

INTERNATIONAL Review of Cytology

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Contents of Previous Volumes

Volume 1

- Some Historical Features in Cell Biology—ARTHUR HUGHES
 Nuclear Reproduction—C. LEONARD HUSKINS
 Enzymic Capacities and Their Relation to Cell Nutrition in Animals—GEORGE W. KIDDER
 The Application of Freezing and Drying Techniques in Cytology—L. G. E. BELL
 Enzymatic Processes in Cell Membrane Penetration—TH. ROSENBERG AND W. WILBRANDT
 Bacterial Cytology—K. A. BISSET
 Protoplast Surface Enzymes and Absorption of Sugar—R. BROWN
 Reproduction of Bacteriophage—A. D. HERSHEY
 The Folding and Unfolding of Protein Molecules as a Basis of Osmotic Work—R. J. GOLDACRE
 Nucleo-Cytoplasmic Relations in Amphibian Development—G. FANK-HAUSER
 Structural Agents in Mitosis—M. M. SWANN
 Factors Which Control the Staining of Tissue Sections with Acid and Basic Dyes—MARCUS SINGER
 The Behavior of Spermatozoa in the Neighborhood of Eggs—LORD ROTHCHILD
 The Cytology of Mammalian Epidermis and Sebaceous Glands—WILLIAM MONTAGNA
 The Electron-Microscopic Investigation of Tissue Sections—L. H. BRETSCHNEIDER
 The Histochemistry of Esterases—G. GOMORI
 AUTHOR INDEX—SUBJECT INDEX

Volume 2

- Quantitative Aspects of Nuclear Nucleoproteins—HEWSON SWIFT
 Ascorbic Acid and Its Intracellular Localization, with Special Reference to Plants—J. CHAYEN

- Aspects of Bacteria as Cells and as Organisms—STUART MUDD AND EDWARD D. DELAMATER
 Ion Secretion in Plants—J. F. SUTCLIFFE
 Multienzyme Sequences in Soluble Extracts—HENRY R. MAHLER
 The Nature and Specificity of the Feulgen Nucleal Reaction—M. A. LESSLER
 Quantitative Histochemistry of Phosphatases—WILLIAM L. DOYLE
 Alkaline Phosphatase of the Nucleus—M. CHÈVREMONT AND H. FIRKET
 Gustatory and Olfactory Epithelia—A. F. BARADI AND G. H. BOURNE
 Growth and Differentiation of Explanted Tissues—P. J. GAILLARD
 Electron Microscopy of Tissue Sections—A. J. DALTON
 A Redox Pump for the Biological Performance of Osmotic Work, and Its Relation to the Kinetics of Free Ion Diffusion Across Membranes—E. J. CONWAY
 A Critical Survey of Current Approaches in Quantitative Histo- and Cytochemistry—DAVID GLICK
 Nucleo-cytoplasmic Relationships in the Development of *Acetabularia*—J. HAMMERLING
 Report of Conference of Tissue Culture Workers Held at Cooperstown, New York—D. C. HETHERINGTON
 AUTHOR INDEX—SUBJECT INDEX

Volume 3

- The Nutrition of Animal Cells—CHARITY WAYMOUTH
 Caryometric Studies of Tissue Cultures—OTTO BUCHER
 The Properties of Urethan Considered in Relation to Its Action on Mitosis—IVOR CORNMANN
 Composition and Structure of Giant Chromosomes—MAX ALFERT
 How Many Chromosomes in Mammalian Somatic Cells?—R. A. BEATTY

The Significance of Enzyme Studies on Isolated Cell Nuclei—ALEXANDER L. DOUNCE

The Use of Differential Centrifugation in the Study of Tissue Enzymes—CHR. DE DUVE AND J. BERTHET

Enzymatic Aspects of Embryonic Differentiation—TRYGGVE GUSTAFSON

Azo Dye Methods in Enzyme Histochemistry—A. G. EVERSON PEARSE

Microscopic Studies in Living Mammals with Transparent Chamber Methods—ROY G. WILLIAMS

The Mast Cell—G. ASBOE-HANSEN

Elastic Tissue—EDWARD W. DEMPSEY AND ALBERT I. LANSING

The Composition of the Nerve Cell Studied with New Methods—SVEN-OLOF BRATTGÅRD AND HOLGER HYDEN

AUTHOR INDEX—SUBJECT INDEX

Volume 4

Cytochemical Micrurgy—M. J. KOPAC
Amoebocytes—L. E. WAGGE

Problems of Fixation in Cytology, Histology, and Histochemistry—M. WOLMAN

Bacterial Cytology—ALFRED MARSHAK

Histochemistry of Bacteria—R. VENDRELY

Recent Studies on Plant Mitochondria—DAVID P. HACKETT

The Structure of Chloroplasts—

K. MÜHLETHALER

Histochemistry of Nucleic Acids—N. B. KURNICK

Structure and Chemistry of Nucleoli—W. S. VINCENT

On Goblet Cells, Especially of the Intestine of Some Mammalian Species—HARALD MOE

Localization of Cholinesterases at Neuromuscular Junctions—R. COUTEAUX

Evidence for a Redox Pump in the Active Transport of Cations—E. J. CONWAY

AUTHOR INDEX—SUBJECT INDEX

Volume 5

Histochemistry with Labeled Antibody—ALBERT H. COONS

The Chemical Composition of the Bacterial Cell Wall—C. S. CUMMINS

Theories of Enzyme Adaptation in Microorganisms—J. MANDELSTAM

The Cytochondria of Cardiac and Skeletal Muscle—JOHN W. HARMAN

The Mitochondria of the Neuron—WARREN ANDREW

The Results of Cytophotometry in the Study of the Deoxyribonucleic Acid (DNA) Content of the Nucleus—R. VENDRELY AND C. VENDRELY

Protoplasmic Contractility in Relation to Gel Structure: Temperature-Pressure Experiments on Cytokinesis and Amoeboid Movement—DOUGLAS MARSLAND

Intracellular pH—PETER C. CALDWELL

The Activity of Enzymes in Metabolism and Transport in the Red Cell—T. A. J. PRANKERD

Uptake and Transfer of Macromolecules by Cells with Special Reference to Growth and Development—A. M. SCHECHTMAN

Cell Secretion: A Study of Pancreas and Salivary Glands—L. C. U. JUNQUEIRA AND G. C. HIRSCH

The Acrosome Reaction—JEAN C. DAN

Cytology of Spermatogenesis—VISHWA NATH

The Ultrastructure of Cells, as Revealed by the Electron Microscope—FRITIOF S. SJÖSTRAND

AUTHOR INDEX—SUBJECT INDEX

Volume 6

The Antigen System of *Paramecium aurelia*—G. H. BEALE

The Chromosome Cytology of the Ascites Tumors of Rats, with Special Reference to the Concept of the Stemline Cell—SAJIRO MAKINO

The Structure of the Golgi Apparatus—ARTHUR W. POLLISTER AND PRISCILLA F. POLLISTER

An Analysis of the Process of Fertilization and Activation of the Egg—A. MONROY

The Role of the Electron Microscope in Virus Research—ROBLEY C. WILLIAMS

The Histochemistry of Polysaccharides—
ARTHUR J. HALE

The Dynamic Cytology of the Thyroid
Gland—J. GROSS

Recent Histochemical Results of Studies
on Embryos of Some Birds and Mam-
mals—ELIO BORGHESE

Carbohydrate Metabolism and Embryonic
Determination—R. J. O'CONNOR

Enzymatic and Metabolic Studies on Iso-
lated Nuclei—G. SIEBERT AND R. M. S.
SMELLIE

Recent Approaches to the Cytochemical
Study of Mammalian Tissues—GEORGE
H. HOGEBOOM, EDWARD L. KUFF, AND
WALTER C. SCHNEIDER

The Kinetics of the Penetration of Non-
electrolytes into the Mammalian Eryth-
rocyte—FREDA BOWYER

AUTHOR INDEX—SUBJECT INDEX

CUMULATIVE SUBJECT INDEX
(VOLUMES 1-5)

Volume 7

Some Biological Aspects of Experimental
Radiology: A Historical Review—F. G.
SPEAR

The Effect of Carcinogens, Hormones, and
Vitamins on Organ Cultures—ILSE
LASNITZKI

Recent Advances in the Study of the
Kinetochore—A. LIMA-DE-FARIA

Autoradiographic Studies with S^{35} -Sulfate
D. D. DZIEWIATKOWSKI

The Structure of the Mammalian Sper-
matozoon—DON W. FAWCETT

The Lymphocyte—O. A. TROWELL

The Structure and Innervation of Lamel-
libranch Muscle—J. BOWDEN

Hypothalamo-neurohypophysial Neurose-
cretion—J. C. SLOPER

Cell Contact—PAUL WEISS

The Ergastoplasm: Its History, Ultrastruc-
ture, and Biochemistry—FRANÇOISE
HAGUENAU

Anatomy of Kidney Tubules—JOHANNES
RHODIN

Structure and Innervation of the Inner

Ear Sensory Epithelia—HANS ENG-
STRÖM AND JAN WERSÄLL

The Isolation of Living Cells from Ani-
mal Tissues—L. M. J. RINALDINI

AUTHOR INDEX—SUBJECT INDEX

Volume 8

The Structure of Cytoplasm—CHARLES
OBERLING

Wall Organization in Plant Cells—R. D.
PRESTON

Submicroscopic Morphology of the Syn-
apse—EDUARDO DE ROBERTIS

The Cell Surface of *Paramecium*—C. F.
EHRET AND E. L. POWERS

The Mammalian Reticulocyte—LEAH MIR-
IAM LOWENSTEIN

The Physiology of Chromatophores—MIL-
TON FINGERMAN

The Fibrous Components of Connective
Tissue with Special Reference to the
Elastic Fiber—DAVID A. HALL

Experimental Heterotopic Ossification—
J. B. BRIDGES

A Survey of Metabolic Studies on Iso-
lated Mammalian Nuclei—D. B.
ROODYN

Trace Elements in Cellular Function—
BERT L. VALLEE AND FREDERIC L. HOCH
Osmotic Properties of Living Cells—
D. A. T. DICK

Sodium and Potassium Movements in
Nerve, Muscle, and Red Cells—I. M.
GLYNN

Pinocytosis—H. HOLTER

AUTHOR INDEX—SUBJECT INDEX

Volume 9

The Influence of Cultural Conditions on
Bacterial Cytology—J. F. WILKINSON
AND J. P. DUGUID

Organizational Patterns within Chromo-
somes—BERWIND P. KAUFMANN, HELEN
GAY, AND MARGARET R. McDONALD

Enzymic Processes in Cells—JAY BOYD
BEST

The Adhesion of Cells—LEONARD WEISS
Physiological and Pathological Changes

- in Mitochondrial Morphology—CH. ROUILLER
- The Study of Drug Effects at the Cytological Level—G. B. WILSON
- Histochemistry of Lipids in Oogenesis—VISHWA NATH
- Cyto-Embryology of Echinoderms and Amphibia—KATSUMA DAN
- The Cytochemistry of Non-Enzyme Proteins—RONALD R. COWDEN
- AUTHOR INDEX—SUBJECT INDEX
- Volume 10
- The Chemistry of Schiff's Reagent—FREDERICK H. KASTEN
- Spontaneous and Chemically Induced Chromosome Breaks—ARUN KUMAR SHARMA AND ARCHANA SHARMA
- The Ultrastructure of the Nucleus and Nucleocytoplasmic Relations—SAUL WISCHNITZER
- The Mechanics and Mechanism of Cleavage—LEWIS WOLPERT
- The Growth of the Liver with Special Reference to Mammals—F. DOLJANSKI
- Cytological Studies on the Affinity of the Carcinogenic Azo Dyes for Cytoplasmic Components—YOSHIMI NAGATANI
- Epidermal Cells in Culture—A. GEDEON MATOLTSY
- AUTHOR INDEX—SUBJECT INDEX
- CUMULATIVE SUBJECT INDEX (VOLUMES 1-9)
- Volume 11
- Electron Microscopic Analysis of the Secretion Mechanism—K. KUROSUMI
- The Fine Structure of Insect Sense Organs—ELEANOR H. SLIFER
- Cytology of the Developing Eye—ALFRED J. COULOMBRE
- The Photoreceptor Structures—J. J. WOLKEN
- Use of Inhibiting Agents in Studies on Fertilization Mechanisms—CHARLES B. METZ
- The Growth-Duplication Cycle of the Cell—D. M. PRESCOTT
- Histochemistry of Ossification—ROMULO L. CABRINI
- Cinematography, Indispensable Tool for Cytology—C. M. POMERAT
- AUTHOR INDEX—SUBJECT INDEX
- Volume 12
- Sex Chromatin and Human Chromosomes—JOHN L. HAMERTON
- Chromosomal Evolution in Cell Populations—T. C. HSU
- Chromosome Structure with Special Reference to the Role of Metal Ions—DALE M. STEFFENSEN
- Electron Microscopy of Human White Blood Cells and Their Stem Cells—MARCEL BESSIS AND JEAN-PAUL THIERY
- In Vivo* Implantation as a Technique in Skeletal Biology—WILLIAM J. L. FELTS
- The Nature and Stability of Nerve Myelin—J. B. FINEAN
- Fertilization of Mammalian Eggs *in Vitro*—C. R. AUSTIN
- Physiology of Fertilization in Fish Eggs—TOKI-O YAMAMOTO
- AUTHOR INDEX—SUBJECT INDEX
- Volume 13
- The Coding Hypothesis—MARTYNAS YČAS
- Chromosome Reproduction—J. HERBERT TAYLOR
- Sequential Gene Action, Protein Synthesis, and Cellular Differentiation—REED A. FLICKINGER
- The Composition of the Mitochondrial Membrane in Relation to Its Structure and Function—ERIC G. BALL AND CLIFFE D. JOEL
- Pathways of Metabolism in Nucleate and Anucleate Erythrocytes—H. A. SCHWEIGER
- Some Recent Developments in the Field of Alkali Cation Transport—W. WILBRANDT
- Chromosome Aberrations Induced by Ionizing Radiations—H. J. EVANS
- Cytochemistry of Protozoa, with Particular Reference to the Golgi Apparatus

and the Mitochondria—VISHWA NATH
AND G. P. DUTTA

Cell Renewal—FELIX BERTALANFFY AND
CHOSEN LAU

AUTHOR INDEX—SUBJECT INDEX

Volume 14

Inhibition of Cell Division: A Critical
and Experimental Analysis—SEYMOUR
GELFANT

Electron Microscopy of Plant Protoplasm
R. BUVAT

Cytophysiology and Cytochemistry of the
Organ of Corti: A Cytochemical The-
ory of Hearing—J. A. VINNIKOV AND
L. K. TITOVA

Connective Tissue and Serum Proteins—
R. E. MANCINI

The Biology and Chemistry of the Cell
Walls of Higher Plants, Algae, and
Fungi—D. H. NORTHCOTE

Development of Drug Resistance by
Staphylococci *in Vitro* and *in Vivo*—
MARY BARBER

Cytological and Cytochemical Effects of
Agents Implicated in Various Patholog-
ical Conditions: The Effect of Viruses
and of Cigarette Smoke on the Cell and
Its Nucleic Acid—CECILIE LEUCHTEN-
BERGER AND RUDOLF LEUCHTENBERGER

The Tissue Mast Wall—DOUGLAS E.
SMITH

AUTHOR INDEX—SUBJECT INDEX

Volume 15

The Nature of Lampbrush Chromosomes
H. G. CALLAN

The Intracellular Transfer of Genetic In-
formation—J. L. SIRLIN

Mechanisms of Gametic Approach in
Plants—LEONARD MACHLIS AND ERIKA
RAWITSCHER-KUNKEL

The Cellular Basis of Morphogenesis and
Sea Urchin Development—T. GUSTAF-
SON AND L. WOLPERT

Plant Tissue Culture in Relation to De-
velopmental Cytology—CARL R. PAR-
TANEN

Regeneration of Mammalian Liver—
NANCY L. R. BUCHER

Collagen Formation and Fibrogenesis
with Special Reference to the Role of
Ascorbic Acid—BERNARD S. GOULD
The Behavior of Mast Cells in Anaphy-
laxis—IVAN MOTA

Lipid Absorption—ROBERT M. WOTTON
AUTHOR INDEX—SUBJECT INDEX

Volume 16

Ribosomal Functions Related to Protein
Synthesis—TORE HULTIN

Physiology and Cytology of Chloroplast
Formation and "Loss" in *Euglena*—
M. GRENSON

Cell Structures and Their Significance for
Ameboid Movement—K. E. WOHL-
FARTH-BOTTERMANN

Microbeam and Partial Cell Irradiation—
C. L. SMITH

Nuclear-Cytoplasmic Interaction with Ion-
izing Radiation—M. A. LESSLER

In Vivo Studies of Myelinated Nerve
Fibers—CARL CASKEY SPEIDEL

Respiratory Tissue: Structure, Histophysi-
ology, Cytodynamics. Part I. Review
and Basic Cytomorphology—FELIX D.
BERTALANFFY

AUTHOR INDEX—SUBJECT INDEX

Volume 17

The Growth of Plant Cell Walls—K.
WILSON

Reproduction and Heredity in Trypano-
somes: A Critical Review Dealing
Mainly with the African Species in the
Mammalian Host—P. J. WALKER

The Blood Platelet: Electron Microscopic
Studies—J. F. DAVID-FERREIRA

The Histochemistry of Mucopolysaccha-
rides—ROBERT C. CURRAN

Respiratory Tissue Structure, Histophysi-
ology, Cytodynamics. Part II. New Ap-
proaches and Interpretations—FELIX D.
BERTALANFFY

The Cells of the Adenohypophysis and

Their Functional Significance—MARC
HERLANT

AUTHOR INDEX—SUBJECT INDEX

Volume 18

The Cell of Langerhans—A. S. BREATH-
NACH

The Structure of the Mammalian Egg—
ROBERT HADEK

Cytoplasmic Inclusions in Oogenesis—
M. D. L. SRIVASTAVA

The Classification and Partial Tabulation
of Enzyme Studies on Subcellular Frac-
tions Isolated by Differential Centrifug-
ing—D. B. ROODYN

Histochemical Localization of Enzyme
Activities by Substrate Film Methods:
Ribonucleases, Deoxyribonucleases, Pro-
teases, Amylase, and Hyaluronidase—
R. DAoust

Cytoplasmic Deoxyribonucleic Acid—
P. B. GAHAN AND J. CHAYEN

Malignant Transformation of Cells *in*
Vitro—KATHERINE K. SANFORD

Deuterium Isotope Effects in Cytology—
E. FLAUMENHAFT, S. BOSE, H. L. CRESPI,
AND J. J. KATZ

The Use of Heavy Metal Salts as Electron
Stains—C. RICHARD ZOBEL AND MI-
CHAEL BEER

AUTHOR INDEX—SUBJECT INDEX

Volume 19

"Metabolic" DNA: A Cytochemical Study
H. ROELS

The Significance of the Sex Chromatin—
MURRAY L. BARR

Some Functions of the Nucleus—J. M.
MITCHISON

Synaptic Morphology on the Normal and
Degenerating Nervous System—E. G.
GRAY AND R. W. GUILLERY

Neurosecretion—W. BARGMANN

Some Aspects of Muscle Regeneration—
E. H. BETZ, H. FIRKET, AND REZNIK

The Gibberellins as Hormones—P. W.
BRIAN

Phototaxis in Plants—WOLFGANG HAUPT

Phosphorus Metabolism in Plants—K. S.
ROWAN

AUTHOR INDEX—SUBJECT INDEX

Volume 20

The Chemical Organization of the Plasma
Membrane of Animal Cells—A. H.
MADDY

Subunits of Chloroplast Structure and
Quantum Conversion in Photosynthesis
RODERIC B. PARK

Control of Chloroplast Structure by Light
LESTER PACKER AND PAUL-ANDRÉ SIE-
GENTHALER

The Role of Potassium and Sodium Ions
as Studied in Mammalian Brain—H.
HILLMAN

Triggering of Ovulation by Coitus in the
Rat—CLAUDE ARON, GITTA ASCH, AND
JACQUELINE ROOS

Cytology and Cytophysiology of Non-
Melanophore Pigment Cells—JOSEPH T.
BAGNARA

The Fine Structure and Histochemistry of
Prostatic Glands in Relation to Sex
Hormones—DAVID BRANDES

Cerebellar Enzymology—LUCIE ARVY
AUTHOR INDEX—SUBJECT INDEX

Volume 21

Histochemistry of Lysosomes—P. B.
GAHAN

Physiological Clocks—R. L. BRAHMA-
CHARY

Ciliary Movement and Coordination in
Ciliates—BELA PARUCA

Electromyography: Its Structural and
Neural Basis—JOHN V. BASMAJIAN

Cytochemical Studies with Acridine
Orange and the Influence of Dye Con-
taminants in the Staining Nucleic Acids
FREDERICK H. KASTEN

Experimental Cytology of the Shoot
Apical Cells during Vegetative Growth
and Flowering—A. NOUGARÈDE

Nature and Origin of Perisynaptic Cells
of the Motor End Plate—T. R. SHAN-
THAVEERAPPA AND G. H. BOURNE

AUTHOR INDEX—SUBJECT INDEX

Volume 22

- Current Techniques in Biomedical Electron Microscopy—SAUL WISCHNITZER
 The Cellular Morphology of Tissue Repair—R. M. H. MCMINN
 Structural Organization and Embryonic Differentiation—GAJANAN V. SHERBET AND M. S. LAKSHMI
 The Dynamism of Cell Division during Early Cleavage Stages of the Egg—N. FAUTREZ-FIRLEFYN AND J. FAUTREZ
 Lymphopoiesis in the Thymus and Other Tissues: Functional Implications—N. B. EVERETT AND RUTH W. TYLER (CAF-FREY)
 Structure and Organization of the Myoneural Junction—C. COËRS
 The Ecdysial Glands of Arthropods—WILLIAM S. HERMAN
 Cytokinins in Plants—B. I. SAHAI SRIVASTAVA
 AUTHOR INDEX—SUBJECT INDEX
 CUMULATIVE SUBJECT INDEX
 (VOLUMES 1-21)

Volume 23

- Transformationlike Phenomena in Somatic Cells—J. M. OLENOV
 Recent Developments in the Theory of Control and Regulation of Cellular Processes—ROBERT ROSEN
 Contractile Properties of Protein Threads from Sea Urchin Eggs in Relation to Cell Division—HIKOICHI SAKAI
 Electron Microscopic Morphology of Oogenesis—ARNE NØRREVANG
 Dynamic Aspects of Phospholipids during Protein Secretion—LOWELL E. HOKIN
 The Golgi Apparatus: Structure and Function—H. W. BEAMS AND R. G. KESSEL
 The Chromosomal Basis of Sex Determination—KENNETH R. LEWIS AND BERNARD JOHN
 AUTHOR INDEX—SUBJECT INDEX

Contents

LIST OF CONTRIBUTORS	v
CONTENTS OF PREVIOUS VOLUMES	xi

Synchronous Cell Differentiation

GEORGE M. PADILLA AND IVAN L. CAMERON

I. Introduction	1
II. Bacterial Systems	3
III. Fungal Systems	7
IV. Protistan Systems	15
V. Metazoan Cells	22
VI. Concluding Remarks	22
References	23

Mast Cells in the Nervous System

YNGVE OLSSON

I. Introduction	27
II. Mast Cells in the Central Nervous System	28
III. Mast Cells in the Peripheral Somatic Nervous System	32
IV. Mast Cells in the Peripheral Autonomous Nervous System	61
V. Concluding Remarks	62
References	63

Developmental Phases in Intermitosis and the Preparation for Mitosis of Mammalian Cells *in Vitro*

BLAGOJE A. NEŠKOVIĆ

I. Introduction	71
II. Methodological Problems of Synchronization	72
III. Phases of Intermitosis	73
IV. Functional Changes in Intermitosis	74
V. Morphological Changes during Intermitosis	77
VI. Some Results of Analyses of Intermitosis Applying the Concepts of Developmental Phases	84
References	96

Antimitotic Substances

GUY DEYSSON

I. Introduction	99
II. Methodology and Experimental Material	100
III. Some Generalities about Antimitotic Substances	103
IV. Spindle Poisons (Mitoclastic Agents)	105
V. Chromosome Poisons (Chromatoclastic Agents)	121
VI. Other Kinds of Antimitotic Action	138
VII. Conclusions	140
References	143

**The Form and Function of the Sieve Tube: A Problem
in Reconciliation**

P. E. WEATHERLEY AND R. P. C. JOHNSON

I. Introduction	149
II. The Structure of the Sieve Tube	152
III. Hypothetical Mechanisms in Relation to the Structure of the Sieve Tube and the Rate of Transport	171
IV. The Physiology of Translocation	182
V. Conclusions	187
References	189

**Analysis of Antibody Staining Patterns Obtained with
Striated Myofibrils in Fluorescence Microscopy
and Electron Microscopy**

FRANK A. PEPE

I. Introduction	193
II. The Use of Antibodies for the Study of the Striated Myofibril	194
III. General Considerations for the Interpretation of Antibody Staining Patterns	208
IV. Analysis of Antibody Staining Patterns in Terms of Distribution, Organi- zation, and Interaction of Protein Molecules in the Myofibril	215
References	228

Cytology of Intestinal Epithelial Cells

PETER G. TONER

I. General	233
II. Epithelial Structure and Function	236

III. Cytopathology	307
IV. Conclusion	323
References	324

Liquid Junction Potentials and Their Effect on Potential Measurements in Biological Systems

P. C. CALDWELL

I. Introduction	345
II. Theoretical Treatment of Junction Potentials	347
III. Tests of Theories of Liquid Junction Potentials	352
IV. The Effects of Liquid Junction Potentials in Measurements of Resting Potentials in Nerve and Muscle	357
V. The Tip Potential of the Ling and Gerard Microcapillary Electrode	366
VI. Conclusion	368
References	370
AUTHOR INDEX	373
SUBJECT INDEX	396

Synchronous Cell Differentiation

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I. Introduction	1
II. Bacterial Systems	3
A. Gene-Directed Enzyme Induction or Activation	3
B. Chromosome Replication	4
C. Germination-Outgrowth-Sporulation	5
III. Fungal Systems	7
A. Myxomycetes	8
B. Cellular Slime Molds	10
C. Aquatic Fungi	10
D. Ascomycetes	13
IV. Protistan Systems	15
A. Unicellular Algae	15
B. Polymorphic Ciliates	16
C. Synchronous Regeneration of Oral Structures	19
D. Encystment in Amebas	19
E. Ameba-Flagellate Transformation	20
F. Trypanosomes	22
V. Metazoan Cells	22
VI. Concluding Remarks	22
VII. References	23

I. Introduction

Synchronous cell differentiation refers to the occurrence of simultaneous cellular transformations throughout a population of cells. Although the induction of cell division synchrony may be a prerequisite for such an experimental situation, it need not be the primary concern of the investigator. In fact, the motivating force for studying a synchronously differentiating system is that it is

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only through the amplification of specific biochemical and morphological changes that analytical methods of cell biology will be successfully employed. We will then be closer to achieving an understanding of the controlling mechanisms in cell specialization.

Various diverse processes presently are being investigated in the field of cellular morphogenesis. One may include the replication of the genetic apparatus, encystment and excystment, sporulation, and germination, as well as certain cases of transient structural and physiological adaptation to environmental shifts. In this discussion we are not concerned with those cases of cellular differentiation commonly found in the embryonic or regenerating systems of metazoan organisms involving a limited number of cells at any given time, but will consider mainly those cellular communities in which synchrony has been induced experimentally throughout the entire population.

It is of some value to consider if cell differentiation as seen in metazoan cells is irreversible (Bell, 1965). That is to say, is there a loss of morphogenetic totipotency which relegates the differentiated cells to a specialized state until its death? Recent nuclear transplantation experiments give strong support to the concept that even in highly differentiated cells the nucleus still retains the totipotency of genetic expression when it is placed into a new and more favorable cytoplasmic environment (Gurdon, 1964). Conversely the stability of the differentiated state, which had been assumed to be maintained only under conditions which preclude cell division, has been found in clonal myogenesis experiments to be independent of the rate of cell division or the total number of divisions (Konigsberg, 1963). On the other hand, dedifferentiation in cultured chondrocytes, characterized by the loss of recognizable form or ability to synthesize chondroitin sulfate, has been demonstrated, although the authors do not categorically state that this is a totally irreversible process (Holtzer *et al.*, 1960). Thus, the extent of irreversibility in the differentiated state is open to question. Perhaps it is the continued interaction between the nucleus, the cytoplasm, and the environment which determines the irreversibility of the differentiated state rather than loss of genetic totipotency. Indeed, most of the examples of cell differentiation which are discussed in this review demonstrate complete reversibility upon appropriate manipulation of the environment.

It is generally assumed that there are universal principles underlying the regulation of the cell state. Such an assumption is most often implicit and derives partly from the mounting evidence that biological systems display the same genetic mechanism for the control of biosynthetic processes, such as the synthesis of specific enzymes, and informational macromolecules, or the development of complex cellular organelles (Bonner *et al.*, 1965; Rutter, 1965; Sager, 1965). A distinction should be made, however, on the level of differentiation being considered. There is no question that all cells from prokaryotic to eukary-

otic types can alter their internal or subcellular organization to meet environmental shifts. For example, the kinetics of bacterial enzyme induction and chromosome replication are radically modified by conditions of growth (Lark, 1966). Likewise, it has been shown that photosynthetic cells can reduce their chloroplast complement to a proplastid level in the absence of a light stimulus. Both of these instances represent what may be called "subcellular differentiation." It is in this area of experimentation that naturally and experimentally synchronized cell systems have been used most successfully (Cameron and Padilla, 1966, Padilla *et al.*, 1968). As expected, much information is being gathered with synchronized cells whose major macromolecular and biosynthetic events are displayed in a well-directed time sequence (Lark, 1966; Sueoka, 1966; Halvorson *et al.*, 1966a). We want to focus attention in this review, however, to a second level of differentiation, that involving the entire cellular complement. This may be called "cellular differentiation," examples of which are described in this review. Perhaps in time we may extend the use of synchronized cells to a study of the evolutionary aspects of gene action in the acquisition of cellular specialization (Moses and Calvin, 1965). For the present we hope that this review will help to widen the scope of the biologist who is interested in cell differentiation and will also introduce him to cellular systems he may not have previously considered.

II. Bacterial Systems

Subcellular differentiation has been studied in synchronously dividing bacteria at three related but distinct levels: (a) Gene-directed enzyme induction or activation, (b) chromosome replication and segregation, and (c) sporulation-germination-outgrowth sequence. We shall consider these areas as they are related to the mechanisms of differentiation.

A. GENE-DIRECTED ENZYME INDUCTION OR ACTIVATION

This constitutes one of the most fertile areas of investigation linking genetics to subcellular differentiation. For instance, it has been demonstrated that the rate of synthesis of repressed enzymes doubles once every cycle in correspondence with a doubling of the genes that govern their formation. Although repressed enzymes may be induced at any given time in the cell cycle, the potential for synthesis of a nonrepressed enzyme most likely also changes discontinuously at a characteristic time in the cycle but not necessarily in direct relation to the time of DNA synthesis. However, the cyclical recurrence for the expression of this potential may still reflect the linear array within the genetic map assigned to the control of a given enzymic function. The timing may be modified by internal as well as external constraints (Goodwin, 1966; Masters and Donachie, 1966;

Masters *et al.*, 1964; Donachie, 1965; Kuempel *et al.*, 1965; see Donachie and Masters, 1968; Helmstetter, 1968; for current reviews). While genes are replicated in an orderly sequence, most likely only once during each cell cycle, it has been also suggested that transcription need not be simultaneous with replication (Masters and Donachie, 1966). Periodic synthesis of an enzyme, which is not being artificially repressed, may also be the outcome of the phenomenon called "end-product repression." That is to say, oscillatory phenomena arise through the interaction of the intracellular concentration of enzymes and their end product (see Goodwin, 1966, Donachie and Masters, 1968, for a full discussion of this subject). These various phenomena are of special significance to our understanding of the mechanism of cellular differentiation, since the elaboration of complex cellular structures ultimately depends on the activation or induction of enzymes involved in the manufacture of specific proteins. Let us now consider the question of chromosome replication; it relates more directly to the elaboration of subcellular subunits in the cytoplasm.

B. CHROMOSOME REPLICATION

Much of the work dates back to the utilization of mutants of *Escherichia coli* that require specific amino acids and nucleic precursors for their growth (Barner and Cohen, 1955). The demonstration (Cairns, 1963) that the bacterial chromosome is in fact a circular structure amenable to analysis by radioautographic techniques has led to the acquisition of much experimental data on the mechanisms of chromosome replication. Lark (1966) recently discussed a model that relates the rate of DNA synthesis and cell division to the processes of chromosome replication and segregation in synchronized cultures of *E. coli*. This model was developed through a mathematical and experimental analysis of the distribution of radioactive precursors of DNA following manipulations of the growth of these bacteria in a variety of experimental conditions. It was shown that the patterns of chromosome replication and segregation may be drastically altered by factors which alter the rate of cell division. The sequence of replication of the bacterial chromosome begins by its attachment through one DNA strand to a proteinaceous cell membrane complex; "the replicator." The other strand of DNA breaks prior to the initiation of replication and becomes temporarily attached to a second membrane site called the "prorepliator" which in turn is linked to a protein complex, the "initiator." (The initiator is thought to be a heritable portion of the chromosome and may also be located in the membrane.) The double DNA helix is thus opened and replication proceeds with the characteristic unwinding of the DNA strands. At the completion of replication the ends of the chromosome attached to the "initiator" are joined at the prorepliator site. The initiator is now converted into the replicator and is