

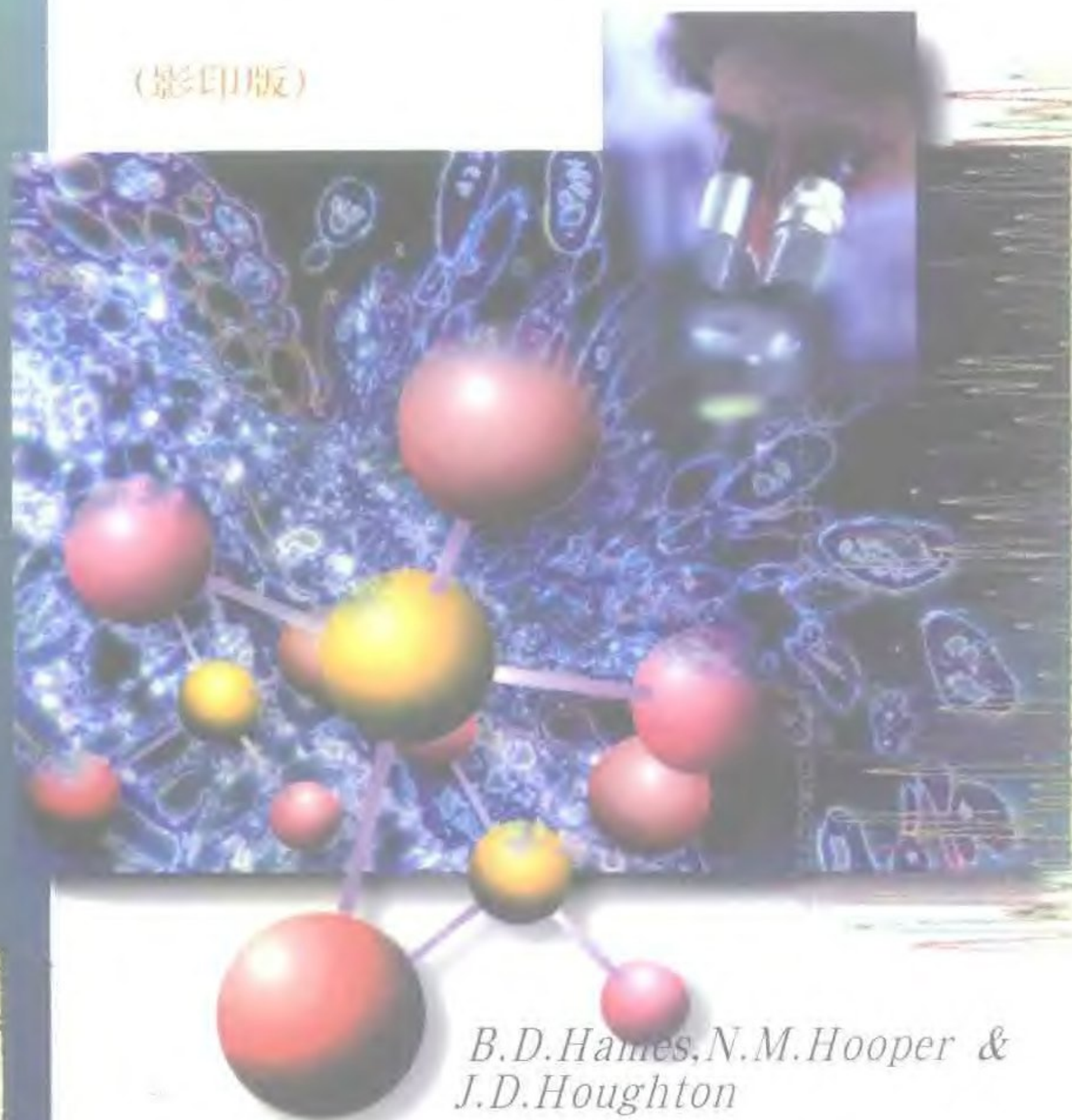
现代生物学精要速览

Instant Notes in

BIOCHEMISTRY

生物化学

(影印版)



*B.D.Hames, N.M. Hooper &
J.D. Houghton*

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*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-流教授编写。它以-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-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

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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	ix
Preface	xi
Section A – Cells and their structure	1
A1 Prokaryote cell organization	1
A2 Eukaryote cell organization	4
A3 Microscopy	9
A4 Subcellular fractionation	14
Section B – Amino acids and proteins	17
B1 Amino acid structure	17
B2 Protein structure	22
B3 Protein structure related to function	28
B4 Protein purification	34
B5 Chromatography of proteins	38
B6 Electrophoresis of proteins	42
B7 Protein sequencing	47
Section C – Enzymes	53
C1 Introduction to enzymes	53
C2 Factors affecting enzyme activity	58
C3 Enzyme kinetics and inhibition	65
C4 Control of enzyme activity	70
Section D – Antibodies	77
D1 The immune system: overview	77
D2 Antibody structure	81
D3 Polyclonal and monoclonal antibodies	85
D4 Antibody synthesis	87
D5 Antibodies as tools	92
Section E – Membranes: structure and function	97
E1 Membrane structure	97
E2 Membrane proteins	104
E3 Transport of small molecules	111
E4 Transport of macromolecules	116
E5 Cell signaling	121
Section F – DNA structure and replication	127
F1 DNA structure	127
F2 DNA organization in chromosomes	131
F3 DNA replication in prokaryotes	135
F4 DNA replication in eukaryotes	140
Section G – RNA synthesis and processing	145
G1 RNA structure	145
G2 Gene transcription in prokaryotes	147
G3 Gene transcription in eukaryotes: overview	151
G4 Expression of eukaryotic protein-coding genes	153
G5 Expression of eukaryotic rRNA and tRNA genes	160
G6 Control of gene transcription in prokaryotes	163
G7 Control of gene transcription in eukaryotes	167
Section H – Protein synthesis and modification	171
H1 The genetic code	171

	H2	Protein synthesis (translation)	174
	H3	Protein targeting	182
	H4	Protein glycosylation	190
Section I		Recombinant DNA technology	195
	I1	Restriction enzymes	195
	I2	Nucleic acid hybridization	200
	I3	DNA cloning	203
	I4	Viruses	208
	I5	DNA sequencing	212
	I6	Polymerase chain reaction (PCR)	215
Section J		Carbohydrate metabolism	219
	J1	Monosaccharides and disaccharides	219
	J2	Polysaccharides and oligosaccharides	225
	J3	Glycolysis	229
	J4	Gluconeogenesis	238
	J5	Pentose phosphate pathway	246
	J6	Glycogen degradation and synthesis	250
	J7	Control of glycogen metabolism	253
Section K		Lipid metabolism	259
	K1	Structures and roles of fatty acids	259
	K2	Fatty acid breakdown	263
	K3	Fatty acid synthesis	270
	K4	Metabolism of triacylglycerols	276
	K5	Cholesterol metabolism	281
	K6	Lipoproteins	287
Section L		Respiration and energy	291
	L1	The citric acid cycle	291
	L2	Electron transport and oxidative phosphorylation	295
	L3	Photosynthesis	306
Section M		Nitrogen metabolism	317
	M1	Nitrogen fixation and assimilation	317
	M2	Amino acid metabolism	321
	M3	The urea cycle	328
	M4	Hemes and chlorophylls	334
Section N		Cell specialization	339
	N1	Muscle contraction	339
	N2	Microtubules, cilia and flagella	345
	N3	Nerve conduction	349
	N4	Collagen	353
Further reading			361
Index			367

ABBREVIATIONS

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

LDL	low density lipoprotein	RER	rough endoplasmic reticulum
Leu	leucine	RF	release factor
LMM	light meromyosin	RFLP	restriction fragment length polymorphism
Lys	lysine	RNA	ribonucleic acid
Met	methionine	RNase	ribonuclease
mV	millivolt	rRNA	ribosomal RNA
mRNA	messenger RNA	rubisco	ribulose biphosphate carboxylase
NAD ⁺	nicotinamide adenine dinucleotide (oxidized)	SDS	sodium dodecyl sulfate
NADH	nicotinamide adenine dinucleotide (reduced)	Ser	serine
NADP ⁺	nicotinamide adenine dinucleotide phosphate (oxidized)	SER	smooth endoplasmic reticulum
NADPH	nicotinamide adenine dinucleotide phosphate (reduced)	snoRNA	small nucleolar RNA
NAM	N-acetylmuramic acid	snoRNP	small nucleolar ribonucleoprotein
NHP	nonhistone protein	snRNA	small nuclear RNA
PAGE	polyacrylamide gel electrophoresis	snRNP	small nuclear ribonucleoprotein
PC	plastocyanin	SRP	signal recognition particle
PCR	polymerase chain reaction	SSB	single-stranded DNA-binding (protein)
PEP	phosphoenolpyruvate	TBP	TATA box-binding protein
PFK	phosphofructokinase	TFII	transcription factor for RNA polymerase II
Phe	phenylalanine	Thr	threonine
P _i	inorganic phosphate	T _m	melting point
pI	isoelectric point	tRNA	transfer RNA
pK	dissociation constant	Trp	tryptophan
PKA	protein kinase A	Tyr	tyrosine
PP _i	inorganic pyrophosphate	UDP	uridine diphosphate
Pro	proline	UMP	uridine monophosphate
PQ	plastoquinone	UTP	uridine 5'-triphosphate
PSI	photosystem I	UV	ultraviolet
PSII	photosystem II	Val	valine
PTI	phenylthiohydantoin	V ₀	initial rate of reaction
Q	ubiquinone (coenzyme Q)	VLDL	very low density lipoprotein
QH ₂	ubiquinol (CoQH ₂)	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)

DNA organization in chromosomes (P2)

Amino acid structure (B1)

Membrane structure (E1)

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

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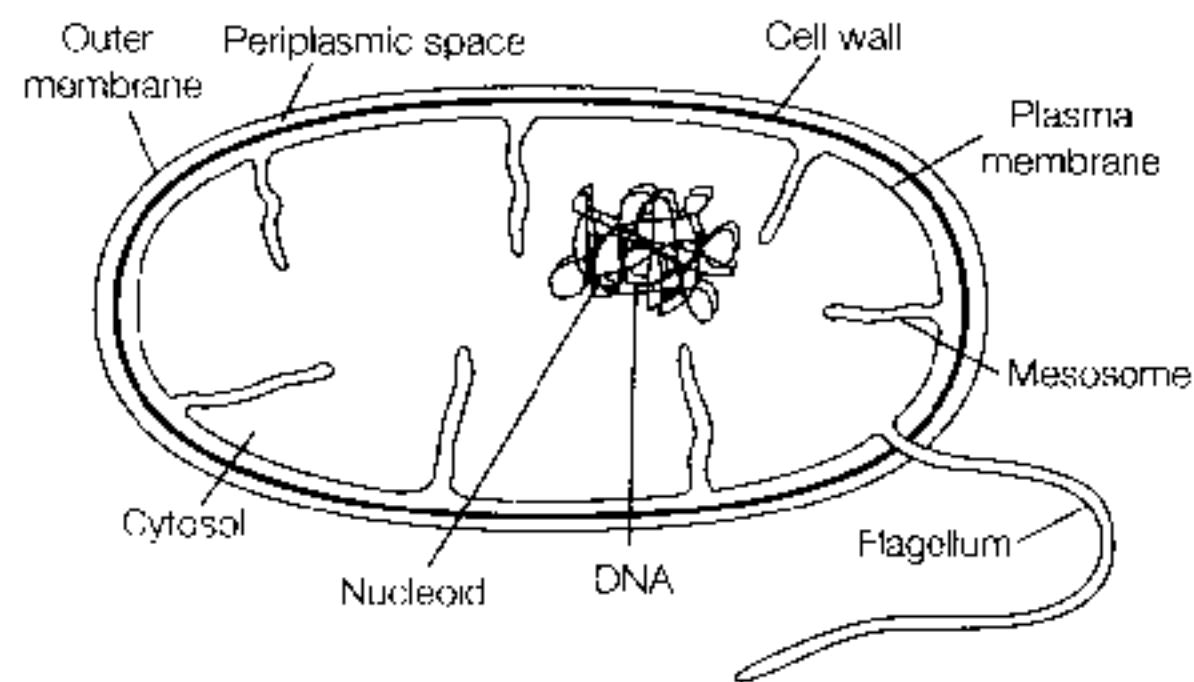


Fig. 1. Prokaryote cell structure

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 $\beta(1-4)$ (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 $\beta(1-4)$ 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.

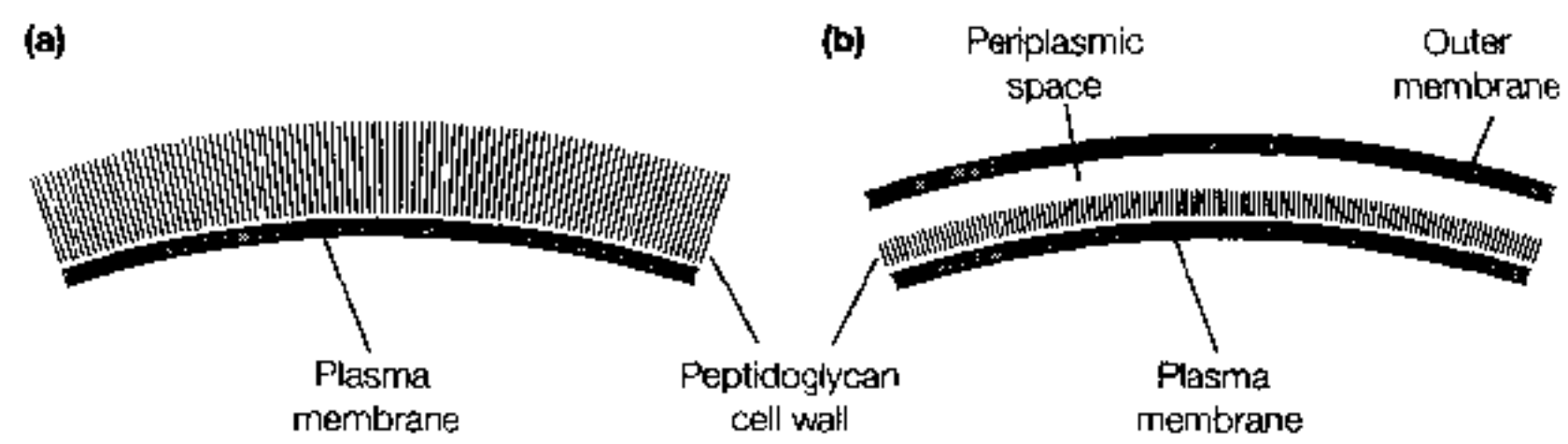


Fig. 2. Cell wall structure of (a) Gram-positive and (b) Gram-negative bacteria.

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 (CO₂) 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).

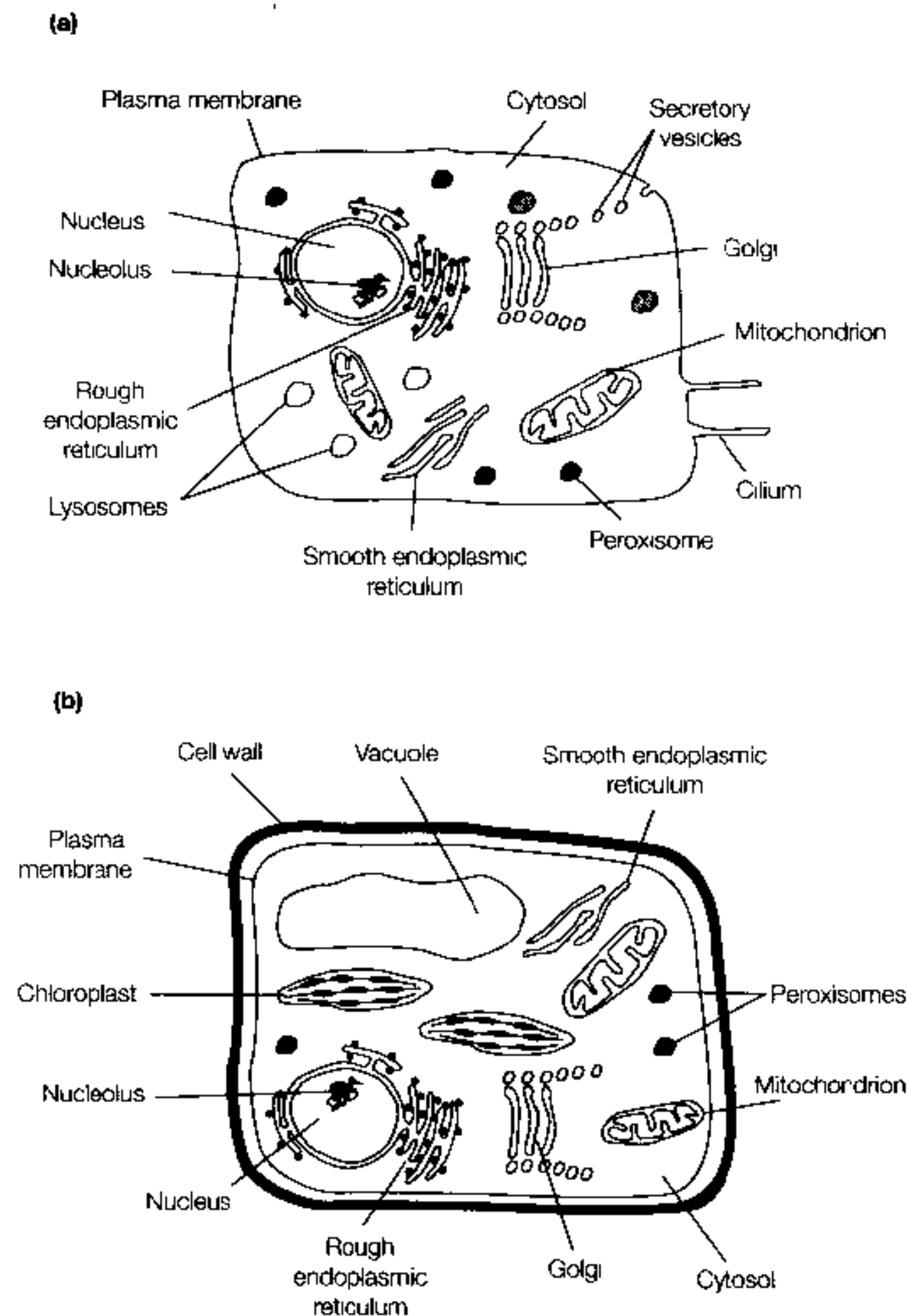


Fig 1. Eukaryote cell structure. (a) Structure of a typical animal cell, (b) structure of a typical plant cell.

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.

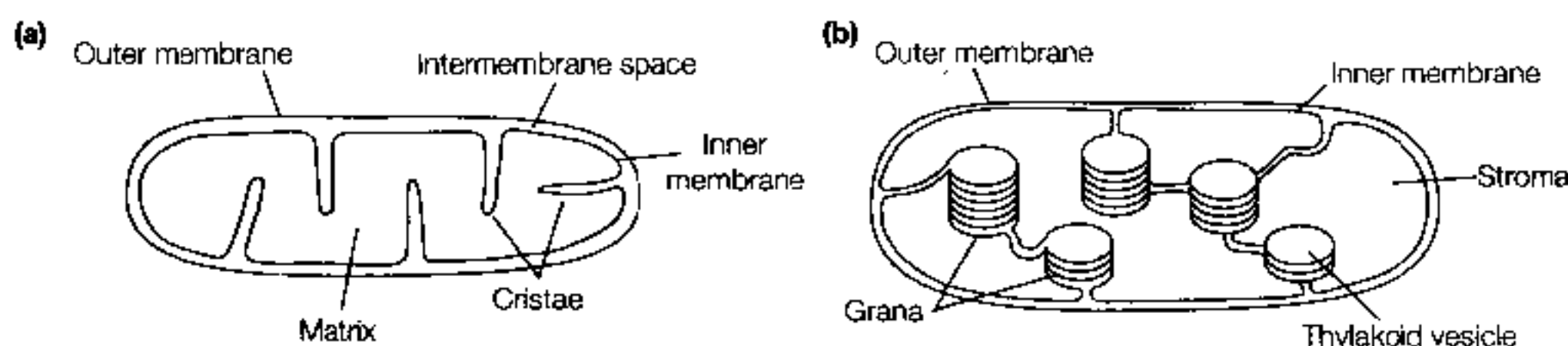


Fig. 2. Structure of (a) a mitochondrion and (b) a chloroplast.

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