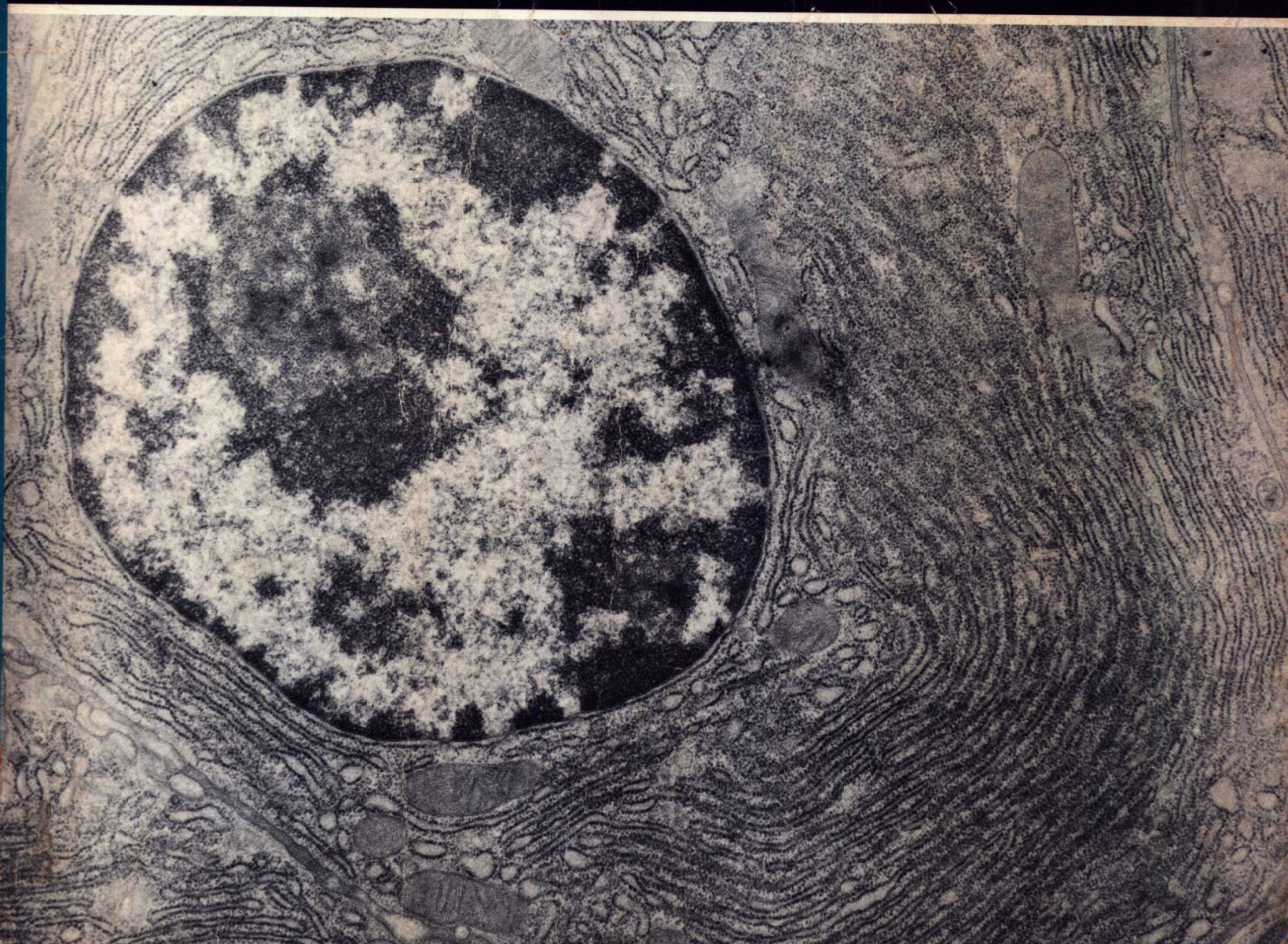
Wolfe

Cell Ultrastructure



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Preface

This book summarizes the important structures of viruses, prokaryotes, and eukaryotic cells. The emphasis is on ultrastructure; the basic information and concepts of cell biology are presented as much as possible in terms of pictures, and text is kept to a minimum. The book aims to provide a supplement for texts in general biology and more advanced courses such as cell biology, genetics, developmental biology, physiology, histology, plant anatomy, and biochemistry that do not include a sufficiently extensive description of cell ultrastructure, particularly in areas of more contemporary interest. With this purpose in mind, the micrographs and descriptions included cover all of the major cell structures in a wide range of prokaryotic and both plant and animal eukaryotic cells.

The first two chapters introduce the primary features of prokaryotic and eukaryotic cells. The following chapters illustrate the major cell parts and organelles, including membranes; the nucleus and its major structures and functions; organelles concerned with cellular energy procurement, the mitochondria, chloroplasts, and peroxisomes; structures associated with protein synthesis, secretion and absorption, including ribosomes, the endoplasmic reticulum, and lysosomes and their roles in endocytosis; microtubules, microfilaments, and their activities in cell motility; the cytoskeleton; cell junctions, extracellular structures of animals, and the cell walls of plants and prokaryotes; mitotic and meiotic cell division; and the structure and function of viruses. An appendix surveys the major techniques and instrumentation used in electron microscopy, including fixation, embedding and sectioning, shadowing and negative staining, freeze-fracture preparations, autoradiography, and a description of the transmission and scanning electron microscopes and their principles of operation. While text is kept to a minimum, care has been taken to include and emphasize the major structural and functional concepts of cell biology.

This book has benefited greatly from the many helpful suggestions made by friends and colleagues who reviewed the text, to whom I give my thanks. I am also indebted to cell biologists throughout the world who generously supplied micrographs, diagrams, and tables for inclusion in the book. I owe particular thanks also to Le and Moss and Paula Shuhert of Wadsworth, who very ably transformed the manuscript into a finished book.

Contents

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1

An Introduction to Cells:
Prokaryotes and Eukaryotes

Cells are the fundamental structural and functional units of all living organisms. Most microorganisms, such as the bacteria and protozoa, exist as single cells that individually carry out all of the activities of life. Although plants and animals and most of the fungi are multicellular, their complex activities still depend on the coordinated activities of individual cells. Any cell of these unicellular or multicellular organisms, if maintained under the proper conditions, may retain all of the qualities of life, grow, and reproduce. If a cell is broken into its subparts, however, the organization of structure and function that we recognize as life is lost. Thus, life as we know it does not exist in units more simple than cells.

Our present-day understanding of cells as the units of life extends from scientific work begun more than three hundred years ago. Cells were first described not long after the first primitive light microscopes became available in the seventeenth century. At this time, in 1665, the Englishman Robert Hooke observed plant cells under the light microscope and published the first descriptions of cells to appear in the scientific literature. Further observations of cells were made by Hooke and by others in the seventeenth and eighteenth centuries. However, nearly two hundred years were to pass before observations of cell structure and function progressed enough for scientists to appreciate the full significance of cells to living organisms. At this time, in the 1830s, 1840s, and 1850s, the German investigators Karl Schleiden, Theodor Schwann, and Rudolf Virchow realized the fundamental importance of cellular organization and stated what is now known as the *cell theory* in much the same form as it is understood today:

1. All living organisms are structured from cells.
2. Cells are the functional units of life.
3. Cells arise only from preexisting cells.

Since this first complete statement of the cell theory, research into cell structure and function has continued at an ever-increasing pace in an effort to determine how cells work and how they are organized internally. Although the results of this effort are still incomplete and research continues today at a more intensive pace than ever before, we have a

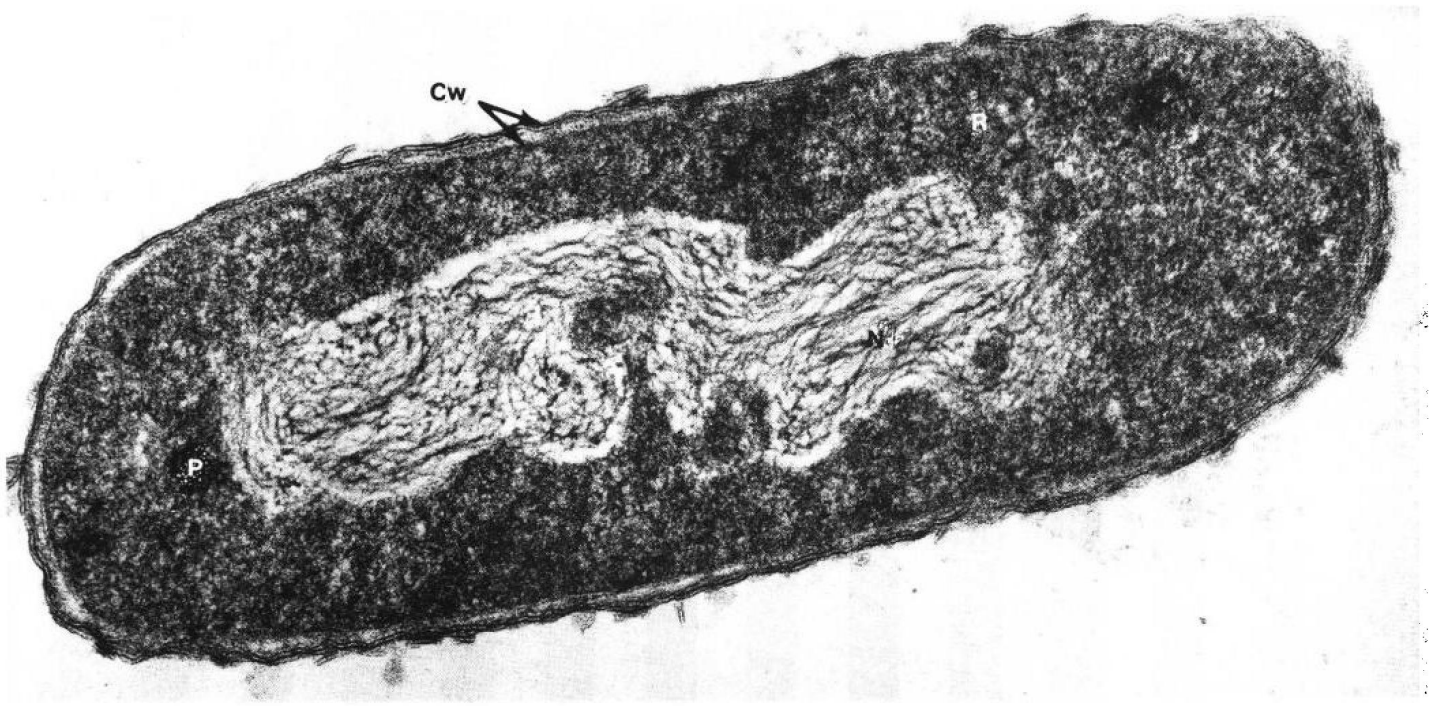

Figure 1-1. *A prokaryotic cell, the bacterium* Escherichia coli. *Cw, cell wall; N, nucleoid; P, polyphosphate body; R, ribosomes. The plasma membrane lies just under the cell wall. × 62,000. Courtesy of G. Cohen-Bazire.*

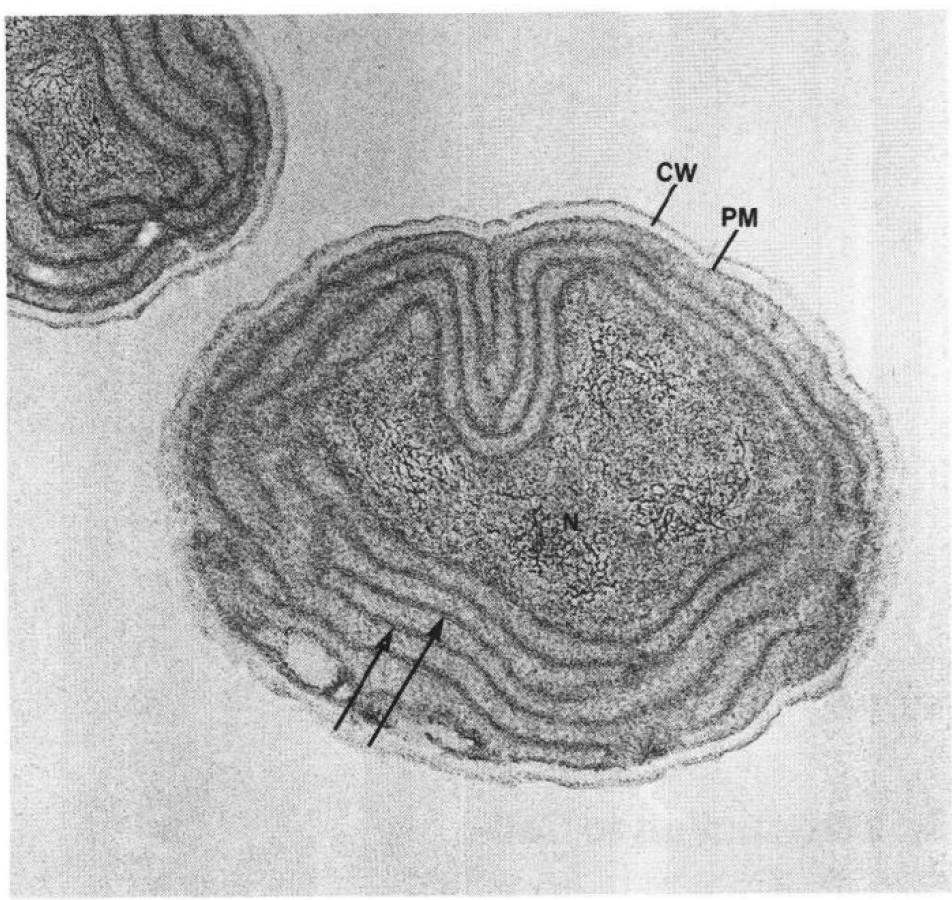

Figure 1-2. *The blue-green alga,* Synechococcus lividus. *The center of the cell is occupied by the nucleoid (N), in which DNA fibers are clearly visible. The cell wall (CW), plasma membrane (PM), and cytoplasmic membranes associated with photosynthesis (arrows) are visible in the cytoplasm. × 60,000. Courtesy of M. R. Edwards and the New York Department of Health, from* Journal of Phycology 4 *(1968): 283.*

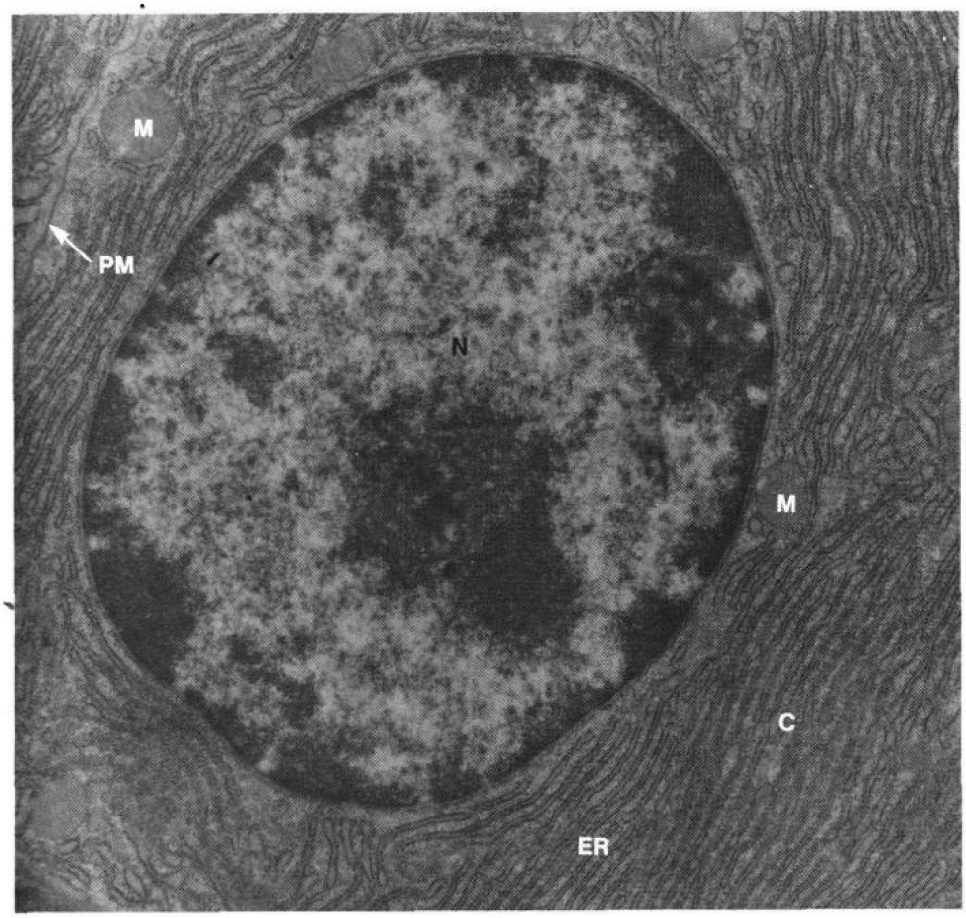

Figure 1-3. *A eukaryotic cell from the pancreas of a rat. N, nucleus; C, cytoplasm; M, mitochondrion; ER, endoplasmic reticulum; PM, plasma membrane. × 16,000. Photograph by the author.*

much greater understanding of cell structure and function today than the early scientists who formulated the cell theory, thanks to the power of modern techniques and methodology. This book serves as an introduction to the internal and surface structures of cells and surveys their functions in sustaining cellular and organismal life.

Cells take highly varied forms in different plants, animals, and microorganisms. They may exist singly, as in the protozoa and bacteria, or packed together by the millions, billions, or trillions, as in larger plants and animals. In size, cells range from the smallest bacteria, just barely visible in the light microscope, to units as large as the hen's egg: The yolk of a hen's egg is a single cell, several centimeters in diameter. Although most cells are roughly spherical in shape, some, like the nerve cells of larger animals, may carry long extensions that are microscopic in diameter but more than a meter in length.

In spite of their varied sizes, shapes, and activities, all cells are divided into two major internal regions that reflect a fundamental division of labor in cell function (Figs. 1-1 to 1-4). The *nuclear region* contains the molecules that store and transmit the hereditary information required for cell growth and reproduction. The second region, the *cytoplasm*, uses the nuclear information to make most of the molecules required for growth and reproduction (some are also made in the nuclear region). The cytoplasm also carries out several additional functions that are vital to life. It contains all of the structures and systems necessary to provide the energy required for cell growth and reproduction. Cell motility also depends entirely on structures forming a part of the cytoplasm. The total living matter of cells, including both the nuclear region and the cytoplasm, is collectively called the *protoplasm.*

Cells are maintained as distinct compartments separate from their environments by *membranes* formed by thin layers of fat- or oil-like molecules called *lipids* in combination with proteins. The lipid layers, which provide the basic framework of membranes, are only two molecules in thickness (see Fig. 2-3). These layers, with their associated proteins, control the movement of molecules between the cell interior and exterior, and between regions within cells. The result is an effective separation of the cell contents from the outside world, and the subdivision of the cell interior into regions with specialized functions.

The cells of all organisms fall into one of two major subdivisions according to the organization of their membranes and the complexity of the nuclear region. The smaller and more primitive subdivision includes only two groups, the bacteria and blue-green algae (Figs. 1-1 and 1-2; the blue-green algae are also called *cyanobacteria*). In the bacteria and blue-green algae, collectively called the *prokaryotes*, cellular membranes are limited to the *plasma membrane*, which covers the entire surface of the cell, and relatively simple inner membranes derived from

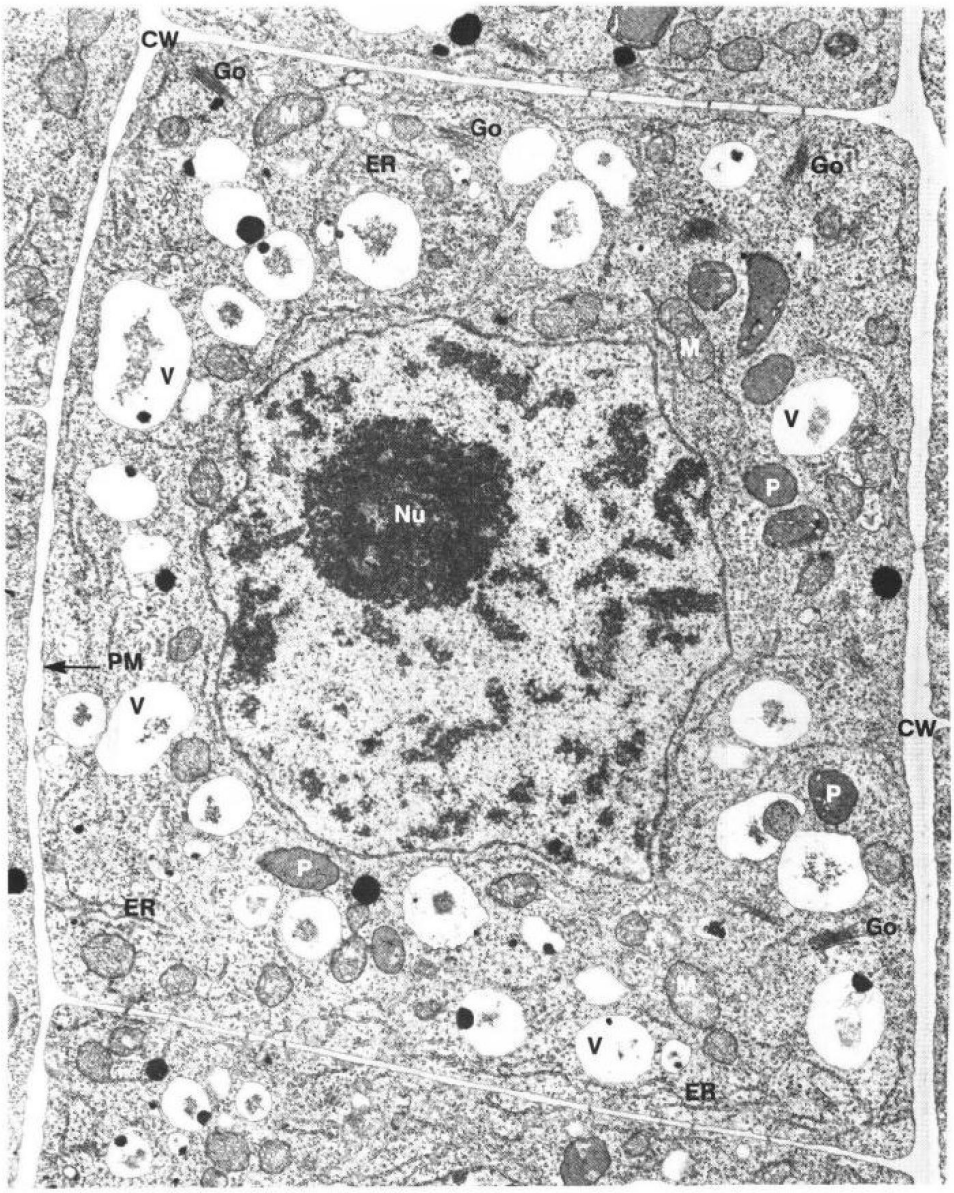

Figure 1-4. *A eukaryotic plant cell from the root tip of* Phleum protense. *N, nucleus; Nu, nucleolus; M, mitochondrion; P, plastid; ER, endoplasmic reticulum; Go, Golgi complex; V, vacuole; PM, plasma membrane; CW, cell wall. × 8,500 Courtesy of B. E. S. Gunning.*

it. No membranes separate the nuclear region from the surrounding cytoplasm in the prokaryotes. The name *prokaryote*—from the Greek *pro* (before) and *karyon* (nucleus)—refers to the primitive organization of the nuclear region in these organisms. Because of its relatively primitive organization, the nuclear region in prokaryotes is termed the *nucleoid*.

The second major division of living organisms, the *eukaryotes*—from *eu* (typical) and *karyon* (nucleus)—includes all of the remaining plants, animals, and microorganisms on the earth. Eukaryotic cells are divided into separate interior compartments by a number of internal membrane systems (see Figs. 1-3 and 1-4). These separate membrane-bound interior structures, called *organelles*, are specialized to carry out the various cellular functions of eukaryotes. The largest and most conspicuous of the internal organelles is the *nucleus*, which forms the nuclear region. In contrast to the nucleoid of prokaryotes, the eukaryotic nucleus is separated from the cytoplasm by a boundary layer of membranes. Other major organelles occur in the cytoplasm. Most conspicuous of these in animal cells are the *mitochondria* and—in plant cells—both mitochondria and *chloroplasts*, organelles that provide energy for cell activities. Also visible as major cytoplasmic organelles are the *endoplasmic reticulum* and *Golgi complex*, membrane systems concerned with the synthesis, modification, and secretion of proteins. The compartmentalization of cell functions in these specialized organelles in eukaryotes, as well as the division of labor among individual cells in multicellular organisms, makes the eukaryotic cell a highly efficient and adaptable unit for the maintenance and evolution of life.

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2

Membranes

Membranes appear as thin barriers about 7 to 8 nanometers in thickness in cells prepared for electron microscopy by embedding and sectioning (Fig. 2-1; Table 2-1 compares the units of measurement used in cell biology). Typically, membranes in sections are imaged in the electron microscope as two dark lines separated by a more lightly stained interspace. Sectioned membranes are rarely more complex in appearance than this simple "railroad track" image (electron microscopy and the major techniques used to prepare cells for viewing in the electron microscope are described in the Appendix).

Work with another technique used to prepare cells for viewing in the electron microscope, the *freeze-fracture* method, indicates that the simple image of membranes seen in sections is deceptive. In the freeze-fracture method (see also Appendix), a tissue sample is frozen almost instantaneously by plunging it in liquid nitrogen. The sample is then fractured by striking it with a sharp knife edge. Because the lipid molecules forming the framework of membranes are fat- or oil-like in character, they produce weakly frozen "faults" that split apart more readily than other cellular regions. As a result, the fracture tends to follow membranes as it travels through the sample. The fracture exposes not only the membrane surfaces but frequently also separates the inner and outer membrane surfaces to expose the membrane interior (Fig. 2-2). Such preparations reveal that most biological membranes are more or less crowded with particles, some embedded only partly within either membrane surface, and some that penetrate entirely through the membranes. Experimental work has shown that the particles are proteins such as enzymes and transport molecules that are responsible for the specialized functions of membranes in different cellular locations. Thus, the structure of membranes is considerably more complex and contains more components than the simple structure suggested by the three-layered railroad track image seen in thin sections.

The contemporary view of the lipid framework supporting membrane structure is based on the tendency of *phospholipid* molecules, the major lipid components of biological membranes, to form stable arrangements called *bilayers* when surrounded by water molecules (Fig. 2-3). The bilayer arrangement depends on the fact that the molecular

structure of phospholipids gives them dual solubility properties. The phospholipids (Fig. 2-4) are built on a backbone structure derived from glycerol, an alcohol that has three reactive groups available for binding other substances (Fig. 2-4a). In the phospholipids two of the reactive groups on glycerol link to long hydrocarbon chains derived from fatty acids. These chains are strongly hydrophobic—from *hydro* (water) and *phobic* (avoiding)—and are most stable when they occupy an environment that excludes water molecules. The remaining reactive group on the glycerol backbone connects to a phosphate group which, in turn, links at its opposite end to a complex chemical group, usually a nitrogen-containing alcohol. The phosphate group and the nitrogenous alcohol, in contrast to the fatty acid chains, are strongly hydrophilic—from *hydro* (water) and *philic* (preferring). These hydrophilic groups, which are most stable in an aqueous environment, tend to extend outward from the glycerol backbone in a direction opposite to the fatty acid chain. The two types of reactive groups give the phospholipids their dual solubility properties, one end of the molecules "preferring" a nonaqueous medium and the other a watery medium. A phospholipid molecule is usually diagramed as it is shown in Figure 2-4b and c, with a circle or sphere representing the hydrophilic end of the molecule and a pair of zigzag lines representing the hydrophobic fatty acid chains.

The bilayer arrangement provides a structure that satisfies the dual solubility properties of phospholipid molecules surrounded by a watery medium, as are the phospholipids of cellular membranes. The hydrophobic "tails" of the two phospholipid layers face each other in the bilayer interior, forming an environment that excludes water. The hydrophilic phosphate-alcohol groups cover the two membrane surfaces, where they face the surrounding water solution. Phospholipid molecules remain stable in the bilayer arrangement because any disturbance of the structure would expose the buried fatty acid chains to the surrounding watery medium or force the phosphate-alcohol groups into the hydrophobic bilayer interior. The same tendency of hydrophobic molecules to associate together in water-excluding environments is responsible for the separate layers formed by oil on water. The structural framework of biological membranes is believed to be a stable phospholipid bilayer of this kind.

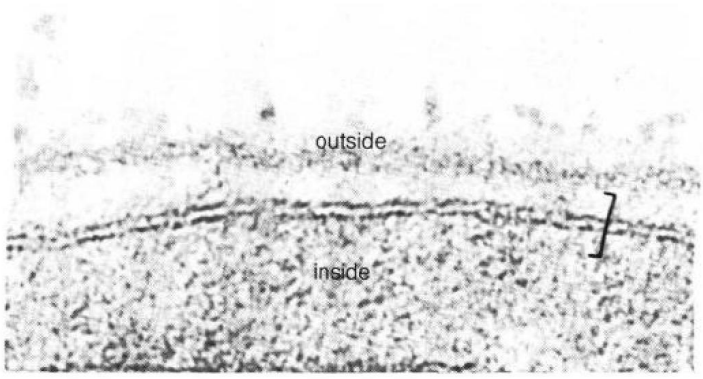

Figure 2-1. *A plasma membrane (bracket) at high magnification, showing the typical trilaminar "railroad track" image obtained for cellular membranes by the preparative techniques most frequently used in electron microscopy. × 240,000. Courtesy of R. B. Park.*

Table 2-1 Units of Measurement Used in Cell Biology

Units	*Equivalence in Millimeters*	*Equivalence in Micrometers*	*Equivalence in Nanometers*	*Equivalence in Angstroms*
Millimeters (mm)	1	1,000	1,000,000	10,000,000
Micrometer (μm)	0.001	1	1,000	10,000
Nanometer (nm)	0.000001	0.001	1	10
Angstrom (A)	0.0000001	0.0001	0.1	1

The micrometer, equivalent to 1/1000 millimeter, is convenient for describing the dimensions of whole cells or larger cell structures such as the nucleus, mitochondria, and chloroplasts. Most cells are between 5 and 200 micrometers in diameter, although some animal eggs may be much larger. Mitochondria are about 1–2 micrometers long and about 0.5 micrometers in diameter; chloroplasts are about 0.5 to 1 micrometer in thickness and 2 to 6 micrometers in diameter. Objects about 200 micrometers (0.2 millimeters) in diameter are just visible to the unaided eye.

Particles roughly the size of ribosomes, microtubules, and virus particles are most often measured in nanometers or Angstroms, units that are useful for descriptions from this level down to particles as small as molecules and atoms. The nanometer, equivalent to 1/1000 micrometer, is difficult to visualize, but with experience a relative appreciation can be made of the size of objects measured in this unit. Lipid molecules, for example, are about 2 nanometers long, and amino acids are about 1 nanometer long. Protein molecules may be 10 nanometers or so in diameter. On the level of cell organelles, membranes are 7.5 to 10 nanometers thick, and ribosomes are about 25 to 30 nanometers in diameter. The electron microscope, incidentally, can "see" objects with diameters as small as 0.7 to 0.8 nanometer. The Angstrom unit, equal to 0.1 nanometer or 1/10,000 micrometer, is employed for measurements in the same size range.

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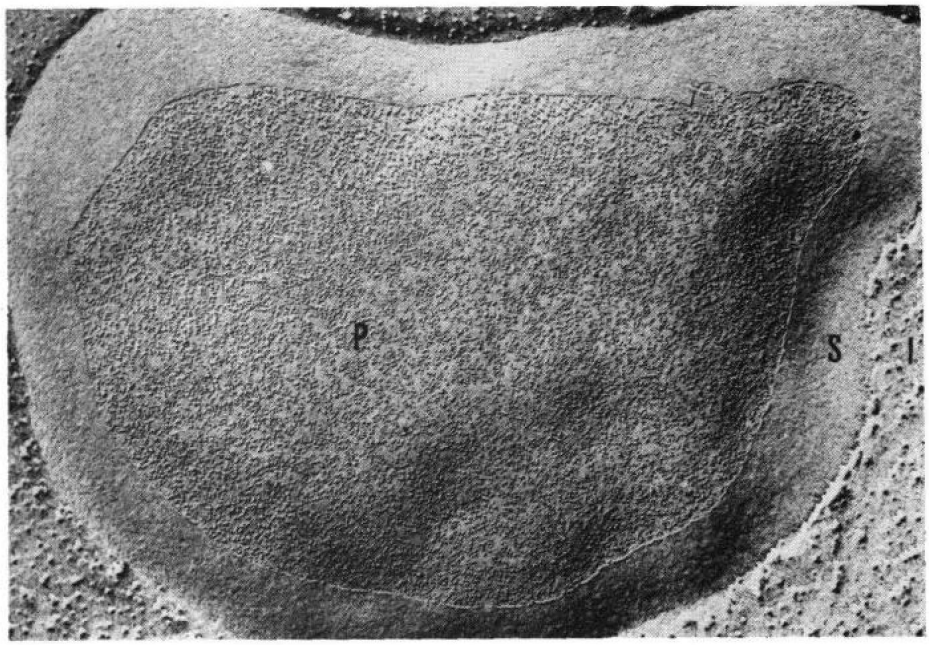

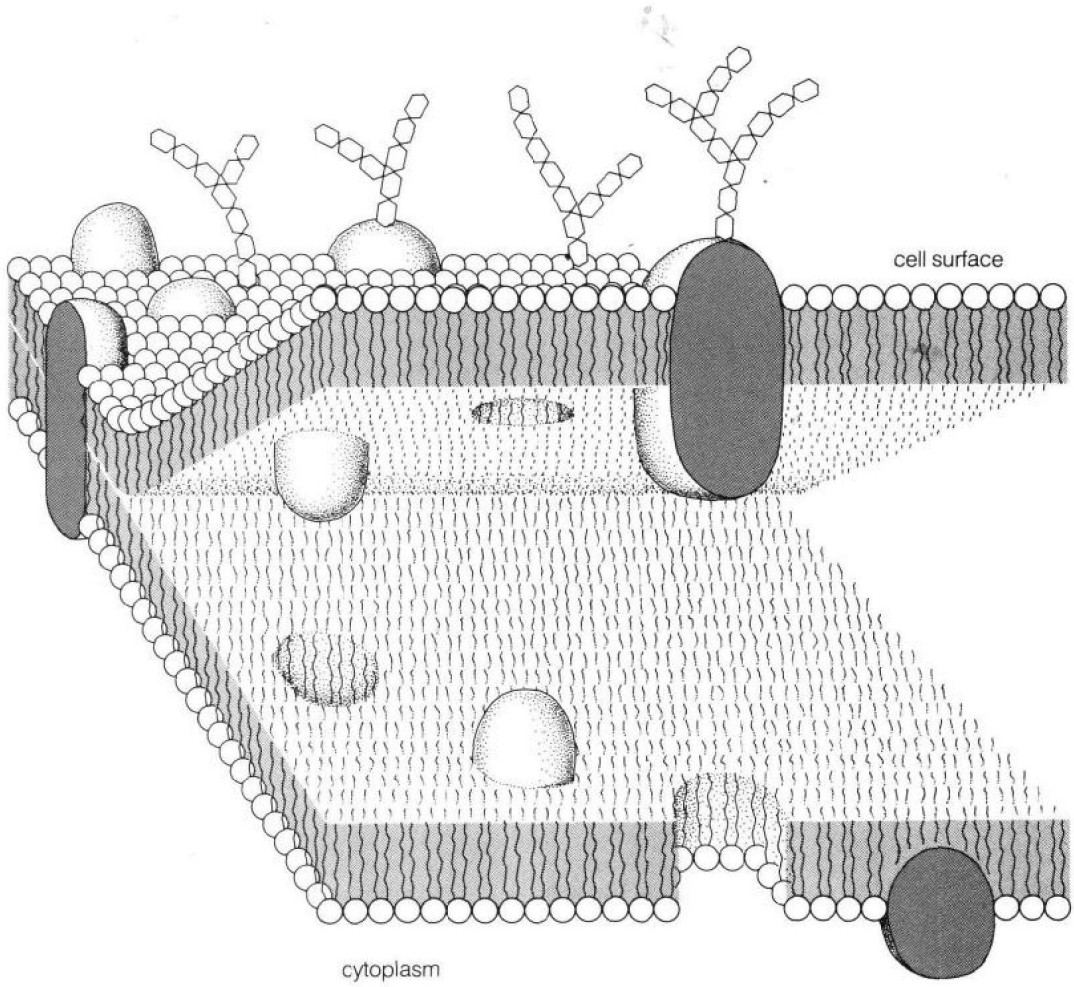

Figure 2-2. *(top) Freeze-fracture preparation of a human red blood cell plasma membrane, showing the particles revealed when the bilayer interior is exposed. The particles are integral proteins suspended within the membrane bilayer. P, membrane particles in bilayer, S, membrane surface; I, ice crystals in the medium surrounding the cell. × 45,000. Courtesy of T. W. Tillack, from* Journal of Cell Biology 45 *(1970): 649, by copyright permission of The Rockefeller University Press. (bottom) Exposure of integral membrane proteins and the membrane interior by fractures that split the bilayer in freeze-fracture preparations.*

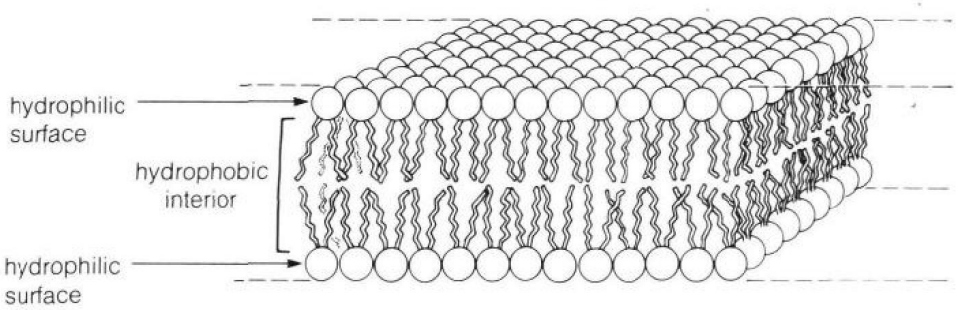

Figure 2-3. *The bilayer structure formed by phospholipids in an aqueous medium. The hydrophilic ends of the phospholipid molecules, represented by the spheres, face the surrounding water solution, and the hydrophobic ends of the molecules, represented by the zigzag lines, associate together in the membrane interior.*

According to the *fluid mosaic model* (Fig. 2-5), the contemporary hypothesis for biological membrane structure proposed in 1966 by S. J. Singer and Garth Nicolson, the bilayers of biological membranes are in a highly fluid state at the temperatures characteristic of living cells. *Fluidity* in this sense means that the fatty acid tails can flex and rotate in the hydrophobic bilayer interior, and that individual phospholipid molecules are free to exchange places rapidly and readily within the same bilayer half (the phospholipid molecules, however, do not readily flip-flop from one bilayer half to the other). This is the "fluid" part of the fluid mosaic model.

Singer and Nicolson deduced the positions of proteins in their model partly from the appearance of freeze-fracture preparations of membranes as shown in Figure 2-2. Noting that the particles identifiable as proteins are suspended individually on and within membranes, Singer and Nicolson proposed that membrane proteins float as units in or on the fluid phospholipid bilayer, like "icebergs in the sea." Some proteins, according to their model, penetrate entirely through the membrane and are exposed on both sides, and some penetrate only part way through. The distribution of proteins in membranes, in units rather than as continuous sheets covering the membrane surfaces, is the "mosaic" part of the fluid mosaic model. Singer and Nicolson called the proteins embedded partly or completely in the phospholipid bilayer *integral* membrane proteins. These proteins are functional parts of membranes. Other proteins attached to membrane surfaces were termed *peripheral* membrane proteins. The peripheral proteins form parts of structures that are associated with the membrane surfaces.

According to the model, the integral membrane proteins are held in suspension in the fluid lipid bilayer by their solubility properties. The proteins that pass entirely through the membrane have two hydrophilic ends and a hydrophobic middle region. The hydrophobic middle regions are held in association with the membrane interior and the hydrophilic ends extend into the watery medium at the membrane surfaces. Integral proteins that extend only partly through the membrane have a hydrophobic end suspended in the membrane interior and a hydrophilic end facing the surrounding watery medium. The proteins remain in stable suspension in the bilayer because, like the bilayer phospholipids, any change in orientation would expose their hydrophobic regions to the watery surroundings or force their hydrophilic ends into the hydrophobic bilayer interior. Within these limitations, the proteins are free to displace phospholipid molecules and move laterally through the fluid bilayer.

Most of the integral proteins are enzymes that catalyze the specialized functions of membranes in different regions of the cell, or transport molecules that provide channels for the movement of selected hydrophilic substances through membranes. Plasma membranes also contain integral proteins with attached carbohydrate groups that act as receptor molecules (several integral proteins bearing carbohydrate groups are shown in Fig. 2-5). The integral proteins bearing hydrophilic carbohydrate groups are typically oriented in plasma membranes with their carbohydrate antennae facing the cell exterior, where they recognize and bind a variety of molecules to the cell surface.

The fluid mosaic model has been supported by the results of a wide variety of experiments and is now accepted as an accurate description of the arrangement of lipid and protein molecules in biological membranes. In this structure, the lipid molecules form the framework of membranes and are essentially similar in structure and function from one membrane to the next. The group of protein molecules present, which varies greatly from membrane to membrane, gives each membrane type its specialized biological functions.

The relationship between membrane structure as described by the fluid mosaic model and the image of membranes seen in thin sections (as in Fig. 2-1) is still unclear. Presumably, the two parallel dark lines in the image, the tracks in the railroad track, correspond to the hydrophilic surface regions of the membranes. These hydrophilic layers include the phosphate groups and nitrogenous alcohols of the membrane phospholipids, and the hydrophilic portions of membrane proteins exposed at the two membrane surfaces. Probably, these darkened surface layers define the limits to which the aqueous solutions used as stains in electron microscopy can penetrate into the membranes. The interior of the membrane probably has its unstained, lighter appearance because little of the staining solution can penetrate into the hydrophobic membrane interior. Although the trilaminar image is frequently less distinct and regular in membranes containing large quantities of enzymatic and transport proteins, such as those of mitochondria and chloroplasts, there is

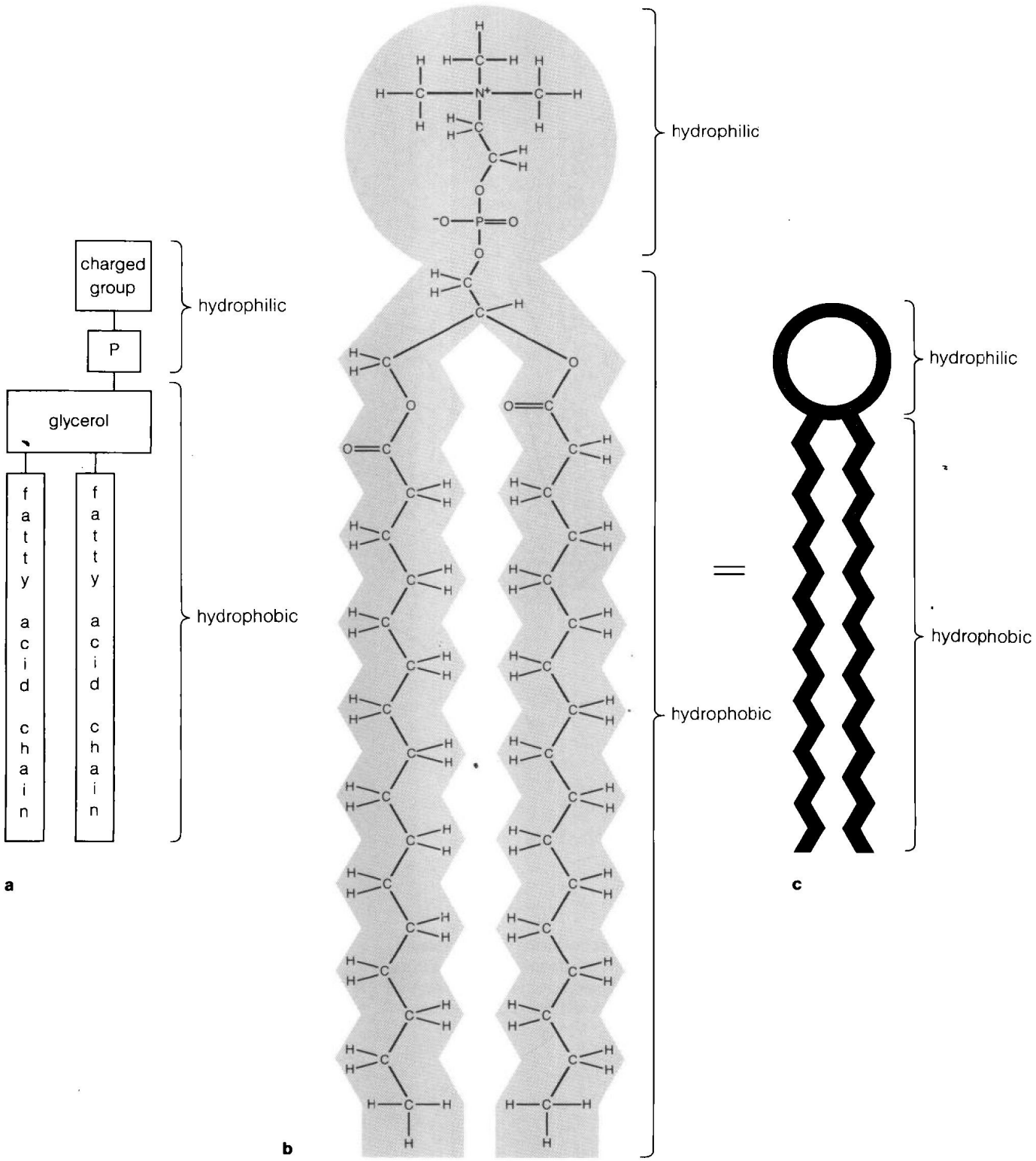

Figure 2-4. *A common membrane phospholipid, phosphatidyl choline. The shaded area in (b) relates the commonly used diagram for a phospholipid, as shown in (c), to the structure of a phospholipid molecule.*

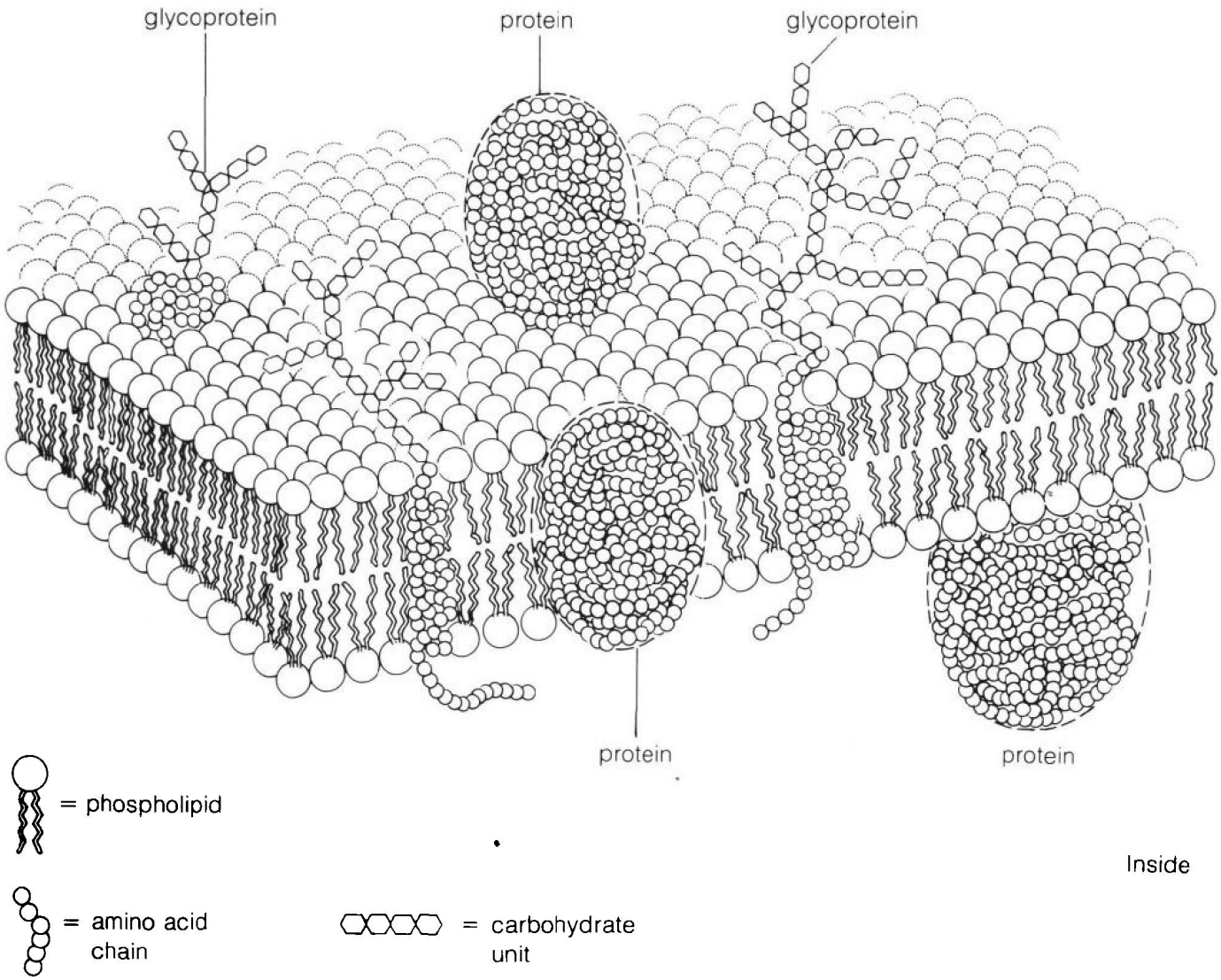

Figure 2-5. *Membrane structure according to the fluid mosaic model. In the model, proteins are suspended as globular units in a fluid bilayer. Integral proteins are deeply embedded in the bilayer; peripheral proteins are attached to the bilayer surfaces. The diagram shows a plasma membrane as proposed in the model, with carbohydrate groups of membrane glycoproteins facing the cell exterior.*

usually little or no hint of visible particles within sectioned membranes corresponding to the abundance of protein-sized particles seen in freeze-fracture preparations.

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3

Prokaryotic Cells

Prokaryctic cells (Figs. 3-1 to 3-3) are comparatively small, usually not much more than a few micrometers long and a micrometer or slightly less in width. The boundary membrane of the cell, the plasma membrane, is surrounded in almost all prokaryotes by a rigid external layer of complex polysaccharide material, the *cell wall*. This external layer may range in thickness from 15 to 100 nanometers or more and may itself be coated with a thick, jellylike *capsule*. The cell wall gives rigidity to prokaryotic cells and, with the capsule, protects the cell within the wall.

The plasma membrane lining the inner surface of the cell wall may be smooth or may include folds or pockets that extend from the surface into the cell interior (as in Figs. 3-2 and 3-3). This membrane carries out a variety of vital functions in prokaryotes in addition to controlling the movement of substances between the cytoplasm and the cell exterior. Many of the molecular systems that carry out oxidations to release energy for cell activities are linked to the plasma membrane in prokaryotes. In the photosynthetic bacteria and in the blue-green algae, the molecules carrying out the absorption and conversion of light to chemical energy are also associated with the plasma membrane and its interior extensions or derivatives. In addition, the plasma membrane is thought to play a part in replication and division of the nuclear material in prokaryotes. Thus many functions that are located in separate, internal membrane-bound organelles in eukaryotes are associated with the plasma membrane or its derivatives in prokaryotes.

Within prokaryotic cells, nucleoids appear as irregularly shaped structures that are less darkly stained than the surrounding cytoplasm. Tightly packed and folded fibers about 3 to 5 nanometers in thickness make up the entire structure of the nucleoid. When isolated by methods designed to remove proteins and reduce breakage, the nucleoid of bacteria proves to contain a single, large DNA molecule in the form of a closed circle. In *Escherichia coli*, the best-studied bacterium, the nucleoid circle contains 1360 micrometers of DNA, equivalent to 4,000,000 base pairs. Other bacteria have circles ranging from about 250 micrometers of included DNA to a maximum not far in excess of the *E. coli* circle, about 1500 micrometers. All of this DNA is packed into the fibrous mass

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