Michael W. Berns

Cells

Second Edition

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Preface to the Second Edition

Since the apparent success of the first edition was due to the simplicity of the approach and the widespread use of high-quality micrographs and diagrams, I have chosen to continue that format in the second edition. In addition, the use of the experimental method has again been stressed.

Most of the chapters have been updated to give the reader a current view, and, in addition, important material omitted from the first edition has been added. For example, the striking omission of viruses has now been rectified in Chapter 1. Several new techniques have been added to Chapter 2, such as freeze-fracture electron microscopy and flow cytometry. In Chapter 3 a more modern description of the nucleosome structure of chromatin has been given, and in Chapter 5 a discussion of cell-cell junctions has been added and amplified with numerous electron micrographs of different junctions. The chapter on cell division has been significantly expanded to encompass the many new observations and "models" being proposed in this area.

However, the greatest change in the second edition is the addition of three new chapters: cell motility/cytoskeleton, genetic engineering, and cellular immunology. The cell motility/cytoskeleton chapter presents the basic information in one of the areas of cell biology that has literally "exploded" during the past five years. This chapter is illustrated and organized much like all the original chapters in the book.

The chapters dealing with genetic engineering and cellular immunology are an attempt to acquaint the beginning student with two areas in cell biology that will not only have tremendous impact in the field of biology in general, but that also have tremendous potential for affecting our everyday lives. These two chapters depart somewhat from the original intent of this book because the material is inherently difficult to get across in a simplistic way (at least that is my experience). It is therefore possible that the beginning student or the nonbiology major may find these two chapters difficult to handle. The instructor should bear this in mind when assigning these two chapters and perhaps supplement with additional material or spend additional time on these subjects in lecture. Of course, even a cursory reading of these chapters will provide the student with the "flavor" of these two exciting fields.

Once again I would like to thank my many friends and colleagues for their constructive criticisms and help. I have taken particular care to modify all the figure legends to give appropriate credit to those persons who were so generous as to provide photos (this is a rectification of a problem in the first edition). I am particularly grateful to the following colleagues for reading and commenting on the new chapters: Brian McCarthy, Jerry Manning, Morrie Granger, George Guttman, and Tim Bradley. I am also indebted to the following people in my laboratory for providing photos as well as helpful comments: Leacky Liaw, Ann Siemens, Marie Wilson, Michael Koonce, Mitzi Kitzes, Robert Walter, James Coulombe, Dodie Nordberg, and Bev Hyndman. In addition, I am extremely grateful to Marie Wilson for her work on the glossary and index.

Michael W. Berns
Irvine, California
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CHAPTER 1

The Diversity of Cells

Nature's variety is boundless. When walking through the woods, across a field, along a stream, through the zoo in a city, or on the vast plains of Africa, one cannot help but be impressed with the diversity of life. Looking through a microscope can be an equally exhilarating experience. The universe of the cell is complex and diverse. Like the world around us, the world of the cell is one of forms specialized for particular types of existence. And as in the larger universe of the plant and animal kingdoms, where one can perceive basic life-sustaining processes common to all organisms, in the cellular world many of the same processes and structures can be found in almost all cells. It seems to be an axiom of nature that where there is diversity, there is also similarity.

Much of cell biology is devoted to the study of structures and functions in specialized cells. The results of these studies are used to formulate the generalizations applied to almost all cells as well as to provide the basic understanding of how a particular cell type carries out its specific functions.

It seems fitting to begin an inquiry into the nature of cell life with a look at nature's diversity. The cell "world" may be broadly divided into prokaryotes (the bacteria, mycoplasmas, and blue-green algae) and eukaryotes (protozoa, sperm and eggs, cells that make up tissues and organs, and so on). Although this book will deal only sketchily with prokáryotic systems, it is important to realize that much of what we know and much of what we are just beginning to perceive about the eukaryotes are based on our understanding of the prokaryotes.

Prokaryotes

Prokaryotes are small, single-cell organisms, usually less than a micrometer (abbreviated μm; 1000 μm = 1 millimeter, abbreviated mm) and generally not larger than 3 μm. Their structural organization is simpler than that of the eukaryotes. They do not have a nucleus (a body containing the hereditary information), and they are lacking in many membranous structures found in the more complex cell types. The hereditary information is contained in a single circular structure that lacks many of the molecular components of the eukaryote hereditary structure called the chromosome. In addition, the prokaryotes seem to lack any kind of special apparatus for cell division. It has been theorized that because these cells divide by a process of fission (by simply splitting in half), and because they do not contain numerous chromosomes that must be separated during division, there has been no need for the prokaryotes to evolve the complex cell-division machinery found in the eukaryotes.

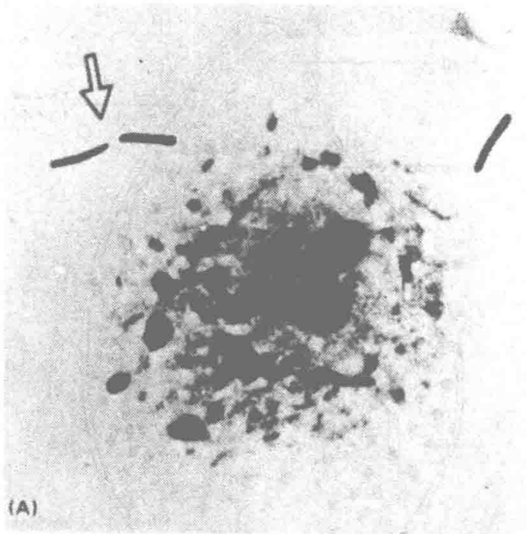
Many of the prokaryotes are surrounded by a rough wall rich in carbohydrates and amino acids. Just below the cell wall is a membrane that has numerous inpockets called mesosomes. The membrane of the prokaryotes exhibits a complex degree of organization. This is not surprising, because the prokaryotic membrane takes on many of the functions (such as cellular respiration) reserved for the internal membranous structures of the eukaryotes. In fact, it has even been speculated (see Chapter 5) that the eukaryotic respiratory (energy-producing) structure, called the mitochondrion, once was a bacterium that, through evolution, became an integral part of the eukaryotic cell respiratory machinery. Although this is only a theory, numerous biologists point to the fact that the bacterial cell membrane contains many of the respiratory proteins found in the mitochondrion.

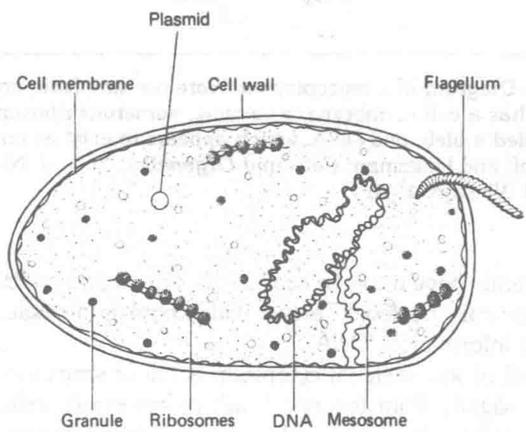
The three major groups of prokaryotes (the bacteria, mycoplasmas, and blue-green algae) are structurally very different (Figs. 1–1, 1–2, and 1–3). One of the common rodlike bacteria is illustrated in Fig. 1–1A and B. A common mycoplasma is depicted in Fig. 1–2, and a blue-green alga is represented in Fig. 1–3. Although all three of these cell types exhibit prokaryotic cytology, their overall organization is quite different.

Bacteria

One of the best-studied bacteria is *Escherichia coli (E. coli)*. It is about 2 μm long and 1 μm wide and contains several thousand different kinds of molecules. It is particularly easy to grow in an artificial medium and reproduces about once every 20 min. This bacterium has both oxygen-requiring (aerobic) and nonoxygen-requiring (anaerobic) respiratory machinery for the breakdown of sugar and contains a special group of proteins called the electron-transport chain for the generation of stored energy in the form of ATP molecules. (See Chapter 6 for a more complete discussion of cellular energetics.) In terms of a biochemical metabolism, *E. coli* is very similar to eukaryotic plant and animal cells.

Structurally, *E. coli* is rodlike and has a typical cell wall and underlying cell membrane. The membrane contains the special regions called mesosomes,





(B)

Figure 1–1 *(A)* **A light micrograph picture of bacteria. Note that they are rod-like. (This is only one form of bacteria; they have several shapes.) The arrow points to two bacteria that have just formed from one as a result of fission. Also note the size of the bacteria in relation to the eukaryote tissue culture cells.** *(B)* **A generalized bacterium. Most bacteria are surrounded by a cell wall, which is attached to the cell membrane at relatively few points. Flagella usually extend from the cytoplasm through the wall. Ribosomes, granules of various kinds, and a circular DNA molecule are found in the cytoplasm, which frequently includes an inward extension of the membrane known as a mesosome. In addition, small cir cular DNA molecules called plasmids have recently been found in the cytoplasm. (After Dyson:** ***Cell Biology*****. Boston: Allyn and Bacon, 1975.)**

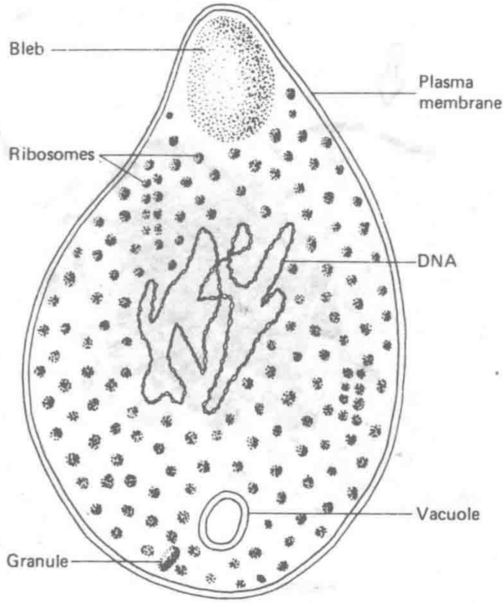


Figure 1–2 Diagram of a mycoplasma. Note the simplistic organization of this organism. It has a cell membrane, a vacuole, numerous ribosomes, an upper extension called a bleb, and DNA, which appears to exist as one large molecule. (After Novikoff and Holtzman: *Cells and Organelles*, 2nd ed. New York: Holt, Rinehart and Winston, 1976.)

which apparently have a role in cellular respiration and cell division. There may be one or several "nucleoid" areas, which contain a single, circular molecule of hereditary information (DNA).

The rest of the bacterial cytoplasm is full of structures called ribosomes, which differ slightly from the ribosomes of eukaryotic cells. These structures are the sites of protein synthesis. In addition, recent studies have revealed the presence of small circular DNA molecules in the cytoplasm called plasmids. These structures are very important in genetic engineering (see Chapter 9).

Mycoplasmas

The mycoplasmas (previously called PPLOs, pleuropneumonialike organisms) are small (0.2 to 0.3 μm) and more simply organized than bacteria. The hereditary material (DNA) is contained in a nonmembrane-bound, nucleuslike region, and it may exist either as strands or as a circular molecule as in the bacteria. However, there is only one tenth the amount of genetic material in mycoplasmas as there is in bacteria. Similarly, the mycoplasmas contain 1/50 to 1/100 the number of bacterial ribosomes per cell. A delimiting cell mem-

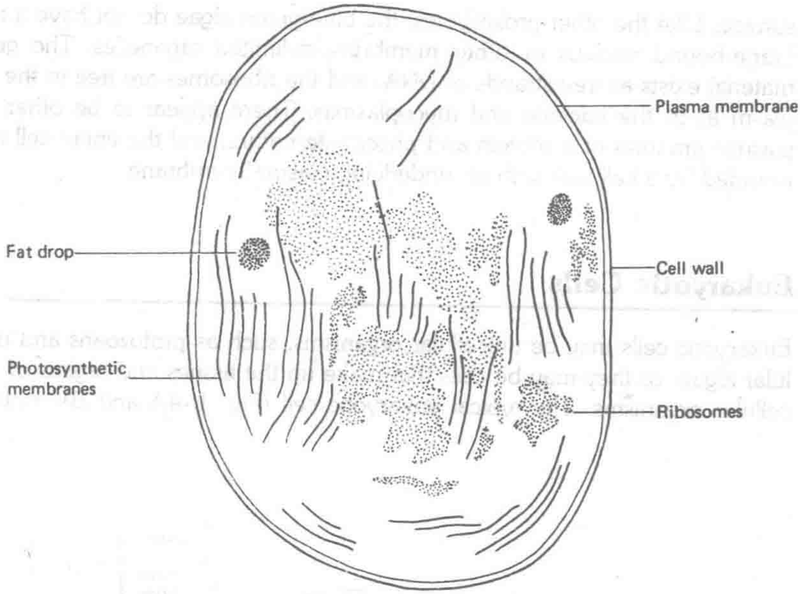


Figure 1–3 Diagram of a blue-green alga. (After Stephens and North: *Biology*. New York: John Wiley & Sons, 1974.)

brane exists, but no cell walls have been detected. A variety of other cytoplasmic inclusions, such as vacuoles and granules, have been detected, but their function is not known. As in other prokaryotes, there are no intracellular membranous structures.

Mycoplasmas have been known to cause certain respiratory diseases in animals and man. They also occur as routine contaminants in eukaryote tissue cultures and currently are of much concern to researchers who use these culture procedures in their studies.

Blue-Green Algae

The blue-green algae are the third major group of prokaryotic organisms. The cellular organization is more complex than that of the other prokaryotes, primarily because of the existence of photosynthetic machinery. The blue-green algae contain chlorophyll as well as other more unusual pigments called phycobilins. The chlorophylls are bound to membranes in flattened rows called lamellae, which give the algal cytoplasm a rather organized and structured appearance. The phycobilins appear to be located in granular structures called cyanosomes, which apparently are attached to the outer lamellar membrane surface. Like the other prokaryotes, the blue-green algae do not have a membrane-bound nucleus or other membrane-delimited organelles. The genetic material exists as free strands of DNA, and the ribosomes are free in the cytoplasm as in the bacteria and mycoplasmas. There appear to be other cytoplasmic granules of a protein and phosphate nature, and the entire cell is surrounded by a cell wall with an underlying plasma membrane.

Eukaryotic Cells

Eukaryotic cells may be unicellular organisms, such as protozoans and unicellular algae, or they may be cells that make up the tissues and organs of multicellular organisms. The typical eukaryotic cell (Fig. 1–4A and B) contains a

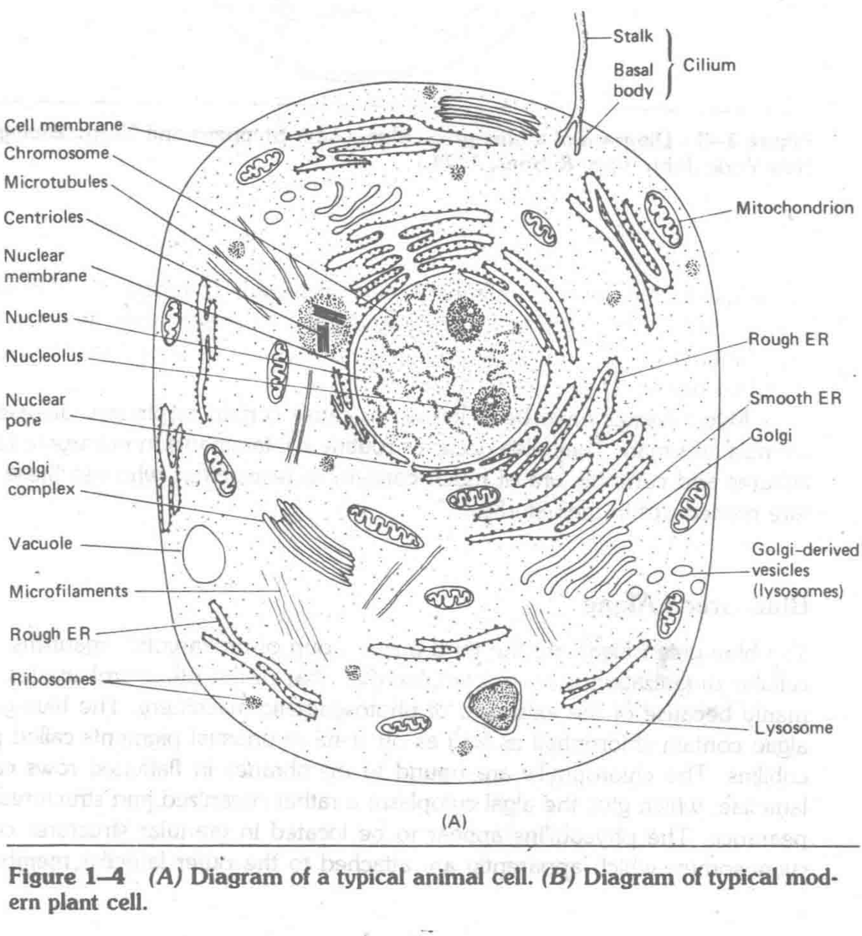


Figure 1–4 ***(A)*** **Diagram of a typical animal cell.** ***(B)*** **Diagram of typical modern plant cell.**

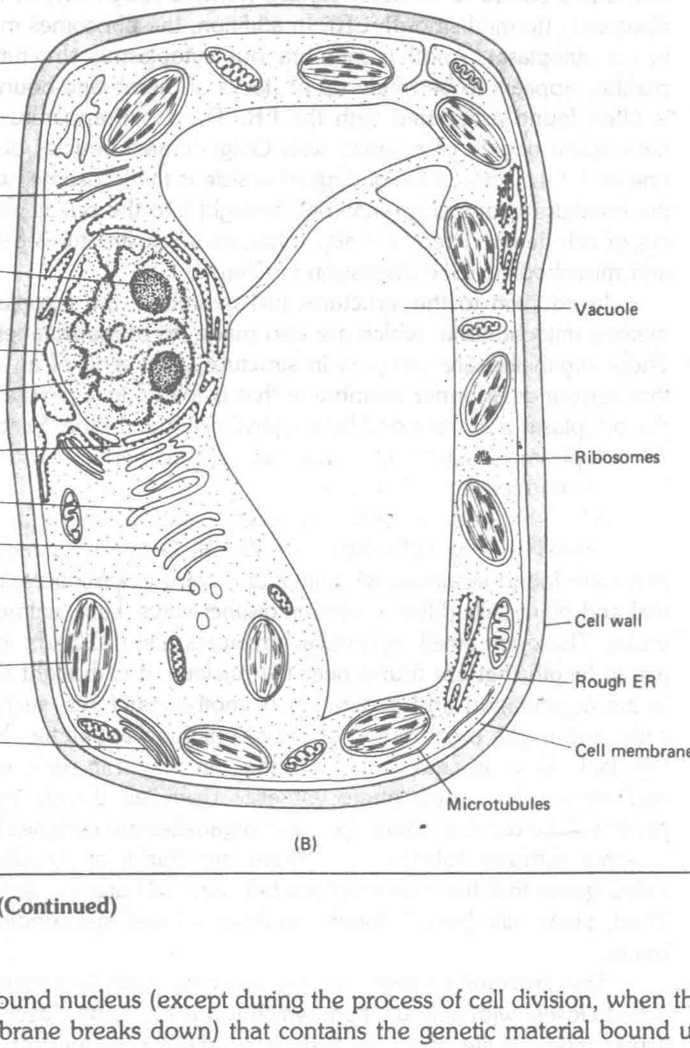


Figure 1–4 (Continued)

membrane-bound nucleus (except during the process of cell division, when the nuclear membrane breaks down) that contains the genetic material bound up in the chromosomes. The chromosomes (see Chapter 3) are rather complex structures consisting of DNA and various protein constituents. They become distinctly visible when the cell undergoes division, and they are nondistinctive (apparently somewhat diffuse) during the phases between division. In addition to the genetic material, the nucleus also contains one or more spherical bodies called nucleoli. Nucleoli function in the production of ribosomes, which are used in the synthesis of proteins. The nuclear membrane contains numerous pores, which provide a means of communication between the nucleus and the cytoplasm.

The cytoplasm of the eukaryotic cell contains many membranous structures (see Chapters 5 and 6). The endoplasmic reticulum, abbreviated ER, often can be seen extending from the area near the nucleus. It may contain ribosomes bound to its outer surface (termed rough ER) or it may be free of ribosomes (termed smooth ER). In addition, the ribosomes may be found free in the cytoplasm. Another membranous cytoplasmic structure, the Golgi apparatus, appears to be made up of stacks of membrane-bound vesicles, and it is often found associated with the ER. The Golgi apparatus also appears to have some degree of polarity, with Golgi-derived vesicles being generated at one end. One type of Golgi-derived vesicle is the lysosome, which functions in the breakdown of foreign materials brought into the cell as well as in the process of cell death. There are also other vacuolar structures called peroxisomes and microbodies. (See discussion in Chapter 5.)

In addition to the structures just described, the cytoplasm contains numerous mitochondria, which are also made up of membranelike components. These organelles are complex in structure, consisting of an outer membrane that surrounds an inner membrane that is folded in a parallel fashion. Finally, the cytoplasm is surrounded by a typical cell membrane. Scattered throughout the cytoplasm of plant and animal cells are filamental structures called microfilaments and microtubules.

All of the aforementioned structures—the nucleus with its chromosomes and nucleoli and the cytoplasm with its ER, Golgi, lysosomes, and mitochondria—are found in almost all animal and plant eukaryotic cells. However, animal and plant cells differ in several distinct ways. First, animal cells have centrioles. These are small, cylindrical structures about 0.2 μm in diameter and 1 μm in length that are found near the nucleus. It is thought that they function in the organization and generation of motile structures, such as cilia and flagella, and in the organization of the cell-division apparatus. Most higher plant cells lack these structures, although they are found in some of the algae. Second, plant cells contain photosynthetic organelles, the chloroplasts and other plastids. Like the mitochondria, these organelles are complex in structure, with a rather intricate substructure. There are stacks of lamellalike membranes called grana that have connections between and are surrounded by a matrix. Third, plant cells have a tough cellulose cell wall surrounding the cell membrane.

The structural diversity among eukaryotic cells is immense. This diversity is tied closely with cell function, which in turn may be closely linked to a particular mode of life. Because there is no division of function between cells in unicellular organisms, the mode of life of the organism is often reflected in a very high degree of structural specialization.

Unicellular Organisms

Protozoa

The protozoans are a diverse group of single-cell organisms in both shape and motility patterns. *Paramecium* (Fig. 1–5) is one of the most common and often