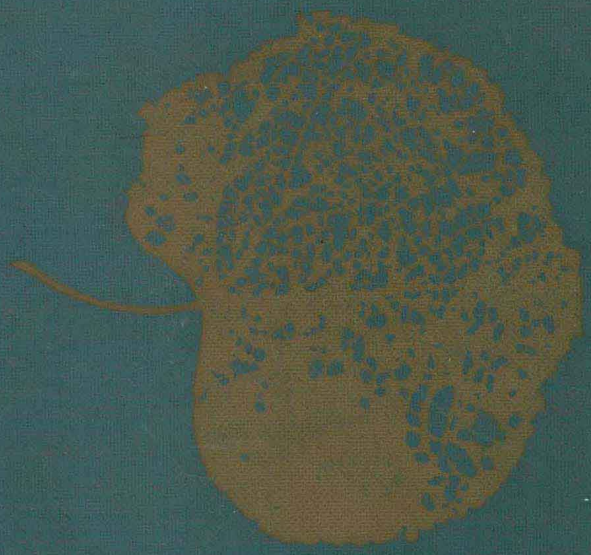

SECOND EDITION

PLANT PHYSIOLOGY

Robert M. Devlin

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University of Massachusetts

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PREFACE

The Second Edition of *Plant Physiology*, like the First Edition, provides the college student with an introduction to the physiology of plants. Although revision in certain parts is extensive, the original organization and aims of the book have been maintained.

The Second Edition includes discussions on the presence of RNA and DNA in mitochondria and chloroplasts, an important discovery with exciting implications. New concepts on chlorophyll and starch synthesis have been added and the possible role of microtubules in cell wall formation is discussed. To Chapter 9 have been added more detailed discussions of the effects of temperature, light, and natural plant-growth hormones on translocation in the phloem. These discussions emphasize the growing interest that this area of plant physiology has attracted. Chapters 10 and 11 have been largely rewritten, giving a detailed and more accurate description of photosynthesis. Particular attention has been given to C. B. van Niel's studies, the "Emerson Effect," the role of ferrodoxin in electron transfer, and the two pigment systems. Chapters 17 and 19, dealing with plant-growth hormones, have been revised to accommodate the many advances that have been made in this area over the last few years. New concepts on auxin translocation and the exciting discovery that IAA is capable of new RNA and protein induction are discussed. An up-to-date description of phototropism and geotropism and a discussion of the newly isolated natural inhibitor abscisin II have been included. In addition, recent work on gibberellins and cytokinins has been given attention, with particular reference to the activity of gibberellins in the mobilization of storage compounds during germination.

Many other changes have been made, including the addition of new illustrations and new references, to make the text a more efficient tool for classroom use.

The book has been organized in a manner to make it applicable to a one- or two-semester course. Adequate coverage of the entire book can be accomplished in a full academic year. With a certain amount of trimming and condensation, it can be used in a one-semester course. It is suggested that students preparing for a course using *Plant Physiology* take general courses in botany and inorganic and organic chemistry. In our time one is "hard put" to distinguish between the fields of biochemistry and physiology, a situation that makes it almost mandatory for a student to be well grounded in certain chemical principles before he undertakes a course in plant physiology.

The book is divided into seven sections, each section covering a specific area of plant physiology. The instructor may start at the beginning of any one section, depending upon the background of his students. In other words, lecture units may conveniently be associated with sections in the book, allowing for closer ties between lecture and text.

Robert M. Devlin

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INTRODUCTION

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THE PLANT CELL—STRUCTURE AND FUNCTIONS OF ITS PARTS

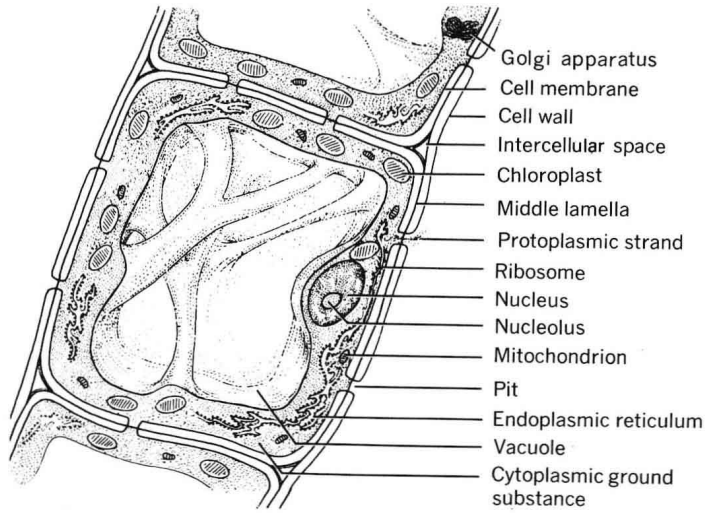
Introduction

Although appearing relatively homogeneous in structure, the plant can actually be thought of as a community of microscopic structures or units called cells. In a most amazing and not as yet completely understood manner, these small units work harmoniously together to give life to the multicellular plant. In the unicellular plant, such as found in the lower forms of plant life (bacteria and algae), the cell is a living individual unit capable of existing in the absence of other cells.

We are on pretty safe ground when we say the cell is the basic unit of life. That is, it is the smallest structure in the universe capable of growth and reproduction. Viruses, considered living units by some, are considerably smaller than cells. No virus, however, has yet been observed that was not associated with a living cell and completely dependent upon it for reproduction. The viruses, then, lacking this important characteristic of self-replication, cannot be called basic units of life.

The size and shape of a plant is due largely to the number, morphology, and arrangement of its cells. For example, in succeeding chapters we will see that the conductive tissues of a plant are made up of cells structurally equipped for the rapid transport of large amounts of water and nutrients. Also in later chapters a definite relationship between cellular structure and function in the leaves and roots of a plant will be discussed. Indeed, it is the purpose of this book to study the physiology of the plant, a study that begins with the plant cell and its parts. A diagrammatic representation of a typical plant cell is shown in Figure 1-1.

Chapter references begin on p. 15.



1-1 A diagrammatic representation of the typical plant cell.

Cell Wall

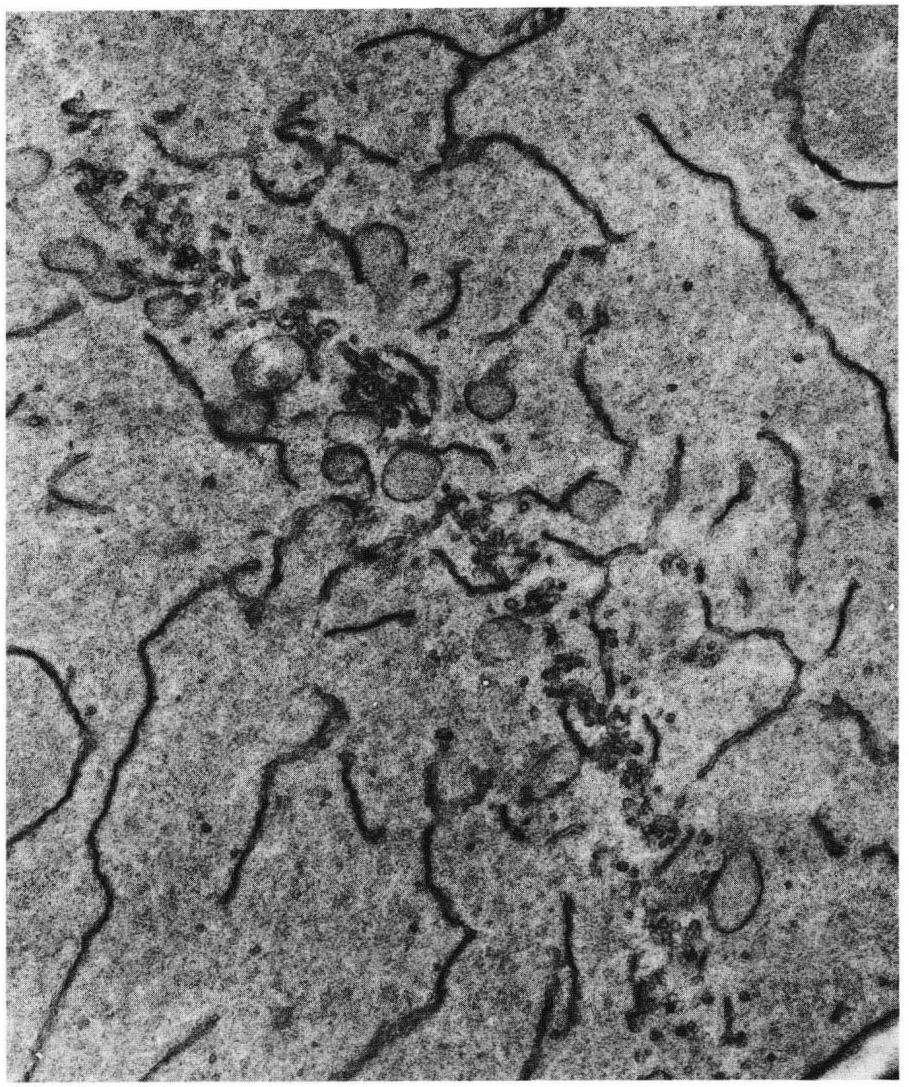
With only a few exceptions, all organisms must have mechanical support of some kind in order to maintain a definite form. In the animal world, this support is either an exoskeleton within which other cells are confined or an endoskeleton to which the other cells cling. In the plant world, however, each individual cell is enclosed in a relatively rigid structure called the *cell wall*, which is lacking in the animal cell. The cell wall is generally thought of as a nonliving part of the cell, which is secreted and maintained by the living portion of the cell called the *protoplast*. However, the designation of nonliving and living properties to different parts of the cell is not entirely correct since its component parts cannot exist apart from each other.

By far the chief structural component of the cell wall is *cellulose*, a compound formed by the stringing together of many thousands of sugar units produced as a result of photosynthesis. A more complete picture of the chemical aspects of cell wall synthesis has been left to a later chapter. In addition to cellulose, pectic compounds, hemicelluloses, lignin, suberin, protein, and cutin represent the chief compounds found in the cell wall.

Cell wall formation

Cell wall formation is initiated during the most advanced stage of mitosis called the telophase (Figure 1-2). Note in Figure 1-2 that tubular fragments of the endoplasmic reticulum appear to have migrated to the equatorial region during telophase. It is thought by many investigators that these fragments participate in the formation of the *cell plate* or *middle lamella*. We may think of the middle lamella as the cementing substance between adjoining cells. One compound in particular, calcium pectate (calcium salt of pectic acid), is most abundant in the middle lamella and acts as an important cementing material between cells. Indeed, the characteristic softening of fruit during the ripening process is caused to a large extent by the pectic substances of the middle lamella becoming more soluble. That is, these substances lose their binding properties through the mediation of pectolytic enzymes, which increase in activity as a fruit matures.

Primary wall The primary wall borders the middle lamella and is the first product of cell wall synthesis by the protoplast. While the cell is enlarging, the primary wall stays relatively thin and elastic, thickening



1-2 Electron micrograph showing early state of cell plate formation in telophase of dividing onion root tip cell. A small portion of each telophase nucleus is seen at the upper right and lower left. The developing cell plate extends diagonally from lower right to upper left. Membrane elements of the endoplasmic reticulum with evidence of branching are present on both sides of the cell plate. In the immediate vicinity of the cell plate the elements of the endoplasmic reticulum are shorter and form a reticulation composed of a close lattice of tubules along the midline between the two cells. (After K. Porter and R. Machado. 1960. Biophys. Biochem. Cytol. 7:167.)

and becoming rigid only after the completion of cell enlargement.

Early investigators believed that the primary wall contained pectic substances, hemicelluloses, and cellulose, with the pectic substances being present in abundance and having a dominant role in the behavior of the wall during cell growth. For example, Kerr (*1951*) has pointed out that the flexibility of the primary wall during cell elongation suggests the presence and importance of pectic substances. However, an analysis of the primary walls of *Avena coleoptile* cells by Bishop et al. (*1958*) showed that hemi-

celluloses were present in much greater concentration than pectic substances. Similarly, Ray (*1958*) and Albersheim (*1958*) have demonstrated that primary walls are low in pectic substances. This information suggests that hemicelluloses and other components of the primary wall play a more important role in the initial stages of cell growth than previously thought.

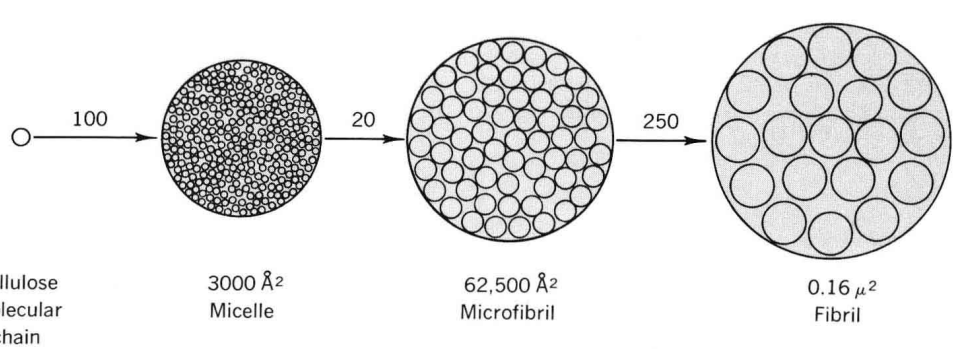
In a study of the wall composition of onion root tip cells, Jensen (*1960*) found that although cell walls of provascular cells were high in pectic substances and hemicelluloses, the cell walls of the cortex and protoderm were low in these compounds. It appears that although all of the common constituents of the cell wall are present in the primary wall, their relative concentrations vary in accordance with the type of cell under investigation.

Secondary wall As the cell matures, the cell wall thickens as layers of cellulose are laid down by the cytoplasm. The wall becomes much less flexible and, finally, almost inelastic. It is understandable, then, why cell elongation ceases with the onset of secondary wall formation. It is the secondary wall that gives the plant cell its structural independence.

By far the most conspicuous constituent of the secondary wall is cellulose. Cell wall layers laid down toward the latter stages of cell growth are, in many cases, almost pure cellulose. A familiar example is the cotton fiber where more than 90% of the wall dry weight is pure cellulose.

Molecular and macromolecular arrangement of cellulose in the cell wall The cell wall may be thought of as a finely interwoven network of cellulose strands of varying complexity and size. The association of molecular cellulose chains has recently been reviewed by Siegel (*1962*) and are as follows. The smallest structural units of the cell wall are the *elementary fibrils* or *micelles*. These so-called micelles are composed of approximately 100 individual cellulose chains and have a cross-sectional area of about 3000 Å^2. The next largest cellulose strand is the *microfibril*, which is thought to be composed of about 20 micelles and to have a cross-sectional area of about 62,500 Å^2 (Figure 1-3). Although the individual cellulose molecular chains cannot be observed even with the electron microscope, the micelles and microfibrils are clearly discernible under the electron microscope. Although accounting for only 20% of the primary wall volume, the microfibril is considered to be the basic structural unit of the cell wall (*Albersheim, 1965*). For example, removal of all noncellulosic material from the cell wall causes very little change in cell shape and most of the mechanical properties of the wall are retained.

An aggregation of about 250 microfibrils will compose a microscopic *fibril* with a cross-sectional area of 0.16 μ^2. A cotton

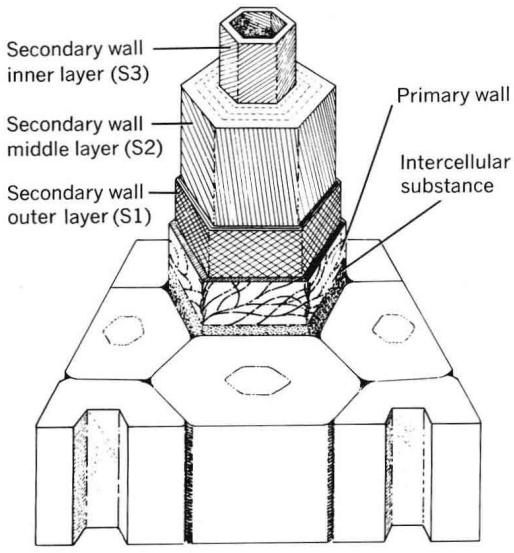


1-3 Diagrammatic representation of the association of molecular cellulose strands showing the approximate cross-sectional area.

fiber, which is visible to the naked eye, may have as many as 1500 fibrils. A little multiplication will show that there are as many as 7.5×10^8 individual molecular cellulose chains in one macroscopic cotton fiber.

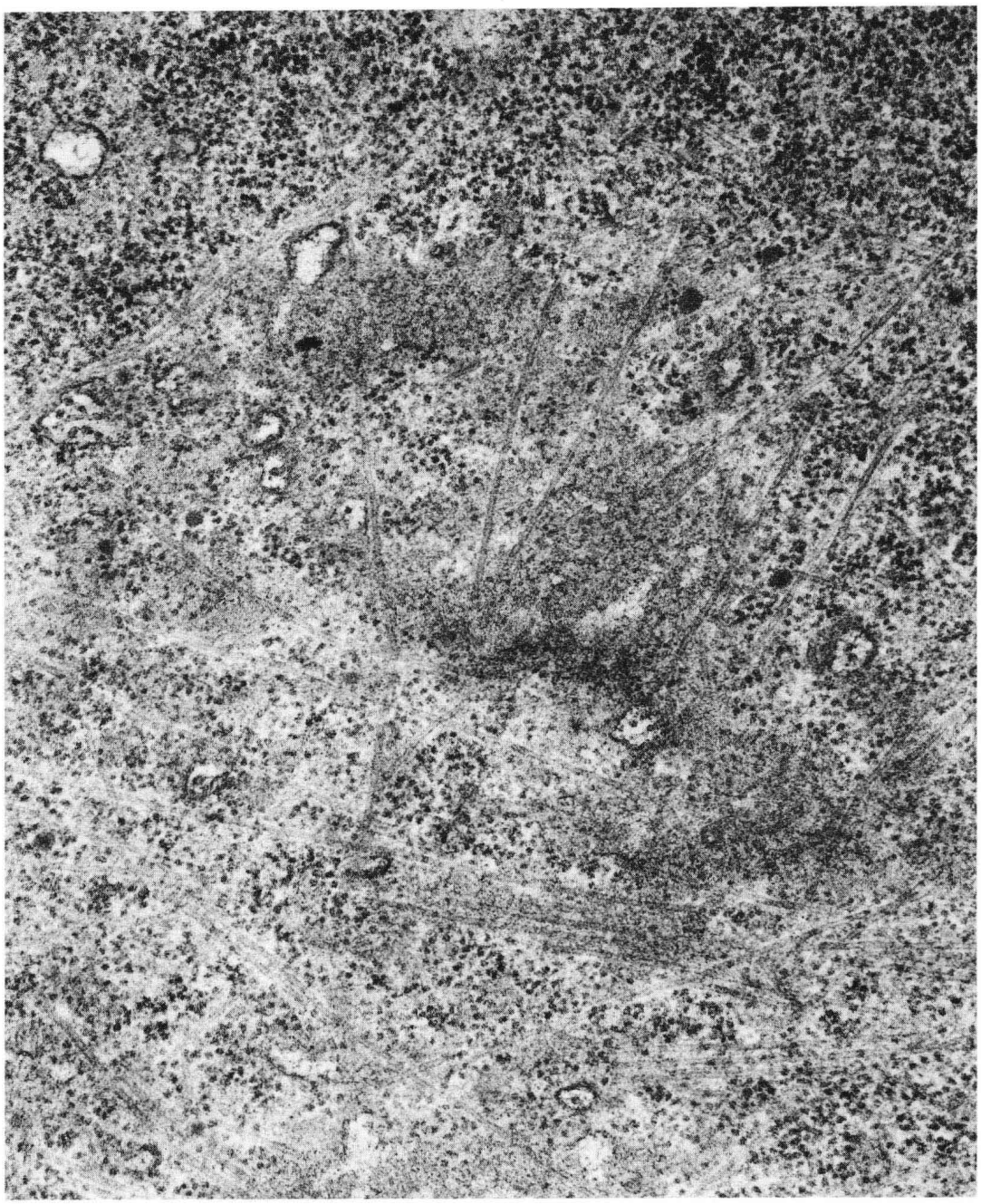
The physical organization of the microfibrils in the primary and secondary wall is quite different. In the primary wall the microfibrils run roughly transverse to the cell axis, but do show a longitudinal orientation at the cell corners. Three distinct layers have been distinguished in the secondary wall, each one having a different microfibril arrangement (Figure 1-4). For example, in the conifer tracheid wall one can distinguish five layers—the middle lamella, a thin primary wall, and a three-layered secondary wall. We can account, then, for nine layers of wall separating the cell cavities of two adjacent tracheids.

In Figure 1-4 two spirals of microfibrils may be seen in the outer layer of the secondary wall forming a rather large angle with the cell axis. In the middle section a steep spiral in addition to concentric rings of microfibrils can be observed. The inner layer is thought to have a flat helical arrangement (*see review by Wardrop and Bland, 1959*).



1-4 A cutaway view of the different layers of the cell wall showing the different arrangement of cellulose microfibrils in each layer. (After A. Wardrop and D. Bland. 1959. Proc. 4th Intl. Congr. of Biochem. Pergamon Press, New York. 2:76).

Site of synthesis Early investigators believed that wall synthesis took place at a distinct cytoplasm-wall interface. However, with the advent of the electron microscope, the consensus of opinion was that the cytoplasm actually penetrated the wall at different localities along the cytoplasm-wall interface (*Preston, 1955; Williams et al., 1955*). Wall synthesis, it was postulated, takes place in these isolated areas. Other investigators adopted a somewhat modified version of the above concept, that wall synthesis takes place where *plasmadesmata* (cytoplasmic strands) penetrate the wall (*Scott et al., 1956; Wardrop, 1958*). Still other investigators believe that the synthesis of microfibrils can take place throughout the wall at areas separate from the cytoplasmic surface (*Beer and Setterfield, 1958*). Apparently, all the precursors necessary for wall synthesis would move to these areas of wall synthesis, most likely through the mediation of plasmadesmata. Whaley, et al., (*1959*) have pointed out the probable importance of the extension of the endoplasmic reticulum to the surface of the protoplast in this respect. Many investigators have noted that microfibrils are laid down in parallel patterns, a circumstance that suggests the participation of related structures in the cytoplasm. Support for this suggestion was given by Ledbetter and Porter (*1964*) on their finding of *microtubules* in the cytoplasm of *Phleum* root cells (Figure 1-5). The microtubules are found very close to the cytoplasm-wall interface and are oriented parallel to the microfibrils laid down in the cell wall. At the present time evidence for the direct involvement of microtubules in microfibril synthesis is lacking. However, the location of microtubules at the cytoplasm-wall interface and their parallel orientation with microfibrils in the cell wall certainly allow



1-5 Electron micrograph of a section cut tangential to a transverse cell wall of a *Phleum* root cell. Numerous microtubules can be seen in the cytoplasm and they all lie in a plane parallel to the transverse wall. (Courtesy of M. C. Ledbetter, Brookhaven National Laboratory.)

for speculation that microtubules are directly involved in microfibril synthesis.

Cell Membrane

Although the cell wall to some extent separates the cell from its environment, it does a very inefficient job in this respect. Most materials in the immediate environment of the cell have no trouble passing through the cell wall. If the cell possessed no other barrier to the entrance of unwanted materials into its interior, life for the cell would indeed be hazardous. In fact, the living cell, as such, could not exist. However, directly adjacent to the interior wall and surrounding the protoplast is a thin, delicate, flexible structure called the *cell membrane* or *plasmalemma*. The importance of this structure to the living cell cannot be overemphasized. Since the membrane encloses the cytoplasm and cytoplasmic inclusions, we can say the membrane contains the living system and in a very real sense protects it.

The cell membrane performs the vital role of regulating the passage of materials in and out of the cell. In other words, the cell membrane is *differentially permeable*, allowing certain materials to pass into the cell but excluding others. In addition, the cell membrane provides only a one-way passage for certain materials into the cell and blocks their passage out. For example, certain essential mineral elements must be accumulated in the cell in higher concentrations than they are found in the cell's immediate environment. Also of major importance to the cell, the membrane blocks to a great extent the penetration of most toxic compounds into the cytoplasm.

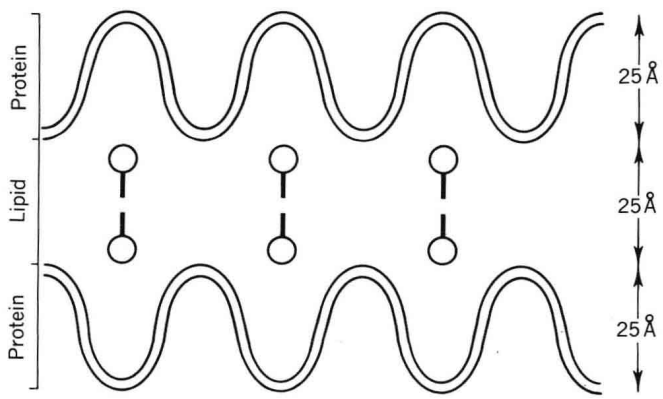
Because of the color similarity between the cell membrane and its cytoplasm, it is very difficult to separately distinguish the two under the light microscope. However, the cell membrane is very clearly shown as a structure separate from the cytoplasm by the electron microscope.

Chemical and physical analyses of the cell membrane suggest that it is a lipoprotein, having a bimolecular lipid center sandwiched between monomolecular layers of protein. Robertson (*1962*) has postulated that the total thickness of the membrane should be about 75 Å. A molecular model representing the cell membrane is given in Figure 1-6.

Inclusions of the Cytoplasm

Endoplasmic reticulum

The cytoplasm of the meristematic cell is interlaced by an elaborate membrane-bound vesicular system called the *endoplasmic reticulum* or *ergastoplasm*. The membranes bounding this system are thought to have a lipoprotein structure somewhat analogous to that of the cell membrane. Although maintaining its general appearance, the endoplasmic reticulum may be-



1-6 A molecular model of the cell membrane showing a bimolecular lipid center bordered by monomolecular layers of protein. (After J. Robertson. 1962. Sci. Am. 206(4): 64.)

come modified during development and during certain activities of the cell.

According to several observations, the endoplasmic reticulum is continuous with the nuclear membrane and extends to the cell surface (*Watson, 1959; Whaley, et al., 1960*). In fact, membranes of this system have been found in the primary walls of some cells and even extending to neighboring cells (*Whaley et al., 1959; Whaley et al., 1960*). Whaley et al. (*1959*) have pointed out that the inclusion of the nuclear membrane with the endoplasmic reticulum provides for extensive surface contact between nuclear material and the cell cytoplasm. Where some strands of the endoplasmic reticulum extend from one cell to the next, the nuclei of both cells may be said to be in direct contact with each other.

A three-dimensional view of the cell will show that the endoplasmic reticulum divides the cytoplasm into numerous small cavities. This compartmentalization of the cytoplasm has drawn a great deal of attention in recent years. Within these compartments certain enzymes and metabolites may be accumulated or excluded—a circumstance, perhaps, of vital importance to the cell. We will see in a later chapter, for example, that a reaction can be forced to move in a certain direction by overloading the system with a certain metabolite and excluding another. Although not completely explored by any stretch of the imagination, the importance of the endoplasmic reticulum to the general functioning of the cell has been fully appreciated.

Mitochondrion

With the possible exception of the nucleus, the *mitochondrion* has been the most studied component of the cell. As a result, our knowledge of the morphology and function of this cytoplasmic inclusion is quite extensive. We will concern ourselves at this time more with the morphology of the mitochondrion than with its function, which is covered in detail in the chapter on respiration.

Energy transfer in mitochondria Because a great deal of the cell's usable energy is provided by the mitochondrion, it is often referred to as the "powerhouse" of the cell. As might be expected, where cellular activity is high, mitochondria tend to accumulate. An example would be the meristematic cell where mitochondria are found in abundance. What is meant when we say mitochondria provide the cell with usable energy? When biological oxidations of proteins, fats, and carbohydrates occur in the cell, energy is released. This is somewhat analogous to the burning of paper or wood where energy is released in the form of heat. However, in the cell, and particularly in mitochondria, much of the energy released is conserved in the form of high-energy phosphate bonds. The most important compound in this respect is adenosine triphosphate (ATP). The advantage of storing energy in this compound is that it can be released and utilized quite readily to drive the energy-consuming reactions of the cell. ATP, then, is synthesized in mitochondria from where it is dispersed throughout the cell to energy-consuming areas.

Mitochondria morphology Let us now consider the structure of the mitochondrion, an area of study where the electron microscope has been a dominant factor. These pleomorphic (many forms) bodies are bounded by a double membrane, which encloses an inner matrix, and range in size from about 0.2 to 3.0μ. Numerous folds, which project deep into the matrix, occur in the inner membrane. Some of these folds have been observed completely bridging the interior of the mitochondrion and connecting with the inner membrane on the opposite side. These projecting folds of the inner membrane are collectively called the *cristae* (Figure 1-7).

The cristae of mitochondria have attracted a great deal of attention because of their