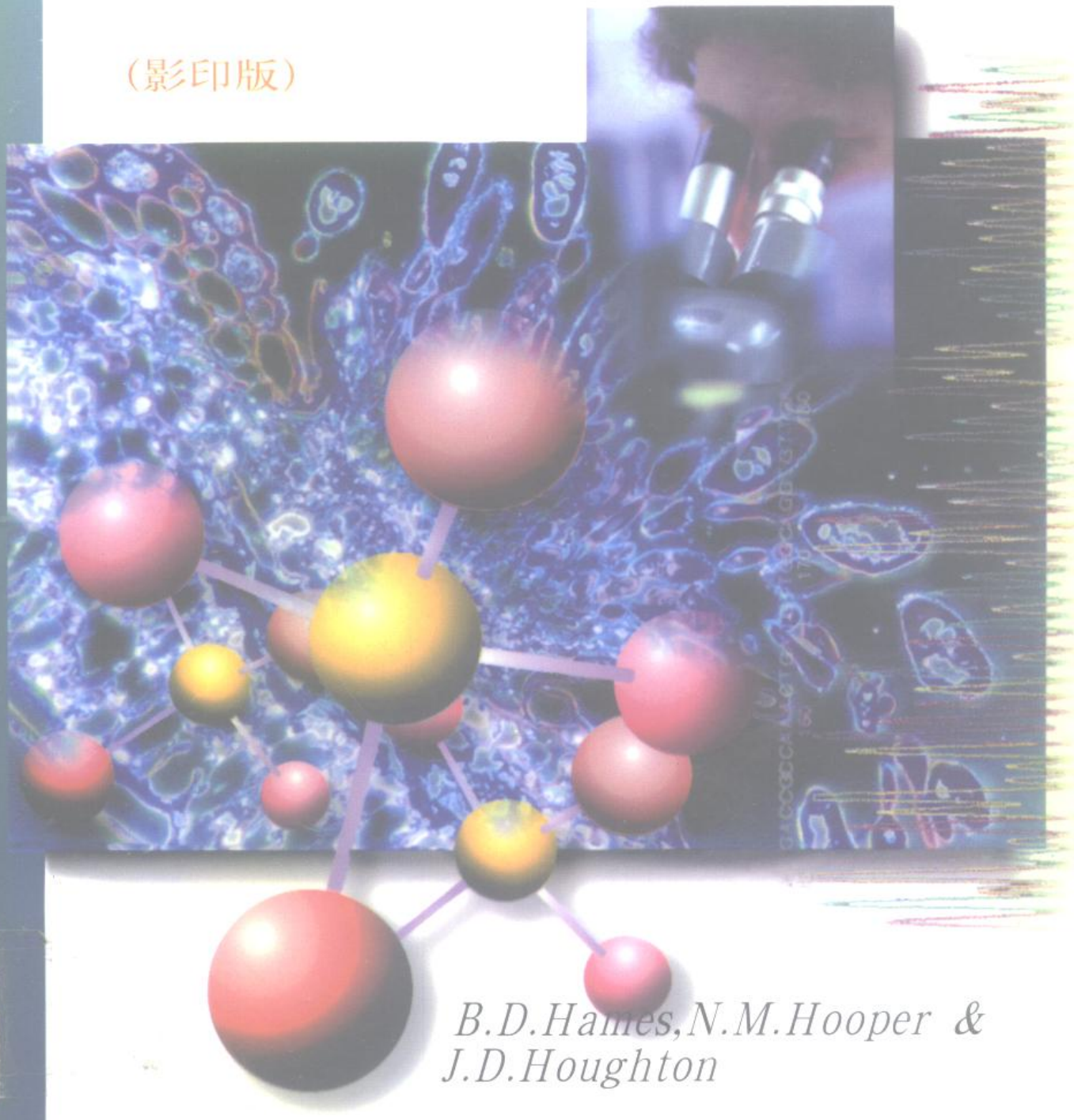
现代生物学精要速览

Instant Notes in BIOCHEMISTRY

生物化学

（影印版）



B.D.Hames, N.M.Hooper &
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内 容 简 介

本套丛书是国外优秀教材畅销榜的上榜教材，面向大学生，由英国著名大学具丰富教学经验的一流教授编写。它以一种风格独特的描述方式，全面、系统地概括了学科的核心内容和前沿动态，并以一种便于学习、利于复习的形式，使学生能快速、准确地掌握知识，很好地指导学习和考试。书中英文使用最为自然、易懂的语句，是提高专业外语的最佳套书。本书是该系列中的生物化学分册，共约 14 个章节。北京大学王镜岩教授大力推荐。

B. D. Hames, N. M. Hooper and J. D. Houghton

Instant Notes in Biochemistry

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PREFACE

The last two decades have seen an astonishing explosion of knowledge in the biological sciences. Today, biology is rightfully center-stage in science studies, fascinating as an academic subject yet also seen as deeply relevant to everyday life. Central to the emergence of biology as a leading subject are the spectacular advances that have been made in biochemistry and its famous offspring, molecular biology. However, exciting though all of this progress undoubtedly is, it poses real problems for modern-day students coming to grips with biochemistry for the first time. Leading textbooks have understandably been tempted into describing new developments soon after they have been reported, growing substantially in size and complexity as they have done so. At ground level, however, the academic appeal and importance of biochemistry and molecular biology has broadened so that many more students now study this subject area as an important subsidiary to their main studies. It is our personal experience as university lecturers that many of these students, as well as many of those studying the subject full-time, now find it difficult to discern core information from that which is more peripheral. It is the difficulty encountered by such students which led directly to us writing this book.

Biochemistry Instant Notes is designed to give students rapid, easy access to the core factual material in a format which facilitates learning and rapid revision. We have divided the book into 70 mainstream topics which together cover core biochemistry at the level we would expect to be attained by a good first/second year student. Indeed the book is based on the first year course taught to over 400 students each year at the University of Leeds. Each topic starts with a short list of 'Key Notes' – a revision checklist – before explaining the subject matter. Figures have been included where these are useful for student understanding but again the approach has been deliberately reductionist, that is, the figures are in monochrome and are drawn in a reasonably simplistic manner which we hope will be more easily remembered by students and more easily reproduced in examinations. Further reading is included at the end of the book for those students who may wish to delve deeper into selected topics of interest.

Section A describes the organization of prokaryotic and eukaryotic cells, microscopy methods that are used to examine cell structure, and the isolation of subcellular fractions for study. Section B covers amino acids and proteins, describing protein structure, the relationship of structure to function, and key methods for the purification and analysis of proteins. Currently there is a wealth of procedures available for protein purification. In line with the philosophy of the book, we have not attempted to be comprehensive but have chosen to cover the core methods used to separate proteins by size and/or charge including affinity chromatography. Protein sequencing is also described. Having learned about protein structure, the student is now ideally placed to study enzyme structure and function in Section C. This section covers factors affecting enzyme activity, enzyme kinetics and inhibition, and the control of enzyme activity *in vivo*. Antibodies are also important proteins, both *in vivo* and as tools for biochemical analysis. These are covered in Section D, which describes not only antibody structure but also the synthesis of antibodies and their use as experimental tools. Biological membranes are the subject of Section E, which describes membrane structure, the transport of small and large molecules across membranes, and cell signaling via membrane receptors. DNA structure and its replication in both prokaryotes and eukaryotes is the subject of Section F. Gene expression in prokaryotes and eukaryotes is covered in Sections G and H, with gene transcription and its regulation, plus RNA processing, described in the first of these two sections, followed by protein synthesis, protein targeting and post-translational modification in Section H. Section I is a brief overview of the key elements of recombinant DNA technology which no modern biochemistry text can justifiably omit. It covers the basics of DNA cloning, explaining the nature and use of restriction enzymes, nucleic acid hybridization and vectors, and DNA sequencing. It ends with a description of the technique which has recently revolutionized

molecular biology, the polymerase chain reaction (PCR). This section is necessarily brief, given the wide scope of the present book. However, students who wish to know more can find this in the companion volume, *Instant Notes in Molecular Biology*.

The important pathways of biochemical metabolism begin to be covered in Section J, which describes the structure of carbohydrates, the pathways of glycolysis and gluconeogenesis, the pentose phosphate pathway, and glycogen degradation and synthesis. Lipid metabolism is the subject of Section K, which also covers lipoprotein structure and function. The citric acid cycle, electron transport, oxidative phosphorylation and photosynthesis are described in Section L. Nitrogen metabolism, including nitrogen fixation and assimilation, amino acid metabolism, the urea cycle and heme synthesis and degradation, is to be found in Section M. Finally, Section N covers selected topics of cell specialization; muscle contraction, cilia and flagella, nerve conduction and collagen.

If you are a student, how should you best use this book? Bear in mind that your course may well teach the different aspects of biochemistry in a different order from those presented here. The topic-led organization is a distinct advantage in this situation since it lets you find the topic you want quickly but citations within each topic direct you elsewhere within the book for related information. Read the main information in a topic first. This explains the subject. Then use the Key Notes as a revision prompt, supplemented with your own notes that you can add to the deliberately wide margins. Bear in mind that the aim of this book is to present only the core facts. Our hope is that our experience as lecturers has enabled us to do much of the hard work you initially face as a new student, of deciding what is the essential information and recording it in an understandable form. However, if you are as fascinated by the subject as we are, we also hope that you will want to learn more. So, to enlarge your knowledge on specific subjects of interest, consult one of the excellent large mainstream textbooks. For more information on a topic that interests you, turn to the Further Reading at the end of the book. This indicates a number of more comprehensive textbooks as well as listing more advanced articles to take you further. If this book rapidly becomes 'dog-eared' by frequent use and makes your task of coming to grips with biochemistry easier, whilst encouraging you to delve deeper into the subject, we will have succeeded in our prime goals.

David Hames
Nigel Hooper

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We would like to acknowledge the patience and support of our families whilst we have spent many hours with drafts of manuscripts rather than with them. We also thank Jonathan Ray, Lisa Mansell and Rachel Robinson at BIOS Scientific Publishers for their encouragement, persistence and for keeping us (almost) to deadlines. Finally, we should acknowledge all the students over the years who, through their responses, have made us realise the importance of teaching the fundamental aspects of biochemistry in a straightforward and hopefully lucid manner.

CONTENTS

ABBREVIATIONS

A	adenine
ACAT	acyl-CoA cholesterol acyltransferase
ACP	acyl carrier protein
ADP	adenosine diphosphate
AIDS	acquired immune deficiency syndrome
Ala	alanine
ALA	aminolaevulinic acid
AMP	adenosine monophosphate
Arg	arginine
Asn	asparagine
Asp	aspartic acid
ATCase	aspartate transcarbamoylase
ATP	adenosine 5′-triphosphate
ATPase	adenosine triphosphatase
bp	base pairs
C	cytosine
cAMP	3′, 5′ cyclic AMP
CAP	catabolite activator protein
cDNA	complementary DNA
CDP	cytidine diphosphate
cGMP	cyclic GMP
CM	carboxymethyl
CMP	cytidine monophosphate
CNBr	cyanogen bromide
CoA	coenzyme A
CoQ	cytochrome Q (ubiquinone)
$CoQH_2$	ubiquinol
CTL	cytotoxic T lymphocyte
CTP	cytosine triphosphate
Cys	cysteine
$\Delta E_0'$	change in redox potential under standard conditions
ΔG	Gibbs free energy
$\Delta G^{\ddagger}$	Gibbs free energy of activation
$\Delta G^{0'}$	Gibbs free energy under standard conditions
d	2′-deoxyribo-
DAG	1,2-diacylglycerol
dATP	deoxyadenosine 5′-triphosphate
dCTP	deoxycytidine 5′-triphosphate
ddNTP	dideoxynucleoside triphosphate
DEAE	diethylaminoethyl
dGTP	deoxyguanosine 5′-triphosphate
DIPF	diisopropylfluorophosphate
DNA	deoxyribonucleic acid
DNase	deoxyribonuclease
DNP	2,4-dinitrophenol
dTTP	deoxythymidine 5′-triphosphate
E	redox potential
EC	Enzyme Commission
EF	elongation factor
eIF	eukaryotic initiation factor
ELISA	enzyme-linked immunosorbent assay
ER	endoplasmic reticulum
F-2,6-BP	fructose 2,6-bisphosphate
FAD	flavin adenine dinucleotide (oxidized)
$FADH_2$	flavin adenine dinucleotide (reduced)
FBPase	fructose bisphosphatase
N-fMet	*N*-formylmethionine
$FMNH_2$	flavin mononucleotide (reduced)
FMN	flavin mononucleotide (oxidized)
GalNAc	*N*-acetylgalactosamine
GDP	guanosine diphosphate
GlcNAc	*N*-acetylglucosamine
Gln	glutamine
Glu	glutamic acid
Gly	glycine
GMP	guanosine monophosphate
GPI	glycosyl phosphatidylinositol
GTP	guanosine 5′-triphosphate
Hb	hemoglobin
HbS	sickle cell hemoglobin
HDL	high density lipoprotein
His	histidine
HIV	human immunodeficiency virus
HMG	3-hydroxy-3-methylglutaryl
HMM	heavy meromyosin
HPLC	high-performance liquid chromatography
hsp	heat shock protein
Hyl	5-hydroxylysine
Hyp	4-hydroxyproline
IDL	intermediate density lipoprotein
IF	initiation factor
Ig	immunoglobulin
IgG	immunoglobulin G
Ile	isoleucine
IP_3	inositol 1,4,5-trisphosphate
IPTG	isopropyl-β-D-thiogalactopyranoside
K	equilibrium constant
K_m	Michaelis constant
LCAT	lecithin–cholesterol acyltransferase
LDH	lactate dehydrogenase

LDL	low density lipoprotein
Leu	leucine
LMM	light meromyosin
Lys	lysine
Met	methionine
mV	millivolt
mRNA	messenger RNA
NAD^+	nicotinamide adenine dinucleotide (oxidized)
NADH	nicotinamide adenine dinucleotide (reduced)
$NADP^+$	nicotinamide adenine dinucleotide phosphate (oxidized)
NADPH	nicotinamide adenine dinucleotide phosphate (reduced)
NAM	*N*-acetylmuramic acid
NHP	nonhistone protein
PAGE	polyacrylamide gel electrophoresis
PC	plastocyanin
PCR	polymerase chain reaction
PEP	phosphoenolpyruvate
PFK	phosphofructokinase
Phe	phenylalanine
P_i	inorganic phosphate
pI	isoelectric point
pK	dissociation constant
PKA	protein kinase A
PP_i	inorganic pyrophosphate
Pro	proline
PQ	plastoquinone
PSI	photosystem I
PSII	photosystem II
PTH	phenylthiohydantoin
Q	ubiquinone (coenzyme Q)
QH_2	ubiquinol ($CoQH_2$)
RER	rough endoplasmic reticulum
RF	release factor
RFLP	restriction fragment length polymorphism
RNA	ribonucleic acid
RNase	ribonuclease
rRNA	ribosomal RNA
rubisco	ribulose bisphosphate carboxylase
SDS	sodium dodecyl sulfate
Ser	serine
SER	smooth endoplasmic reticulum
snoRNA	small nucleolar RNA
snoRNP	small nucleolar ribonucleoprotein
snRNA	small nuclear RNA
snRNP	small nuclear ribonucleoprotein
SRP	signal recognition particle
SSB	single-stranded DNA-binding (protein)
TBP	TATA box-binding protein
TFII	transcription factor for RNA polymerase II
Thr	threonine
T_m	melting point
tRNA	transfer RNA
Trp	tryptophan
Tyr	tyrosine
UDP	uridine diphosphate
UMP	uridine monophosphate
UTP	uridine 5′-triphosphate
UV	ultraviolet
Val	valine
V_0	initial rate of reaction
VLDL	very low density lipoprotein
V_{max}	maximum rate of reaction

A1 PROKARYOTE CELL ORGANIZATION

Key Notes

Prokaryotes

Prokaryotes (bacteria and blue-green algae) are the most abundant organisms on earth. A prokaryotic cell does not contain a membrane-bound nucleus. Bacteria are either cocci, bacilli or spirilla in shape, and fall into two groups, the eubacteria and the archaebacteria.

Cell structure

Each prokaryotic cell is surrounded by a plasma membrane. The cell has no subcellular organelles, only infoldings of the plasma membrane called mesosomes. The deoxyribonucleic acid (DNA) is condensed within the cytosol to form the nucleoid. Some prokaryotes have tail-like flagella.

Bacterial cell walls

The peptidoglycan (protein and oligosaccharide) cell wall protects the prokaryotic cell from mechanical and osmotic pressure. A Gram-positive bacterium has a thick cell wall surrounding the plasma membrane, whereas Gram-negative bacteria have a thinner cell wall and an outer membrane, between which is the periplasmic space.

Related topics

Eukaryote cell organization (A2)
Amino acid structure (B1)
Membrane structure (E1)
DNA organization in chromosomes (F2)
Microtubules, cilia and flagella (N2)

Prokaryotes

Prokaryotes are the most numerous and widespread organisms on earth, and are so classified because they have no defined membrane-bound nucleus. Prokaryotes range in size from 0.1 to 10 μm, and have one of three basic shapes: spherical (**cocci**), rodlike (**bacilli**) or helically coiled (**spirilla**). They can be divided into two separate groups: the **eubacteria** and the **archaebacteria**. The eubacteria are the commonly encountered bacteria in soil, water and living in or on larger organisms, and include the Gram-positive and Gram-negative bacteria, and cyanobacteria (photosynthetic blue-green algae). The archaebacteria grow in unusual environments such as salt brines, hot acid springs and in the ocean depths, and include the sulfur bacteria and the methanogens.

Cell structure

Like all cells, a prokaryotic cell is bounded by a **plasma membrane** that completely encloses the cytosol and separates the cell from the external environment. The plasma membrane, which is about 8 nm thick, consists of a lipid bilayer containing proteins (see Topic E1). Although prokaryotes lack the membranous subcellular organelles characteristic of eukaryotes (see Topic A2), their plasma membrane may be infolded to form **mesosomes** (*Fig. 1*). The mesosomes may be the sites of deoxyribonucleic acid (DNA) replication and other specialized enzymatic reactions. In photosynthetic bacteria, the mesosomes contain the proteins and pigments that trap light and generate adenosine triphosphate (ATP). The aqueous cytosol contains the macromolecules [enzymes, messenger ribonucleic

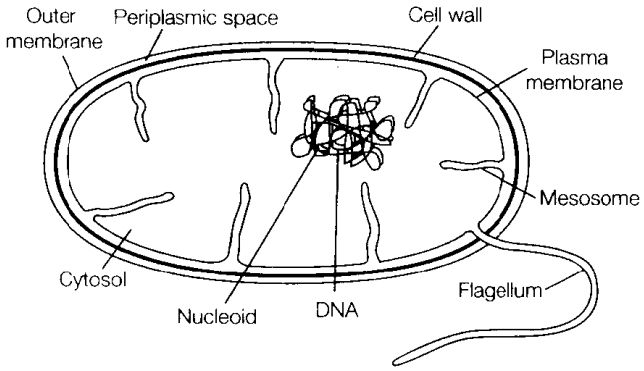

Fig. 1. Prokaryote cell structure.

acid (mRNA), transfer RNA (tRNA) and ribosomes], organic compounds and ions needed for cellular metabolism. Also within the cytosol is the prokaryotic 'chromosome' consisting of a single circular molecule of DNA which is condensed to form a body known as the **nucleoid** (*Fig. 1*) (see Topic F2). Many bacterial cells have one or more tail-like appendages known as **flagella** which are used to move the cell through its environment (see Topic N2).

Bacterial cell walls

To protect the cell from mechanical injury and osmotic pressure, most prokaryotes are surrounded by a rigid 3–25 nm thick **cell wall** (*Fig. 1*). The cell wall is composed of **peptidoglycan**, a complex of **oligosaccharides** and **proteins**. The oligosaccharide component consists of linear chains of alternating *N*-acetylglucosamine (GlcNAc) and *N*-acetylmuramic acid (NAM) linked β(1–4) (see Topic J1). Attached via an amide bond to the lactic acid group on NAM is a **D-amino acid**-containing tetrapeptide. Adjacent parallel peptidoglycan chains are covalently cross-linked through the tetrapeptide side-chains by other short peptides. The extensive cross-linking in the peptidoglycan cell wall gives it its strength and rigidity. The presence of D-amino acids in the peptidoglycan renders the cell wall resistant to the action of **proteases** which act on the more commonly occurring L-amino acids (see Topic B1), but provides a unique target for the action of certain **antibiotics** such as **penicillin**. Penicillin acts by inhibiting the enzyme that forms the covalent cross-links in the peptidoglycan, thereby weakening the cell wall. The β(1–4) glycosidic linkage between NAM and GlcNAc is susceptible to hydrolysis by the enzyme **lysozyme** which is present in tears, mucus and other body secretions.

Bacteria can be classified as either **Gram-positive** or **Gram-negative** depending on whether or not they take up the **Gram stain**. Gram-positive bacteria (e.g. *Bacillus polymyxa*) have a thick (25 nm) cell wall surrounding their plasma membrane, whereas Gram-negative bacteria (e.g. *Escherichia coli*) have a thinner (3 nm) cell wall and a second **outer membrane** (*Fig. 2*). In contrast with the plasma membrane (see Topic E3), this outer membrane is very permeable to the passage of relatively large molecules (molecular weight > 1000 Da) due to **porin proteins** which form pores in the lipid bilayer. Between the outer membrane and the cell wall is the **periplasm**, a space occupied by proteins secreted from the cell.

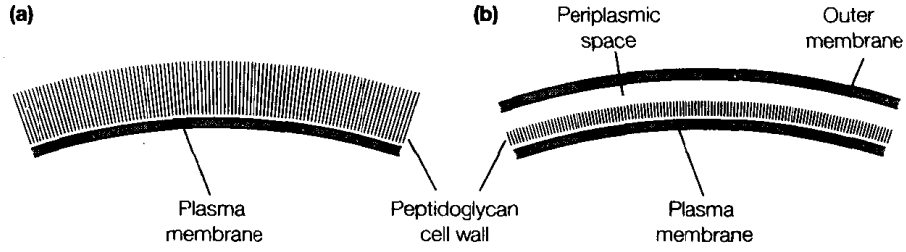

Fig. 2. Cell wall structure of (a) Gram-positive and (b) Gram-negative bacteria.

A2 EUKARYOTE CELL ORGANIZATION

Key Notes

Eukaryotes

Eukaryotic cells have a membrane-bound nucleus and a number of other membrane-bound subcellular (internal) organelles, each of which has a specific function.

Plasma membrane

The plasma membrane surrounds the cell, separating it from the external environment. The plasma membrane is a selectively permeable barrier due to the presence of specific transport proteins. It is also involved in receiving information when ligands bind to receptor proteins on its surface, and in the processes of exocytosis and endocytosis.

Nucleus

The nucleus stores the cell's genetic information as DNA in chromosomes. It is bounded by a double membrane but pores in this membrane allow molecules to move in and out of the nucleus. The nucleolus within the nucleus is the site of ribosomal ribonucleic acid (rRNA) synthesis.

Endoplasmic reticulum

This interconnected network of membrane vesicles is divided into two distinct parts. The rough endoplasmic reticulum (RER), which is studded with ribosomes, is the site of membrane and secretory protein biosynthesis and their post-translational modification. The smooth endoplasmic reticulum (SER) is involved in phospholipid biosynthesis and in the detoxification of toxic compounds.

Golgi apparatus

The Golgi apparatus, a system of flattened membrane-bound sacs, is the sorting and packaging center of the cell. It receives membrane vesicles from the RER, further modifies the proteins within them, and then packages the modified proteins in other vesicles which eventually fuse with the plasma membrane or other subcellular organelles.

Mitochondria

Mitochondria have an inner and an outer membrane separated by the intermembrane space. The outer membrane is more permeable than the inner membrane due to the presence of porin proteins. The inner membrane, which is folded to form cristae, is the site of oxidative phosphorylation, which produces ATP. The central matrix is the site of fatty acid degradation and the citric acid cycle.

Chloroplasts

Chloroplasts in plant cells are surrounded by a double membrane and have an internal membrane system of thylakoid vesicles that are stacked up to form grana. The thylakoid vesicles contain chlorophyll and are the site of photosynthesis. Carbon dioxide (CO_2) fixation takes place in the stroma, the soluble matter around the thylakoid vesicles.

Lysosomes

Lysosomes in animal cells are bounded by a single membrane. They have an acidic internal pH (pH 4–5), maintained by proteins in the membrane that pump in H^+ ions. Within the lysosomes are acid hydrolases; enzymes involved in the degradation of macromolecules, including those internalized by endocytosis.

Peroxisomes

Peroxisomes contain enzymes involved in the breakdown of amino acids and fatty acids, a byproduct of which is hydrogen peroxide. This toxic compound is rapidly degraded by the enzyme catalase, also found within the peroxisomes.

Cytosol

The cytosol is the soluble part of the cytoplasm where a large number of metabolic reactions take place. Within the cytosol is the cytoskeleton, a network of fibers (microtubules, intermediate filaments and microfilaments) that maintain the shape of the cell.

Plant cell wall

The cell wall surrounding a plant cell is made up of the polysaccharide cellulose. In woody plants, the phenolic polymer called lignin gives the cell wall additional strength and rigidity.

Plant cell vacuole

The membrane-bound vacuole is used to store nutrients and waste products, has an acidic pH and, due to the influx of water, creates turgor pressure inside the cell as it pushes out against the cell wall.

Related topics

- Microscopy (A3)
- Transport of macromolecules (E4)
- Cell signaling (E5)
- DNA organization in chromosomes (F2)
- Protein targeting (H3)
- Electron transport and oxidative phosphorylation (L2)
- Photosynthesis (L3)
- Microtubules, cilia and flagella (N2)

Eukaryotes

A eukaryotic cell is surrounded by a **plasma membrane**, has a membrane-bound nucleus and contains a number of other distinct **subcellular organelles** (*Fig. 1*). These organelles are membrane-bounded structures, each having a unique role and each containing a specific complement of proteins and other molecules. Animal and plant cells have the same basic structure, although some organelles and structures are found in one and not the other (e.g. chloroplasts, vacuoles and cell wall in plant cells, lysosomes in animal cells).

Plasma membrane

The plasma membrane envelops the cell, separating it from the external environment and maintaining the correct ionic composition and osmotic pressure of the cytosol. The plasma membrane, like all membranes, is impermeable to most substances but the presence of specific proteins in the membrane allows certain molecules to pass through, therefore making it **selectively permeable** (see Topic E3). The plasma membrane is also involved in communicating with other cells, in particular through the binding of ligands (small molecules such as hormones, neurotransmitters, etc.) to **receptor proteins** on its surface (see Topic E5). The plasma membrane is also involved in the **exocytosis** (secretion) and **endocytosis** (internalization) of macromolecules (see Topic E4).

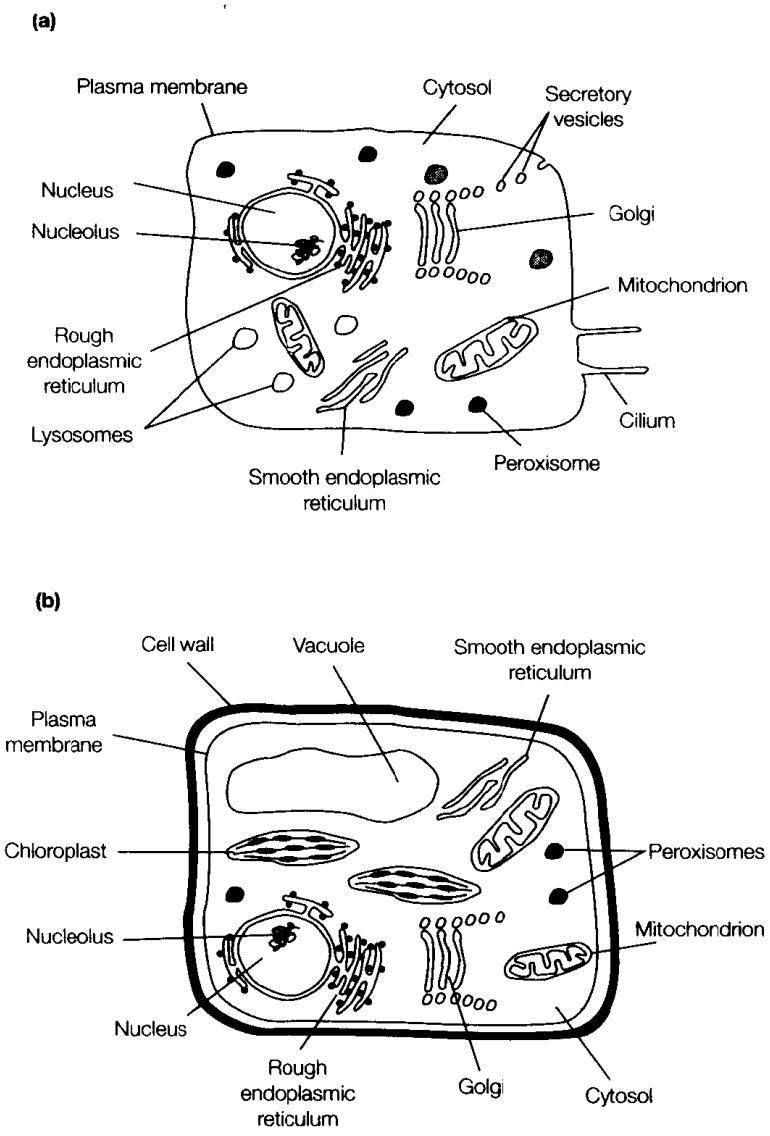

Fig. 1. Eukaryote cell structure. (a) Structure of a typical animal cell, (b) structure of a typical plant cell.

Nucleus

The nucleus is bounded by two membranes, the **inner and outer nuclear membranes**. These two membranes fuse together at the **nuclear pores** through which molecules [messenger ribonucleic acid (mRNA), proteins, ribosomes, etc.] can move between the nucleus and the cytosol. Other proteins, for example those involved in regulating gene expression, can pass through the pores from the cytosol to the nucleus. The outer nuclear membrane is often continuous with the rough endoplasmic reticulum (RER). Within the nucleus the **DNA** is tightly coiled around **histone proteins** and organized into complexes called **chromosomes** (see Topic F2). Visible under the light microscope (see Topic A3) is the **nucleolus**, a subregion of the nucleus which is the site of ribosomal ribonucleic acid (rRNA) synthesis.

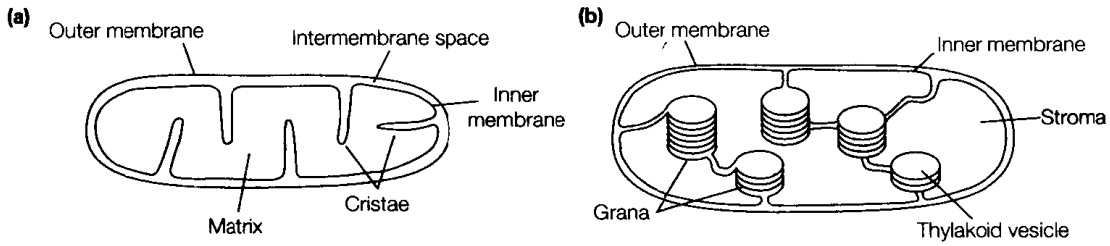

Fig. 2. Structure of (a) a mitochondrion and (b) a chloroplast.

Endoplasmic reticulum

The endoplasmic reticulum (ER) is an interconnected network of membrane vesicles. The **rough endoplasmic reticulum (RER)** is studded on the cytosolic face with **ribosomes**, the sites of **membrane and secretory protein biosynthesis** (see Topic H2). Within the lumen of the RER are enzymes involved in the **post-translational modification** (glycosylation, proteolysis, etc.) of membrane and secretory proteins (see Topic H4). The **smooth endoplasmic reticulum (SER)**, which is not studded with ribosomes, is the site of **phospholipid biosynthesis**, and is where a number of **detoxification reactions** take place.

Golgi apparatus

The Golgi apparatus, a system of flattened membrane-bound sacs, is the **sorting center** of the cell. Membrane vesicles from the RER, containing membrane and secretory proteins, fuse with the Golgi apparatus and release their contents into it. On transit through the Golgi apparatus, further **post-translational modifications** to these proteins take place and they are then sorted and packaged into different vesicles (see Topic H3). These vesicles bud off from the Golgi and are transported through the cytosol, eventually fusing either with the plasma membrane to release their contents into the extracellular space (a process known as **exocytosis**; see Topic E4) or with other internal organelles (lysosomes, peroxisomes, etc.).

Mitochondria

A mitochondrion has an **inner and an outer membrane** between which is the **intermembrane space** (*Fig. 2a*). The outer membrane contains **porin proteins** which make it permeable to molecules of up to 10 kDa. The inner membrane, which is considerably less permeable, has large infoldings called **cristae** which protrude into the **central matrix**. The inner membrane is the site of oxidative phosphorylation and electron transport involved in ATP production (see Topic L2). The central matrix is the site of numerous metabolic reactions including the citric acid cycle (see Topic L1) and fatty acid breakdown (see Topic K2). Also within the matrix is found the mitochondrial DNA which encodes some of the mitochondrial proteins.

Chloroplasts

Chloroplasts also have **inner and outer membranes**. In addition, there is an extensive internal membrane system made up of **thylakoid vesicles** (interconnected vesicles flattened to form discs) stacked upon each other to form **grana** (*Fig. 2b*). Within the thylakoid vesicles is the green pigment **chlorophyll** (see Topic M4), along with the enzymes that trap light energy and convert it into chemical energy in the form of ATP (see Topic L3). The **stroma**, the space surrounding the thylakoid vesicles, is the site of carbon dioxide (CO_2) fixation