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Elements of CYTOLOGY

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PREFACE

THE cell is the fundamental unit of structure and function in a living organism. Yet recent advances in cytology have shown that particular constituents of the cell have specialized biological roles. Consequently, in contemporary experimental cytology, the cell is reduced to its component parts, which are then studied in great detail with new techniques and instruments. The subcellular particles, however, have no real independence in the general scheme of biological activity, as Laurence Picken points out: *

> The proper attitude is to accept the cell as given, as an organism. At its own level of organization it is a unity; and it remains a unity, though with our analytical mental equipment we conceive it more easily as a plurality of discriminated organelles. Those attributes of the whole unit which we are always seeking to project into its components are only true *of the whole,* no matter how far we succeed in resolving the unit into smaller and smaller components.

Cytologists today are not content with a mere identification and description of a cell and of cellular components and activities. These are meaningful only when related to the heredity, physiology, and development of the whole organism. Emphasizing the experimental evidence for the interdependence of genetics, biochemistry, and development by indicating how cytology links certain aspects of these sciences, this approach to the study of cytology is thus contemporary rather than historical, although constructed on a morphological basis. The critical and significant achievements of cytologists from the seventeenth century to the present are treated in a summary. Providing a comprehensive, balanced survey of the field of cytology for the undergraduate or graduate student and stressing the dynamics of the discipline by introducing the reader to the experimental literature, the presentation meets the needs of both the student with only a basic background in biology and chemistry and the advanced student.

The text is divided into three parts, The Cytoplasm, The Nucleus, and Nucleocytoplasmic Relations, which are further divided into short chapters dealing with specific cellular components or cellular behavior. This arrangement permits an instructor to adapt the subject matter to

* *The Organization of Cells,* Oxford Univ. Press, London, 1960, p. 164.

his class requirements. A list of references for further reading follows each chapter.

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NORMAN S. COHN

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SUMMARY OF HISTORICAL EVENTS

We shall not cease from exploration
And the end of all our exploring
Will be to arrive where we started
And know the place for the first time.
——T. S. ELIOT, *Four Quartets*

1590

Z. JANSSEN and H. JANSSEN produced the first operational compound microscope.

1661

M. MALPIGHI (1628–1694) discovered capillaries; confused blood corpuscles with fat globules; suggested cells when referring to "utricles" and "saccules."

1665

R. HOOKE (1635–1703), first curator of the Royal Society of London, described cork and other cells; introduced the term *cell;* published *Micrographia.*

1674

A. VAN LEEUWENHOEK (1632–1723) improved microscope lens systems by grinding; observed sperm, bacteria, and protozoa; observed, but did not identify, nuclei in blood cells.

1682

N. GREW (1641–1712) described bladders and pores in wood and pith; published two illustrated volumes on the microscopic anatomy of plants.

1759

C. F. WOLFF (1738–1794), founder of embryology, made reference to "little globules which may be distinguished under a microscope."

1809

J. B. LAMARCK (1744–1829) stated the importance of the cell in the living organism.

1823

J. B. AMICI (1784–1860) observed the development of the pollen tube.

1824

R. J. H. DUTROCHET (1776–1847) separated cells of *Mimosa* by boiling in nitric acid; "All organic tissues are actually globular cells . . . united only by simple adhesive forces."

1825

F. V. RASPAIL (1794–1878) used iodine for the detection of starch; developed the frozen-section technique; beginning of cytochemistry.

1828

R. BROWN (1773–1858) observed what is known as the Brownian movement.

1830

AMICI observed the entrance of the pollen tube into the ovary.

1830–1837

J. E. PURKINJE (1787–1869) studied the anthers of flowering plants, the oöcyte nucleus of the hen's egg, and ciliary movement; introduced the term *protoplasm;* used microscopes with a resolution of just under 1 micron.

1833

BROWN discovered the cell nucleus in a flowering plant.

1835

H. VON MOHL (1805–1872) described cell division and emphasized the importance of protoplasm.

1838

M. J. SCHLEIDEN (1804–1881) observed nucleoli; provided an explanation of the cellular derivation of plant tissues; formulated the cell concept, although with erroneous views.

1839

T. SCHWANN (1810–1882) applied the cell concept to animals.

1845

A. DONNÉ (1801–1878) studied spermatozoa, using photomicroscopy for the first time, with L. FOUCAULT.

1846

K. NÄGELI (1817–1891) showed that plant cells arise from the division of pre-existing cells.

AMICI showed that the egg in the ovary is stimulated to develop into an embryo by the entrance of the pollen tube.

1849

W. HOFMEISTER (1824–1877) studied nuclear division in *Tradescantia* stamen hairs; observed fertilization.

1855

R. VIRCHOW (1821–1902) confirmed the principle that cells arise only from pre-existing cells ("Omnis cellula e cellula").

1858

VIRCHOW published *Cellular Pathology,* showing the importance of the cell in disease and cancer.

1865

G. MENDEL (1822–1884) developed the fundamental principles of heredity (rediscovered independently by CORRENS, DE VRIES, and TSCHERMAK in 1900).

1867

L. ST. GEORGE discovered what was later called the *Golgi apparatus.*

1870

W. HIS (1831–1904) invented the microtome.

1871

F. MIESCHER (1844–1895) isolated nuclei and nucleoprotein.

1873

H. FOL (1845–1892) described spindle and astral rays.

1876

O. HERTWIG (1849–1922) studied reproduction in the sea urchin; concluded that fertilization involves the union of sperm and egg nuclei.

1877

E. ABBE (1840–1908) produced oil immersion objectives with a resolution of 0.25 micron.

1879

FOL showed that only one sperm enters the egg in fertilization.

1881

E. G. BALBIANI (1825–1899) discovered larval salivary gland chromosomes in *Chironomus.*

1882

W. FLEMING (1843–1915) proposed the term *mitosis;* showed that chromosomes split longitudinally during nuclear division, and formation of daughter nuclei; refined techniques of fixation and staining; suggested a correlation between *chromatin* and nucleic acid.

1883

E. VAN BENEDEN (1845–1910) showed that in *Ascaris* the number of chromosomes in the gametes is half that in the body cells.

W. ROUX (1850–1924) proposed that the chromosomes contain the units of heredity.

1884

E. STRASBURGER (1844–1912) described fertilization in angiosperms.

1886

R. ALTMANN (1852–1901) stained the granular components of the cytoplasm (including the mitochondria) and suggested that they have a role in cellular respiration.

ABBE developed apochromatic lenses.

1887

VAN BENEDEN discovered the central body and indicated that it is the origin of the aster.

1888

T. BOVERI (1862–1915) described the centriole.

W. WALDEYER (1836–1921) introduced the term *chromosome*.

STRASBURGER showed that when gametes are formed the chromosome number is halved in the cell divisions preceding pollen grain and embryo sac formation.

1892

A. WEISMANN (1834–1914) indicated the importance of the germ plasm as independent from the body cells and as the only carrier of inherited variations, in his theory of "continuity of the germ plasm"; stated that the chromosomes are the most important part of the nucleus.

BOVERI described meiosis in *Ascaris*.

1898

C. GOLGI (1844–1926) described the Golgi apparatus in nerve cells.

1899

C. BENDA discovered and named the mitochondria in spermatozoa and other cells.

1900

C. GARNIER introduced the term *ergastoplasm*.

K. E. CORRENS, H. DE VRIES, and E. TSCHERMAK rediscovered the fundamental principles of heredity, first developed by MENDEL in 1865.

1901

DE VRIES (1848–1935) postulated the occurrence of mutations in hereditary material in his work with *Oenothera*.

STRASBURGER introduced the term *plasmodesmata*.

1902

C. E. MCCLUNG (1870–1946) identified the sex chromosomes in *Hemiptera*.

W. S. SUTTON (1876–1916) showed the significance of reduction division proposed the chromosome theory of heredity.

1903

E. BUCHNER received the Nobel Prize for discovery of the first enzyme.

BOVERI showed the importance of the chromosomes in development.

1904

MEVES demonstrated the presence of mitochondria in plant cells.

1905

J. B. FARMER coined the term *maiosis* (meiosis) with J. E. MOORE.

1907

R. G. HARRISON developed techniques for growing tissues in culture.

1909

F. A. JANSSENS indicated that chiasmata are produced by exchanges between chromatids of nonhomologous chromosomes.

1915

T. H. MORGAN (1866–1945) published *The Mechanism of Mendelian Heredity;* correlated genetic studies with cytological studies in *Drosophila.*

1920

A. F. BLAKESLEE discovered trisomics in *Datura.*

1921

C. B. BRIDGES observed triploid intersexes in *Drosophila.*

1923

BRIDGES discovered duplications, deficiencies, and translocations.

1924

FEULGEN and H. ROSSENBECK described a test for the presence of DNA.

1926

A. H. STURTEVANT discovered inversions.

1927

H. J. MULLER studied the production by X rays of mutations in animals.

1928

J. STADLER studied the production by X rays of mutations in plants.

1931

STERN presented cytological proof of crossing over in *Drosophila.*

H. B. CREIGHTON and B. MCCLINTOCK presented cytological proof of crossing over in corn.

1932

M. KNOLL and E. RUSKA produced one of the first electron microscopes.

1935

F. ZERNICKE introduced the principle of phase-contrast microscopy.

1938

T. CASPERSSON began development of ultraviolet photomicrography for the study of nucleic acids.

1944

O. T. AVERY, C. M. MCLEOD, and M. MCCARTY showed the significance of DNA as the hereditary material by studies of transformation in bacteria.

1946

MULLER received the Nobel Prize for work in radiation genetics.

1948

A. BOIVIN, R. VENDRELY, and C. VENDRELY showed the quantitative constancy of DNA in different cells of the same organism.

1952

R. BRIGGS and T. J. KING made nuclear transplants in embryonic studies and showed the importance of nuclei in differentiation.

1953

J. D. WATSON and F. H. C. CRICK proposed a model for the DNA molecule.

1956

S. OCHOA succeeded in the in vitro synthesis of polyribonucleotides.

A. KORNBERG demonstrated the in vitro synthesis of polydeoxyribonucleotides.

P. I. MARCUS, S. J. CIECIURA, and T. T. PUCK developed methods for growing human cells in culture.

1958

G. W. BEADLE, E. L. TATUM, and J. LEDERBERG received the Nobel Prize for work in the field of genetics.

1959

F. SANGER received the Nobel Prize for determination of the amino acid sequence in insulin.

OCHOA received the Nobel Prize for the in vitro synthesis of polyribonucleotides.

KORNBERG received the Nobel Prize for the in vitro synthesis of polydeoxyribonucleotides.

1962

WATSON and CRICK, with M. H. F. WILKINS, received the Nobel Prize for their model of the DNA molecule.

REFERENCE: A. Hughes, *A History of Cytology,* Abelard-Schuman, New York, 1959.

CONTENTS

PART III
Nucleocytoplasmic Relations

PART I

The Cytoplasm

CHAPTER ONE

Morphology and Chemistry

With the advent of the electron microscope, a relatively recent event in the history of the biological sciences, the physical and chemical organization of the cell became a subject of intensive and rewarding study. Prior to the availability of this remarkable instrument, information pertaining to the structure of the cytoplasm was rather sparse. This is not to imply that nothing was known about its construction, but the details of structure were not clear. In the years following 1940, several types of instruments were developed that removed many of the limitations imposed upon the study of cells. Not only was there a need for an increase in magnification, but there were, and still are in some cases, needs for techniques to permit the study of cells under more natural conditions of life and growth than were possible with existing methods. Some of these techniques and instruments will be described in Chapter Two.

One might question a morphological approach to the study of the cell on the basis of its value to an understanding of cell function, but this objection has little justification. It is necessary to determine the framework of the cell in which the various activities take place. For this reason, the use of techniques involving the electron microscope and other optical instruments has provided a rapid advance toward an understanding of cell function as well as cell structure. As is the nature of science, the information obtained from a variety of studies is not always accurate in terms of the actual cellular condition. The handling of cells for observation often changes them in such a way as to increase the possibility of misinterpretation of the observed material. This problem is related to the earlier statement concerning the desirability of studying cells under normal living conditions rather than under artificial conditions created in the laboratory by the use of available techniques. In addition to the problem of inaccuracy of observations or the determination of the actual cellular structure and behavior, there are sometimes as many interpretations of the