A TEXTBOOK OF

HISTOLOGY

By ALEXANDER A. MAXIMOW
Late Professor of Anatomy, University of Chicago

and WILLIAM BLOOM
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SIXTH EDITION

With 986 Illustrations, 257 in Color, on 580 Figures

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DERECHOS RESERVADOS CONFORME A LA LEY
PARA LA REPUBLICA MEXICANA

PREFACE TO THE SIXTH EDITION

The intent of this book now, as it was when begun twenty-six years ago by Professor Maximow, is to present a morphological and functional description of the minute structure of the human body.

As with all sciences during this quarter century, histology has undergone marked changes. When this book first appeared, morphological and biochemical endocrinology, electrical and biochemical neurology, and the histochemical and biophysical study of the submicroscopic structure of protoplasm were just entering an era of intense activity and significance.

The progressively rapid rate of increasing knowledge is producing many specialized facets of histology which are beyond the ken and competence of one person. It is accordingly a relief to me to be able to place the responsibility for some parts of this book largely on Professors P. P. H. DeBruyn, W. L. Doyle and I. Gersh. However, I have retained such final responsibility for the text as is required to promote unity, and to maintain it a textbook for medical students with the hope that it avoids becoming a series of specialized monographs.

Large sections of the book have been rewritten, and there are marked changes in content and illustrations and, in places, in point of view. Professor Doyle has written a new introductory chapter to correlate the submicroscopic, biochemical and enzymatic constitution of cells with their structure and function as determined with the optical microscope. He has also revised the discussion of renal function.

Professor DeBruyn revised and shortened the chapters on blood, connective tissue, blood formation and destruction, lymphatic system and spleen. His most important change has been to bring into the chapter on connective tissue most of the material dealing with inflammation and the macrophage system. He has also moved the discussion of the origin of connective tissue fibers to this chapter. The chapter on the thymus has been placed after that on the spleen.

Professor Gersh has written new descriptions of the endocrine glands (except the pineal). In expanding this material he has made a separate chapter for each gland. In these chapters and in those on the "target" organs he has included new illustrations showing endocrine effects. He has also revised and expanded the chapters on epithelium and glands.

To include new developments in the science I have shortened most of the chapters without deletion of essential material, particularly those on the eye, ear, male and female generative systems, nervous tissue, skin, muscle, and the digestive tract except the teeth. Few changes have been made in the descriptions of the respiratory portion of the lung (revised by Professor Loosli for the last edition) and the mammary gland. In many places, material previously in small type is now in large type.

For aid in revising the nervous tissue I am greatly indebted to Professor Patrick Wall, who made many helpful criticisms and suggestions. In response to many requests I have included several low-power photomicrographs of the central nervous system. Professor W. H. Taliaferro has revised the discussion of the physiology of the spleen. Professor F. C. McLean, as in previous editions, has contributed to the revision of the chapter on bone, and my wife has rewritten the chapter on cartilage from a more functional point of view.

There are four new colored plates by Mrs. E. Bohlman Patterson, one each in chapters I, IV, VII and XV. Seventeen photomicrographs in color are from the new atlas of von Herrath and Abramow, published by the G. Thieme Verlag. There are five new electron micrographs and several new photomicrographs by phase contrast. In addition, forty-six new photomicrographs were taken by Mr. Jean Crunelle. Abbreviations have been replaced by spelling out the labels on several of the figures, of which the most important are the two color plates showing the development of bone marrow cells.

I have been favored and assisted by suggestions, corrections and criticisms from many histologists here and abroad. In this place I cannot thank all who have contributed in this way to this revision, but among them I am particularly indebted to Professors M. Block, D. Bodian, R. G. Murray, I. Schour and J. W. Wilson.

WILLIAM BLOOM

April, 1952

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ACKNOWLEDGMENTS FROM PAST EDITIONS

FROM THE FIRST EDITION

At the time of his death in December, 1928, Professor Maximow was writing a Text-book of Histology. This was to be based as far as possible, both as to text and figures, on human material, and the functional aspects of the structures described were to be emphasized. For this work he had collected much new material and had made many new illustrations. He had completed the sections on the male and female generative organs, the urinary tract, the organs of special sense, and epithelium. In rough manuscript he left the sections on the blood and connective tissue, the gastro-intestinal tract, the blood vascular and lymphatic systems, the spleen, the integument, and the mammary gland.

None of the chapters on the Nervous Tissue were written by Professor Maximow in their present form. His papers included some notes and drawings which were helpful in a general way as indicative of the line of treatment contemplated. There was also available the Russian text of 1918 in which the nervous tissues are treated very fully. A complete translation of these Russian chapters and the notes and drawings were placed in the hands of Professor Maximow's colleague, Professor C. Judson Herrick, and these served as the basis upon which the present text was written. . . . These chapters, accordingly, are to be regarded not as a posthumous publication, but as an entirely new formulation of the theme, the responsibility for which rests chiefly with Professor Herrick.

I am indebted to Dr. N. Hoerr for writing the description of the suprarenal bodies.

I have written the sections on the biliary and respiratory systems, the pancreas, the endocrine glands (with the exception of the suprarenals) and the introductory chapter. In all of these sections I have conformed, in general, with Professor Maximow's ideas on these subjects. In addition, I have thoroughly revised the sections on cartilage, bone and muscle, which were based on translations of parts of his Principles of Histology (Russian), and his rough manuscript on the blood vascular and lymphatic systems, the spleen, integument, mammary gland, gastro-intestinal tract, the blood, connective tissue, and the blood-forming and destroying tissues.

Throughout the work of editing and completing this book I have profited greatly by frequent consultations with Professor Bensley.

FROM THE FOURTH EDITION

The obtaining of very early implantations of chimpanzee and human ova makes it possible to include a brief description of the early stages of human placentation. Professor G. W. Bartelmez has generously contributed this new material and also a thorough revision of the rest of the chapter dealing with the female generative system.

With each revision of this book I am encouraged to face the enormous literature by the liberal help which I have received from friends and colleagues in various biological fields. I am indebted to Professor R. R. Bensley for revising the section on protoplasm, to Professor S. W. Becker for some of the changes in the chapter on the skin, to Professor E. A. Boyden for extending the description of the biliary passages, and to Professor E. M. K. Geiling for aid with the chapter on the endocrine glands. Professor S. Polyak has revised the chapters on the nervous system and the eye and has omitted some of the details of both chapters, espe-

cially of the latter. The appearance of his monograph on the retina makes it unnecessary to have the description of this structure as detailed as it was in the previous edition. Professor W. H. Taliaferro has contributed to the discussion of the macrophages and the spleen. Dr. E. Conway Mahon has helped in the revision of much of the text.

FROM THE FIFTH EDITION

Professor William L. Doyle has revised the section on protoplasm and written most of the discussion of its submicroscopic organization. Professor Clayton G. Loosli has recast the description of the respiratory portion of the lung. The chapter on bone has been rewritten in collaboration with my co-worker in this field, Professor Franklin C. McLean. Professors Peter De Bruyn, Eugene M. K. Geiling, Ralph W. Gerard, Franklin C. McLean and William H. Taliaferro and Dr. Roy Grinker made many helpful suggestions for other topics.

The treatment of the hemopoietic tissues has been abbreviated and fairly extensive changes made in the sections on muscle and the endocrine glands. I have condensed parts of the chapter on the nervous tissue which was prepared for the last two editions by Professor Stephen Polyak. I have also rewritten much of the chapter on the female generative system. This chapter was revised in previous editions by Professor George W. Bartelmez, who contributed a description of early human placentation to the fourth edition.

William Bloom

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I. INTRODUCTION

Histology is concerned with the structural characteristics of the cells and tissues of living organisms and with the relationships of their structure to function. It involves the organization of cell types into tissues which have characteristic intercellular environments, and deals with the contributions of the various tissues to the formation of organs. Most of the basic information has been obtained by observation of living or preserved specimens with a microscope.

Although the microscope has been used for nearly 300 years for the study of minute anatomy, modern histology began with an outburst of investigation in the third and fourth decades of the nineteenth century and received its greatest impetus from Schwann's conclusion that nucleated cells are the basis of the formation of all animals and plants. His idea was received with great enthusiasm "because it gave the key to a multitude of known facts and the direction for new, planned investigations" (Henle, 1841).

The succeeding century of intensive histological investigation may be divided into several fairly distinct periods, each with different immediate aims and philosophies. But the entire history has been characterized by the desire for further knowledge of the origin and function of the parts of animals and plants as evidenced by minute structure.

As most tissues and organs are too thick to be examined directly with the microscope, the histologists of a hundred years ago examined thin membranes and scrapings and teasings of thick organs. These teasings disrupted topographic relations, and the cells soon died. With their imperfect microscopes and with the aid of only a few reagents, such as acetic acid, it seems remarkable that the histologists saw as much as they did.

The study of living and surviving cells was replaced to a large extent during the next fifty years by the investigation of details made visible in dead cells through the introduction of methods for the preservation of tissues, cutting them in thin slices and staining them with a variety of dyes. Such studies were made possible by great improvements in microscopes and microtomes and a host of "fixing" and staining methods. During this period there was accumulated a great mass of descriptive embryological, histological and histopathological data. Basic processes in the life history of the unicellular and multicellular organisms were recognized, such as their modes of reproduction, and the occurrence of growth, multiplication, differentiation and death of cells.

About the turn of the century a new period began, characterized by attempts at interpretation of structure in terms of function and by renewed interest in correlating living and dead appearances. As one of the results of

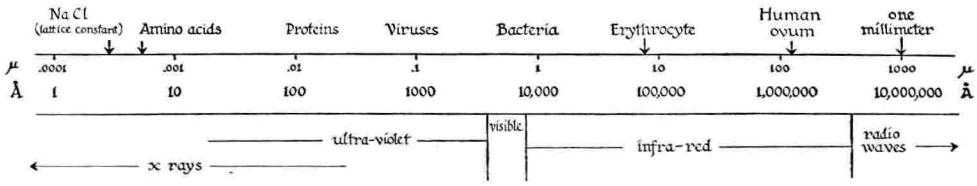

Fig. 1. Comparison of dimensions of molecules and cells with wavelengths of various radiations. Logarithmic scale. (Courtesy of A. B. Hastings, T. Young and J. B. Hoag.)

this study, a number of investigators began to look on all sectioned material as artefact and to accept as true only what could be seen in living cells. This view was soon modified, because some of the so-called artefacts of fixation have been shown to be important components of living cells. On the whole, however, the skeptical period has caused the histologist to realize that he must use all the methods of investigation, that all of them together are insufficient, and that new ones must be developed. Out of this era several significant methods of cell study developed, such as tissue culture, transplantation to foreign tissues, including the anterior chamber of the eye, the use of transparent windows in rabbit ears, and micromanipulation devices.

Today, newer methods in histology, recognizing the advances in physiology and biochemistry, are concerned with a more precise description of structure in terms of chemical composition and biochemical activities, and with the exploitation of new physical instruments capable of revealing finer structural details.

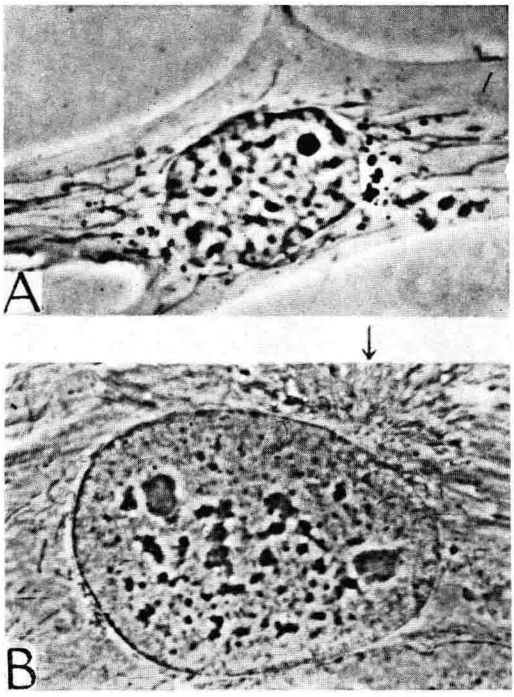

Fig. 2. Phase-contrast photomicrographs of newt cells in tissue culture. A, Outstretched macrophage; the largest nuclear body is the nucleolus; long mitochondria are prominent in the cytoplasm. B, Portion of fibroblast, showing nucleoli and chromatin particles in the nucleus. The arrow points to the concentration of mitochondria about the clearer cytocentrum adjacent to the nucleus. 900 ×. (Courtesy of L. Wang.)

The Microscope. With the aid of an optical microscope one can distinguish objects as individual particles if they are not less than 0.2 micron apart. The resolving power of a microscope is dependent on the wavelength of the light and the light-gathering capacity (numerical aperture) of the objective. The best oil immersion objects have a numerical aperture of 1.4, but most histological work is done with lenses of numerical aperture 1.0 or less. By reducing the wavelength of light it is possible to increase the resolving power of the microscope to 0.1 micron with ultraviolet light. Particles smaller than the limit of resolution can be seen by the light reflected from them in dark-field illumination of the ultramicroscope, but it is not possible to determine their dimensions or shape precisely. From Figure 1 it can be seen that it should be possible to photograph individual molecules, provided one uses wavelengths which are sufficiently short and lenses with sufficiently high numerical apertures. As appropriate instruments are developed, the field of histology will merge more closely with that of structural chemistry. Electron beams have much shorter wavelengths than light, and magnetic lenses have been developed so that, at 100 kilovolts, a resolution of 30 angstrom units is achieved. With this resolving power the morphology of virus and protein molecules can be viewed directly on the fluorescent screen of the electron microscope or photographed.

The light microscope has also been improved by the development of phase-contrast microscopy. Most colorless structures embedded in colorless protoplasm, unless they are highly refractile, are seen indistinctly, if at all. If these structures are of different refractive index from that of protoplasm, the phase-contrast device provides differences in light intensity which reveal the structures. (See Figures 2, 3 and 11.)

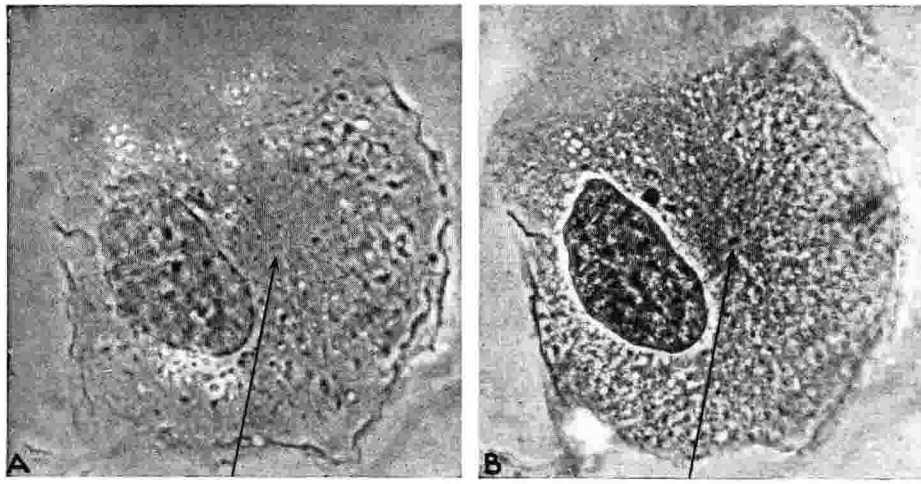

Fig. 3. Photomicrograph by phase-difference microscopy of a macrophage of newt in tissue culture. A, Before fixation; B, same cell in 95 per cent alcohol thirty four minutes after fixation in Zenker-formol. The arrows point to the centrioles. 800 ×. (After Buchsbaum.)

CELL STRUCTURE

Protoplasm. Although special techniques of tissue culture and microdissection permit the study of living tissue, the great mass of work done in both normal and pathological histology is based on preserved material which has been appropriately stained. Figure 3 demonstrates that much of the structural appearance of the living cell can be preserved by appropriate treatment. The more stable elements of cell structures are quite well preserved by a variety of procedures, and the stains hematoxylin and eosin reveal them in a manner which is easily reproducible in any laboratory. Accordingly, these procedures have become standardized for most medical teaching and pathological studies.

To appreciate the action of preservatives and stains on biological material, it is necessary to have some understanding of the nature of the living substance—protoplasm. For reasons which are not obvious, protoplasm in higher organisms characteristically occurs in the form of cells which are bounded by a so-called *plasma* or *cell membrane* and which contain a subdivision, the *nucleus*, bounded by a *nuclear membrane*; the material in which the nucleus is embedded is the *cytoplasm* (Fig. 4). The plasma membrane regulates the interchange of materials between the cell and its environment. The nature of the invisible surface membrane of the cell is still in doubt. This membrane, estimated as 100 to 200 angstrom units thick, is usually described as differentially permeable; that is, the membrane acts selectively, in unknown fashion, to permit the accumulation within the cell of some solutes and not of others. The extensive body of knowledge dealing with this topic has been thoroughly reviewed by Davson and Danielli and by Höber et al.

By microdissection it has been determined that the cell membrane is somewhat resistant and highly elastic and that, when it is destroyed at one point on a cell, a new membrane is soon formed from the cytoplasm.

Between the nucleus and the cytoplasm is another membrane, called the nuclear membrane (Fig. 4). By microdissection it has been shown that the nuclear membrane is quite tough and slightly elastic, and that, when it is punctured, the nuclear content may run out, although nuclei usually "set" as a viscous gel when they are injured. Electron micrographs of a nuclear membrane reveal a thicker structure (400 angstrom units) with the appearance of regularly arranged pores.

Taking the cytoplasm as typical protoplasm, we find that it has a consistency which may vary from that of a liquid to a rather firm gel. It presents the appearance of an optically clear (hyaline) continuous sub-

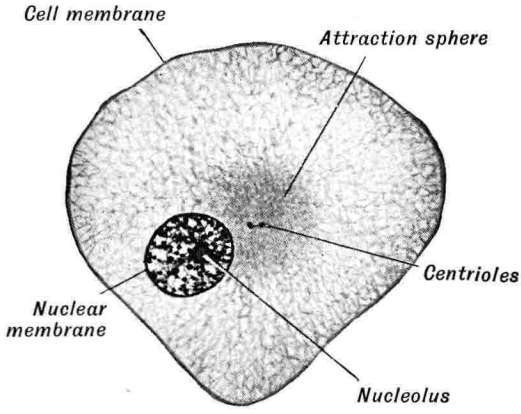

Fig. 4. Interstitial cell from the ovary of a rabbit. Iron-hematoxylin stain. 1300 ×. (A.A.M.)

stance in which certain visible particles are embedded. Many of these are products of cell activity, but others, such as *mitochondria* (p. 14), are to be regarded as organelles of the cell. The chemical composition of protoplasm is properly the domain of biochemistry, but certain aspects are essential to a consideration of structure.

Composition. As the cell may be considered to be an organized set of systems in dynamic equilibrium with their environments, it is not surprising that many of the common chemical elements are to be found in protoplasm. The human body has the following percentage composition on a fresh weight basis: oxygen, 65; carbon, 18; hydrogen, 10; nitrogen, 3; calcium, 2; phosphorus, 1.1; potassium, 0.35; sulfur, 0.25; sodium, 0.15; chlorine, 0.15; magnesium, 0.05; iron, 0.004. In addition to these, traces of two dozen or so other elements normally found in living organisms are vital to life. However, on the basis of the number of molecules and ions present, a table of the composition of the body would have a different aspect; thus there are 1.7 times more hydrogen atoms in the body than all the other atoms put together.

An analysis of protoplasm reveals the presence of water, inorganic ions and innumerable naturally occurring organic compounds, some of which may be broadly classed as proteins, carbohydrates, lipid substances, their combinations, their constituents and their precursors. Preeminent in the architecture of cells are the proteins.

Some proteins vary from one cell type to another and are specific for organ and species. Other proteins seem to be of common occurrence. Important constituents of nucleus and cytoplasm are the nucleoproteins (p. 7). Carbohydrates occur in animal cells as glycogen and its hydrolytic products and also combined with proteins and lipids. Intracellular fats vary from minute droplets of neutral fats in many types of cells to large accumulations in the fat cells which are specialized for the storage of these substances. Although more complex lipids such as sterols and phosphatides are widely dispersed in cells, they are only rarely demonstrated by visual means.

Protoplasm contains much potassium, little sodium, small amounts of magnesium, and even less calcium; the heavy metals are present in traces. Of the anions, bicarbonate and phosphate predominate; chloride is present in small amounts if at all, except in red blood cells. This contrasts strongly with the body fluids, in which sodium salts, especially the chloride, predominate (Figs. 5 and 30).

Extracellular and Intracellular Phases of Tissue. The chemical composition of different tissues from the same animal or of the same tissue from different animals differs widely, and it is surprising that any deductions of biological significance can be made from chemical analyses. The distribution of materials extracellularly and intracellularly has been described by Hastings as follows: Quantitative analyses of various tissues were made for water, hemoglobin, fat, total protein, collagen, elastin, chloride, bicarbonate, phosphate, magnesium, calcium, potassium and sodium. For a relatively homogeneous tissue, such as muscle, heart or liver, by expressing analytical results on a fat-free, blood-free basis, by assuming that chloride is extracellular and that its concentration in extracellular fluid is equal to that in blood plasma, save for a small correction due to the Donnan equilibrium, it is possible to calculate the following: (1) the proportions of the tissue that constitute the extracellular and

intracellular phases (extracellular phase = extracellular fluid plus collagen and elastin; intracellular phase = intracellular fluid plus intracellular proteins); (2) the ionic composition of the extracellular fluid (this can be fairly completely specified); (3) the concentration of certain constituents of intracellular fluid. Further analytical studies are needed in order to complete the ionic composition of intracellular fluid.

Figure 5 is a graphic interpretation of analytical data obtained on the skeletal muscle of the dog. Concentrations in milliequivalents per kilogram of water are plotted vertically; amounts of intracellular and extracellular solids and fluids are plotted horizontally. The points of interest are (1) The extracellular solids (cross-hatched area) plus extracellular fluid (clear areas) comprise about 17 per cent of the muscle mass. (2) The extracellular fluid has an ionic composition nearly like that of blood plasma. Note that it is rich in sodium, chloride and bicarbonate, and low in potassium, calcium and magnesium. (3) The intracellular phase amounts to about 83 per cent. The water concentration of the intracellular phase is 75 per cent and remains remarkably constant. (4) The principal cations of the intracellular fluid are potassium and magnesium, and the principal anions are protein and organic phosphates. Under normal conditions the intracellular fluid contains little sodium and practically no chloride. The intracellular concentration of the bicarbonate radical is only about one third that of extracellular fluid, and from this the intracellular *p*H has been calculated to be about 6.8.

In view of the freedom with which potassium exchanges between extracellular and intracellular fluids, the maintenance of a thirty-fold gradient of potassium between these two fluids requires a fuller explanation than is as yet available. The opinion, recently current, that this gradient depends upon a pumplike mechanism which uses part of the energy derived from the metabolism of the cell, is now being displaced by the belief that the high concentration of potassium in the muscle fiber may be derived as a consequence of the Donnan equilibrium plus a specific affinity between potassium and myosin. (See also page 150.)

The data for skeletal muscle are similar, though quantitatively slightly different, for

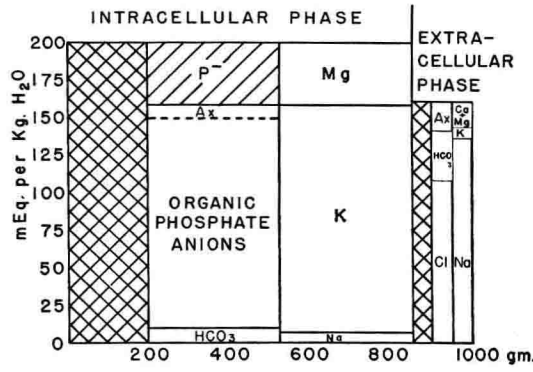

Fig. 5. Diagram of constitution of skeletal muscle. Concentrations in milliequivalents per kilogram of water are plotted vertically; amounts of intracellular and extracellular solids and fluids are plotted horizontally. The solids are represented as cross-hatched areas and the fluids as clear ones. For details, see text (p. 4, 5). (Courtesy of A. B. Hastings.)

heart muscle and liver. A similar treatment of analytical data obtained on brain and kidney is not practical, owing to their heterogeneous nature.

Chemical Architecture. It is frequently stated that protoplasm is a complex colloidal system which provides a variety of interfaces and phase boundaries at which biochemical reactions take place. But such a concept is hardly adequate in view of the degree of integration of the activities which is present in living systems. It has therefore been postulated that cells have some kind of macromolecular skeleton which provides numerous surfaces of highly specific configuration arranged as a more or less continuous phase permeated by components in true solution. If there is such a "cytoskeleton," it would have to be in dynamic equilibrium with the more fluid continuous phase. In a sense the architecture of the cell is that of a factory carrying out certain processes in connection with specialized structures, but it is a factory in which the raw materials, the machinery and the end products are continually inter-

changing. At one moment an amino acid molecule may be considered a potential source of food, and at another moment it may be incorporated in a protein of the metabolic machinery.

The use of isotopic tracers has led to the view that cellular structures and their chemical reaction systems are in dynamic equilibrium with an intracellular pool of metabolites composed of many small organic molecules. Thus the significance of the classical distinction betwen endogenous metabolism and exogenous metabolism disappears (Schoenheimer).

Enzymes. In the transformation from food substance to constituents of living protoplasm and in the numerous metabolic processes furnishing energy, a fundamental component of each of the mechanisms is the *enzyme* which catalyzes the reaction. Now the variety of systems which operate simultaneously in a single cell appears to be relatively large compared to the number of distinct morphological structures which we can distinguish optically. Furthermore, since in many metabolic reactions there must be a coupling between the energy-producing (*exergonic*) oxidative reactions and the energy-using (*endergonic*) synthetic processes, some sort of structural organization, such as a "cytoskeleton," is required to compartmentalize the processes. This concept of a cytoarchitecture is compatible with the observed specificity of many enzymes. Among the more important groups of enzymes are those catalyzing *oxidations, reductions, hydrolyses* and *phosphorylations*; esters are split by *esterases* and peptide bonds by *peptidases*, and so on. It may be assumed that reversal of the hydrolytic processes is frequently accompanied by (coupled to) exergonic reactions.

Owing to the remarkable specificity of many enzymes, it is not always necessary that there be a compartment for each reaction, if that were in fact possible. The oxidation of carbohydrates, for example, involves the stepwise conversion of one compound into another in a sequence of reactions each of which is catalyzed by an enzyme specific for that step. By introducing the initial compound into an appropriate solution containing three purified enzymes, one may observe that the highly specific end product of the third reaction is produced as well as if its immediate precursor had been supplied. This sequential organization of processes without benefit of any structure has been termed by Dixon "organization by specificity," and this concept is of major significance for an understanding of the physiology of protoplasm.

Several qualitative histochemical methods have demonstrated the presence of particular enzymes, notably *phosphatase*, within cells and tissues. In a few instances, quantitative studies have also been made (Figs. 236, 359). It is, however, difficult to deduce the physiological role of the enzymes from their localization in relatively high concentration (cf. Danielli). Actually, the demonstration of a spatial correlation between morphological units and chemical mechanisms involves difficulties of practical and theoretical nature. A large literature of circumstantial evidence relating the configuration of cellular structures to processes significant in particular tissues is accumulating rapidly. (See reviews by Dempsey and Wislocki; Moog.) It is also evident from the biochemical differences observed between the metabolism of tissue slices, minces and extracts that certain processes are inactivated (and others initiated) when cellular organization is disrupted. Only after suitable precautions may the structural elements be isolated in more or less intact condition for examination of their chemical mechanisms.

In multicellular animals, and more particularly in the higher forms, many cells are specialized for the execution of particular functions. These may be classified as dealing primarily with (1) the *vegetative existence* of the cell, (2) its *growth* and *reproduction*, and (3) its *special functions*. The vegetative activities of the cell, defined as the minimum of activities necessary for its continued existence, are concerned chiefly with its energy metabolism (or respiration), with the assimilation of food and the elimination of waste materials.

The processes by which energy is released

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