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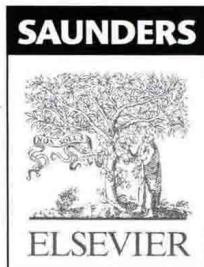
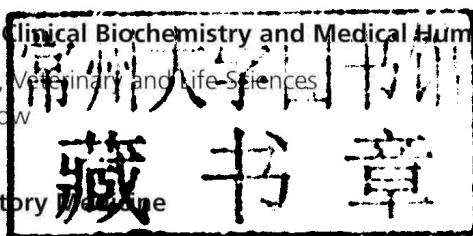
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FOURTH EDITION

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BIOCHEMISTRY

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Preface

We now present the 4th edition of *Medical Biochemistry*. Our aim remains, as before, to provide biochemical foundation for the study of clinical medicine – with down-to-earth practical relevance.

A textbook is a snapshot of a field as it exists at the time of writing. Such ‘photographic’ metaphor is appropriate here, because biochemistry undergoes constant change; in the period since the publication of the 3rd edition it has probably changed faster than ever before.

While core metabolic pathways remain largely unchanged, our understanding of underlying regulatory mechanisms is better, thanks to the progress in identifying signaling pathways. In many instances, these pathways have become targets for drugs, and underpin the impressive therapeutic progress in fields such as oncology.

Since completion of the Human Genome Project, genome-wide association studies and bioinformatic analyses have allowed us to put together a new picture of genetic regulation, the hallmarks of which are interactions between multiple, heterogeneous transcription factors and gene promoters, and the emerging field of epigenetics.

Behind this are, as had happened many times before in the history of science, major advances in methodology, including rapidly expanding genetic screening. The common denominator between methodologies now employed in genetic research laboratories and hospital clinical labs has been the advent of robotics and bioinformatics, and therefore the ability to process – and interpret – an ever-increasing amount of data.

This edition has again been substantially updated. We have rewritten the chapters on lipids, glucose homeostasis, nutrition and biochemical endocrinology, and added a section on the effects of exercise on muscle development and cardiovascular health. The chapter on the -omics incorporates new directions in proteomics, metabolomics and recombinant DNA technology.

This edition also benefits from the expertise of new authors who have shared their perspectives on signaling, fat and

glycoconjugate metabolism, exercise biochemistry, nutrition, and blood coagulation processes.

We have expanded the chapter on the GI tract as an important interface between the organism and the environment, and now have a separate short chapter on kidney function. In both we provide more information on membrane transport systems. We remain convinced that the biochemistry of water and electrolyte balance is as important for future clinicians as the key metabolic pathways – and deserve more emphasis in the biochemistry curricula.

We have updated literature and web references throughout the textbook. At the same time we were able to eliminate some web links in this edition, because search engines and websites such as Wikipedia and YouTube now provide quick access to so many rapidly evolving resources.

Throughout the text we strive to explain complex issues as simply as possible, but try hard not to become superficial. Unfortunately, new fields come with new terminologies and numerous additions to scientific slang. The discovery of new genes and new signaling pathways means new names and acronyms. We identify them here not as material to be committed to memory, but to help build a knowledge framework without oversimplification. The fact that some chapters may seem complex to the uninitiated may also reflect the true state of knowledge – the complexity, or even a touch of confusion, often present before a coherent picture emerges.

The Question Bank (Self-Assessment) and many more resources are available at the Elsevier website, www.student-consult.com, to which the reader is referred. Student Consult also provides links to other Elsevier biomedical textbooks which integrate and build on knowledge of medical biochemistry. There is also a companion publication, *Medical Biochemistry Flash Cards*, which provides means for quick revision.

As before, we welcome comments, criticisms and suggestions from our readers. Many of these suggestions are incorporated in this 4th edition. There is no better way to continue the improvement of this text.

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Dedication

To inspirational academics
Inquisitive students
And all those who want to be good doctors

Acknowledgments

First of all, we wish to thank our contributors for sharing their expertise with us and for fitting the writing – again – into their busy research, teaching and clinical schedules. In the 4th edition, we welcome several new contributors: Catherine Bagot, Norma Frizzel, Koichi Honke, Fredrik Karpe, Matthew Kostek, Jennifer Logue, Alison Michie, Matthew Priest, Ryoji Nagai and Ian Salt. We are delighted that they have joined us.

We were saddened by the death of our good friends and contributors to previous editions, A. Michael Wallace and Alan D. Elbein.

As in the previous editions, we greatly valued the excellent secretarial assistance of Jacky Gardiner in Glasgow.

We are very grateful to students and academics from universities around the world who continue to provide us with comments, criticisms and suggestions.

The key to the whole project has been, of course, the Elsevier team. Our thanks go to Nani Clansey, Senior Development Editor, who enthusiastically steered the project through, and also to Meghan K. Ziegler and Madelene Hyde who formulated the strategy. We are very grateful to the production staff, Anne Collett, Samuel Crowe and Andrew Riley who gave the book its final form.

Our inspiration to change and improve this text comes also from ‘the field’ – from the issues, questions and decisions that arise in our everyday clinical practice, in the outpatient clinics and during wardrounds. Therefore a final thank you goes to all our clinical colleagues and doctors in training.

Abbreviations

A	adenine	BMR	basal metabolic rate
ABC	ATP-binding cassette	BNP	brain natriuretic peptide
ACE	angiotensin-converting enzyme	bp	base pair
acetyl-CoA	acetyl coenzyme A	2,3-BPG	2,3-bisphosphoglycerate
ACh	acetylcholine	BUN	blood urea nitrogen equivalent of (but not the same as) serum urea
ACP	acyl carrier protein		body weight
ACTase	aspartate carbamoyl transferase	bw	cytosine
ACTH	adrenocorticotrophic hormone	C	carbonic anhydrase
ADC	AIDS-dementia complex	CA	caspase-dependent endonuclease
ADH	alcohol dehydrogenase	CAD	carboxyaminoimidazole
ADH	antidiuretic hormone (also known as AVP)	CAIR	ribonucleotide
ADP	adenosine diphosphate	cAMP	cyclic AMP
AE	anion exchanger	CAT	catalase
AFP	α -fetoprotein	CD	cluster designation: classification system for cell surface molecules
AGE	advanced glycoxidation (glycation) endproduct	CDG	congenital disorders of glycosylation
AHF	antihemophilic factor	CDGS	carbohydrate-deficient glycoprotein syndromes
AICAR	5-aminoimidazole-4-carboxamide ribonucleotide	CDK	cyclin-dependent kinase
AIDS	acquired immunodeficiency syndrome	CDKI	cyclin-dependent kinase inhibitor
AIR	5-aminoimidazole ribonucleotide	CDP	cytidine diphosphate
ALDH	aldehyde dehydrogenase	CFTR	cystic fibrosis transmembrane conductance regulator
ALP	alkaline phosphatase	cGMP	cyclic GMP
ALT	alanine aminotransferase	CGRP	calcitonin gene-related peptide
AML	acute myeloblastic leukemia	CML	chronic myeloid leukemia
AMP	adenosine monophosphate	CMP	cytidine monophosphate
ANP	atrial natriuretic peptide	CNS	central nervous system
APC	adenomatous polyposis coli (gene)	COAD	chronic obstructive airways disease (synonym: COPD)
apoA, B, etc.	apolipoprotein A, B, etc.	COMT	catecholamine-O-methyl transferase
APRT	adenosine phosphoribosyl transferase	COPD	chronic obstructive pulmonary disease (synonym: COAD)
APTT	activated partial thromboplastin time	CoQ ₁₀	coenzyme Q ₁₀ (ubiquinone)
AQP	aquaporin	COX-1	cyclooxygenase-1
ARDS	acute respiratory distress syndrome	CK	creatine phosphokinase (also CPK)
ARE	antioxidant response element	CPK	creatine phosphokinase (also CK)
AST	aspartate aminotransferase	CPS I, II	carbamoyl phosphate synthetase I, II
ATF	activation transcription factor	CPT I, II	carnitine palmitoyl transferase I, II
ATM	ataxia telangiectasia-mutated gene	CREB	cAMP-response element-binding protein
ATP	adenosine triphosphate	CRGP	calcitonin-related gene peptide
AVP	arginine-vasopressin (same as antidiuretic hormone)	CRH	corticotropin-releasing hormone
AZT	azido-2',3'-dideoxythymidine		
Bcl-2	B cell lymphoma protein 2		
BMI	body mass index		

CRP	C-reactive protein	FGAR	formylglycinamide ribonucleotide
CSF	cerebrospinal fluid	FGF	fibroblast growth factor
CT	calcitonin	FHH	familial hypocalciuric hypercalcemia
CTP	cytidine triphosphate	FMN	flavin mononucleotide
CVS	chorionic villous sampling	FMNH ₂	reduced flavin mononucleotide
DAG	diacylglycerol	FRAXA	fragile X syndrome
DCC	'delete in colon carcinoma' gene	Fru-1,6-BP	fructose-1,6 bisphosphate
dNPs	deoxynucleotides	Fru-2,6-BP	fructose-2,6 bisphosphate
ddNPs	dideoxynucleotides	Fru-2,6-BPase	fructose-2,6 bisphosphatase
DEAE	diethylaminoethyl	Fru-6-P	fructose-6-phosphate
DGGE	denaturing-gradient gel electrophoresis	FSF	fibrin-stabilizing factor
DHAP	dihydroxyacetone phosphate	FSH	follicle-stimulating hormone
DIC	disseminated intravascular coagulation	G	guanine
DIPE, DFP	diisopropylphosphofluoride	G3PDH	glyceraldehyde-3-phosphate dehydrogenase
DNA	deoxyribonucleic acid	GABA	γ-amino butyric acid
DNP	2,4-dinitrophenol	GAG	glycosaminoglycan
dNTPs	deoxynucleotides triphosphates	Gal	galactose
Dol-P	dolichol phosphate	Gal-1-P	galactose-1-phosphate
Dol-PP-GlcNAc	dolichol pyrophosphate- <i>N</i> -acetylglucosamine	GalNAc	<i>N</i> -acetylgalactosamine
DOPA	dihydroxyphenylalanine	GalNH ₂	galactosamine
DPPC	dipalmitoyl phosphatidyl choline	GAP	guanosine-triphosphatase activating protein
DVT	deep vein thrombosis	GAPDH	glyceraldehyde-3-phosphate dehydrogenase
EBV	Epstein-Barr virus	GAR	glycinamide ribonucleotide
ECF	extracellular fluid	GDH	glutamate dehydrogenase
ECM	extracellular matrix	GDP	guanosine diphosphate
EDRF	endothelium-derived relaxing factor (nitric oxide)	GDP-Fuc	guanosine diphosphate-L-fucose
EDTA	ethylenediaminetetraacetic acid	GDP-Man	guanosine diphosphate-mannose
EF-1, 2	elongation factor-1,2	GEAP	glial fibrillary acidic protein
EFAs	essential fatty acids	γGT	γ-glutamyl transferase
EGF	epidermal growth factor	GH	growth hormone
eIF-3	eukaryotic initiation factor 3	GHRH	growth hormone-releasing hormone
EMSA	electrophoretic mobility shift assay	GIP	glucose-dependent insulinotropic peptide
ENaC	epithelial sodium channel	GIT	gastrointestinal tract
ER	endoplasmic reticulum	GK	glucokinase
ERK	extracellular signal-regulated kinase	Glc	glucose
ESR	erythrocyte sedimentation rate	Glc-1-P	glucose-1-phosphate
FACIT	fibril-associated collagen with interrupted triple helices	Glc-6-P	glucose-6-phosphate
FAD	flavin adenine dinucleotide	Glc-6-Pase	glucose-6-phosphatase
FADD	a 'death domain' accessory protein	GlcN-6-P	glucosamine-6-phosphate
FADH ₂	reduced flavin adenine dinucleotide	GlcNAc	<i>N</i> -acetylglucosamine
FAICAR	5-formylaminoimidazole-4-carboxamide ribonucleotide	GlcNAc-1P	<i>N</i> -acetylglucosamine-1-phosphate
FAP	familial adenomatous polyposis	GlcNAc-6-P	<i>N</i> -acetylglucosamine-6-phosphate
Fas	apoptosis signaling molecule: a 'death domain' accessory protein (CD95)	GlcNH ₂	glucosamine
FBPase	fructose bisphosphatase	GlcUA	D-glucuronic acid
FDP	fibrin degradation product	GLP-1	glucagon-like peptide-1
		GLUT	glucose transporter (GLUT-1 to GLUT-5)
		GM ₁	monosialoganglioside 1
		GMP	guanosine monophosphate

GnRH	gonadotropin-releasing hormone	IRE-BP	IRE-binding protein
GP1b-IXa (etc.)	glycoprotein receptor 1b-IXa (etc.)	IRMA	immunoradiometric assay
GPx	glutathione peroxidase	ITAM	immunoreceptor tyrosine activation motif
GRE	glucocorticoid response element	ITIM	immunoreceptor tyrosine inhibition motif
GSH	reduced glutathione	JAK	Janus kinase
GSSG	oxidized glutathione	JNK	Jun N-terminal kinase
GTP	guanosine triphosphate	K	equilibrium constant
GTPase	guanosine triphosphatase	kb	kilobase
5-HIAA	5-hydroxyindoleacetic acid	kbp	kilobase pair(s)
5-HT	5-hydroxytryptamine	KCCT	kaolin-cephalin clotting time
Hb	hemoglobin	KIP2	cell cycle regulatory molecule
HBOC	Hb-based oxygen carrier	K_m	Michaelis constant
HCM	hypercalcemia associated with malignancy	LACI	lipoprotein-associated coagulation inhibitor
Hct	hematocrit	LCAT	lecithin: cholesterol acyltransferase
HDL	high-density lipoprotein	LDH	lactate dehydrogenase
HGF-R	hepatocyte growth factor receptor	LDL	low-density lipoprotein
HGP	Human Genome Project	LH	luteinizing hormone
HGPRT	hypoxanthine-guanine phosphoribosyl transferase	LPL	lipoprotein lipase
HIV	human immunodeficiency virus	LPS	lipopolysaccharide
HLA	human leukocyte antigen (system)	LRP	LDL-receptor-related protein
HLH	helix-loop-helix (motif)	M-CSF-R	macrophage colony-stimulating factor receptor
HMG	hydroxymethylglutaryl	malonyl-CoA	malonyl coenzyme A
HMWK	high-molecular-weight kininogen	Man	mannose
HNPCC	hereditary nonpolyposis colorectal cancer	Man-1-P	mannose-1-phosphate
hnRNA	heteronuclear ribonucleic acid	Man-6-P	mannose-6-phosphate
HPLC	high-performance liquid chromatography	MAO	monoamine oxidase
HPT	hyperparathyroidism	MAPK	mitogen-activated protein kinase (a superfamily of signal-transducing kinases)
HRT	hormone replacement therapy	Mb	myoglobin
HTGL	hepatic triglyceride lipase	MCHC	mean corpuscular hemoglobin concentration
HTH	helix-turn-helix (motif)	MCP-1	monocyte chemoattractant protein-1
ICAM-1	intracellular cell adhesion molecule-1	MCV	mean corpuscular volume
ICF	intracellular fluid	MDR	multidrug resistance
IDDM	insulin-dependent diabetes mellitus (term now substituted by Type 1 diabetes mellitus)	MEKK	mitogen-activated protein kinase kinase
IDL	intermediate-density lipoprotein	MEN IIA	multiple endocrine neoplasia type IIA
IdUA	L-iduronic acid	met-tRNA	methionyl-tRNA
IEF	isoelectric focusing	MGUS	monoclonal gammopathy of uncertain significance
IFN- γ	interferon- γ	MHC	major histocompatibility complex
Ig	immunoglobulin	miRNAs	micro RNAs
IGF	insulin growth factor	MMPs	matrix metalloproteinases
IGF-1	insulin-like growth factor 1	MPO	myeloperoxidase
IL	interleukin (IL-1 to IL-29)	mRNA	messenger ribonucleic acid
IMP	inosine monophosphate	MRP	multidrug resistance-associated protein
Inr	initiator (nucleotide sequence of a gene)		
IP ₁ I-1-P ₁ , I-4-P ₁ (etc.)	inositol monophosphates		
IP ₂ , I-1, 3-P ₂ , I-1, 4-P ₂	inositol bisphosphates		
IP ₃ , I-1, 4, 5-P ₃	inositol trisphosphate		
IRE	iron response element		

MS	mass spectrometry	PEPCK	phosphoenolpyruvate
MSH	melanocyte-stimulating hormone		carboxykinase
MSUD	maple syrup urine disease	PF3	platelet factor 3
MyoD	muscle cell-specific transcription factor	PFK-1 (-2)	phosphofructokinase 1 (2)
Na ⁺ /K ⁺ -ATPase	sodium-potassium ATPase	PGG ₂	prostaglandin G ₂ (etc.)
NABQI	N-acetyl benzoquinoneimine	PGK	phosphoglycerate kinase
NAC	N-acetylcysteine	PGM	phosphoglucomutase
NAD ⁺	nicotinamide adenine dinucleotide (oxidized)	PHHI	persistent hyperinsulinemic hypoglycemia of infancy
NADH	nicotinamide adenine dinucleotide (reduced)	PHP	pseudohypoparathyroidism
NADP ⁺	nicotinamide adenine dinucleotide phosphate (oxidized)	Pi	inorganic phosphate
NADPH	nicotinamide adenine dinucleotide phosphate (reduced)	PI-3-K	phosphoinositide-3-kinase
NANA	N-acetylneuraminic acid (sialic acid)	PIP ₂ /PIP ₃	phosphatidylinositol bisphosphate/trisphosphate
ncRNAs	noncoding RNAs	PK	pyruvate kinase
NF	nuclear factor	PKA/PKC	protein kinase A/C
NF-II	type II neurofibromatosis	PKU	phenylketonuria
NGF	nerve growth factor	PL	phospholipase A, etc.
NHE	sodium-hydrogen exchanger	PLA/PLC	phospholipase A/C
NIDDM	noninsulin-dependent diabetes mellitus (term now substituted by Type 2 diabetes mellitus)	PMA	phorbol myristic acetate
NKCC1	Na-K-Cl co-transporter 1 (etc.)	PNS	peripheral nervous system
NMDA	N-methyl-D-aspartate	PPARs	peroxisome proliferator-activated receptors
NPY	neuropeptide Y	PPi	inorganic pyrophosphate
NSAID	nonsteroidal antiinflammatory drug	PRL	prolactin
nt	nucleotide (as measure of size/length of a nucleic acid)	PrP	prion protein
1,25(OH) ₂ D ₃	1,25-dihydroxy vitamin D ₃	PRPP	5-phosphoribosyl- α -pyrophosphate
OGTT	oral glucose tolerance test	PS	phosphatidylserine
8-oxoG	8-oxo-2'-deoxyguanosine	PT	prothrombin time
OxS	oxidative stress	PTA	plasma thromboplastin antecedent
3-PG	3-phosphoglycerate	PTH	parathyroid hormone
p38RK	p38-reactivating kinase	PTHrP	parathyroid hormone-related protein
Pa	pascal	PTK	protein tyrosine kinase
PA	phosphatidic acid	PTPase	phosphotyrosine phosphatase
PAF	platelet-activating factor	Py	pyrimidine base (in a nucleotide sequence)
PAGE	polyacrylamide gel electrophoresis	R	receptor (with qualifier, not alone)
PAI-1	plasminogen activator inhibitor-1	RAIDD	a 'death domain' accessory protein
PAPS	phosphoadenosine phosphosulfate	Rb	retinoblastoma protein
PC	phosphatidyl choline	RBC	red blood cell
PC	pyruvate carboxylase	RDS	respiratory distress syndrome
PCR	polymerase chain reaction	RER	rough endoplasmic reticulum
PDE	phosphodiesterase	RFLP	restriction fragment length
PDGF	platelet-derived growth factor	RIP	polymorphism
PDH	pyruvate dehydrogenase		a 'death domain' accessory protein
PDK	phosphatidylinositol dependent kinase	RKK	p38RK homologue of MEK
PE	phosphatidyl ethanolamine	RNA	ribonucleic acid
PEP	phosphoenolpyruvic acid	RNAi	RNA interference
		RNAPol I/II	RNA polymerase I/II
		RNR	ribonucleotide reductase
		RNS	reactive nitrogen species
		ROS	reactive oxygen species
		S	Svedberg unit

SACAIR	5-aminoimidazole-4-(<i>N</i> -succinylcarboxamide) ribonucleotide	TB	tuberculosis
SAM	<i>S</i> -adenosyl methionine	TBG	thyroid-binding globulin
SAPK	stress-activated protein kinase	TCA	tricarboxylic acid cycle
SCIDS	severe combined immunodeficiency syndrome	TCT	thrombin clotting time
scuPA	single-chain urinary-type plasminogen activator	TEG	thromboelastography
SD	standard deviation	TF	transcription factor (with qualifier)
SDS	sodium dodecyl sulfate	TFPI	tissue factor pathway inhibitor
SDS-PAGE	sodium dodecyl sulfate-polyacrylamide gel electrophoresis	TG	triglyceride (triacylglycerol)
SEK	SAPK homologue of MEK	TGF(- β)	transforming growth factor- β
SER	smooth endoplasmic reticulum	T_{\max}	K _m for facilitated transport protein
ser-P	serine phosphate	TNF	tumor necrosis factor
SGLT	Na ⁺ -coupled glucose symporter	TNF-R	tumor necrosis factor receptor
SH	(Figs only) steroid hormone	tPA	tissue-type plasminogen activator
SH2	Src-homology region-2	TRADD	a 'death domain' accessory protein
SIADH	syndrome of inappropriate antidiuretic hormone secretion	TRAFF	a 'death domain' accessory protein
siRNAs	small interfering RNAs	TRH	thyrotropin-releasing hormone
snRNA	small nuclear RNA	TSH	thyroid-stimulating hormone (thyrotropin)
SOD	superoxide dismutase	TTP	thymidine triphosphate
SPCA	serum prothrombin conversion accelerator	TXA ₂	thromboxane A ₂
Src	a protein tyrosine kinase	U	uridine
SRE	steroid response element	UCP	uncoupling protein
SREBPs	sterol regulatory element-binding proteins (SREBP 1a, SREBP 1c)	UDP	uridine diphosphate
SRP	signal recognition particle	UDP-Gal	UDP-galactose
SSCP	single-strand conformational polymorphism	UDP-GalNAc	UDP- <i>N</i> -acetylgalactosamine
SSRI	selective serotonin reuptake inhibitor	UDP-Glc	UDP-glucose
STAT	signal transducer and activator of transcription	UDP-GlcNAc	UDP- <i>N</i> -acetylglucosamine
SUR	sulfonylurea receptor	UDP-GlcUA	UDP glucuronic acid
T	thymine	UMP	uridine monophosphate
T ₃	tri-iodothyronine	uPA	urinary-type plasminogen activator
T ₄	thyroxine	UTR	untranslated region
TAG	triacylglycerol (triglyceride)	UV	ultraviolet
TAP	transporter associated with antigen presentation	VCAM-1	vascular cell adhesion molecule 1
		VDCC	voltage-dependent calcium channel
		VIP	vasoactive intestinal peptide
		VLDL	very low-density lipoprotein
		vWF	von Willebrand factor
		WAF1	cell cycle regulator
		X-SCID	X-linked severe combined immunodeficiency
		XMP	xanthine monophosphate
		XO	xanthine oxidase
		ZP3	zona pellucida 3 glycoprotein