (Fig. 1–6). These are bounded by double membranes; the inner membrane is the origin of a series of thin internal membranes in which are situated the enzymes that participate in the orderly transport of electrons from oxidizable substances to oxygen. Between these membranes are other enzymes involved in the oxidation of carbon compounds to carbon dioxide.

The cells of green plants contain chloroplasts, which are more complicated in structure and function than the chromatophores of procaryotes. They are composed of parallel layers of leaflike membranes, or lamellae, that are not connected with the bounding membranes. They contain the chlorophyll and carotenoid photosynthetic pigments and the enzymes that participate in the fixation of carbon dioxide and formation of carbohydrate. The chromatophores of procaryotes, by contrast, lack the enzymes that fix carbon dioxide. The highly organized structure of a chloroplast is illustrated in Figure 1–7.

The walls of eucaryotic cells, when present, are usually composed of relatively simple organic or inorganic substances, such as the polysaccharide, cellulose, and monosaccharide polymers like mannans and xylans. Most animal cells do not possess a rigid wall.

Membranes of eucaryotic cells contain sterols, whereas those of procaryotes usually lack them. The differences in cell wall and membrane composition are the only consistent chemical differences between procaryotes and eucaryotes.

Flagellated eucaryotic cells possess flagella of microscopic size but of "advanced" design. They are composed of 20 fibrils arranged in a distinctive pattern: nine pairs of fibrils are distributed more or less evenly around two fibrils situated near the center (Fig. 1–8). Each fibril of a eucaryotic cell is approximately the same size as each flagellum of a procaryotic organism.

Differences between procaryotic and eucaryotic cells are summarized in Table 1–1.

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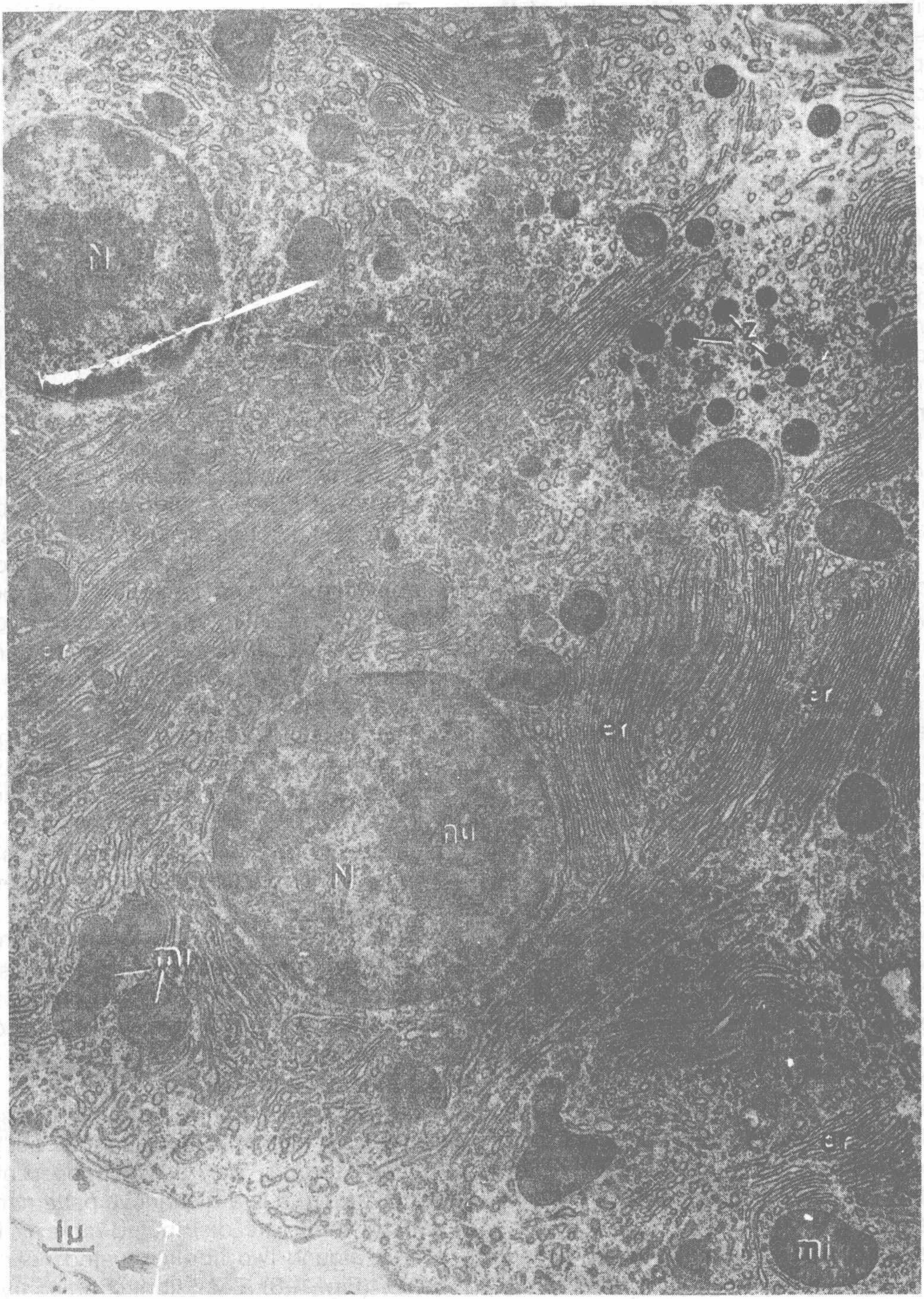

Figure 1–5. *Elect on micrograph of a cell of the eucaryotic type (pancreas). The membranous endoplasmic reticulum* (er) *is co ıspicuous, as is the nucleus* (N), *bounded by a double membrane and containing a nucleolus* (nu). *The mitochondria* (mi) *are also filled with thin membranes. Magnification: 7000X. (Courtesy of K. R. Porter, from DeRobertis, Saez, and DeRobertis: Cell Biology, 6th ed. Philadelphia, W. B. Saunders Co., 1975.)*