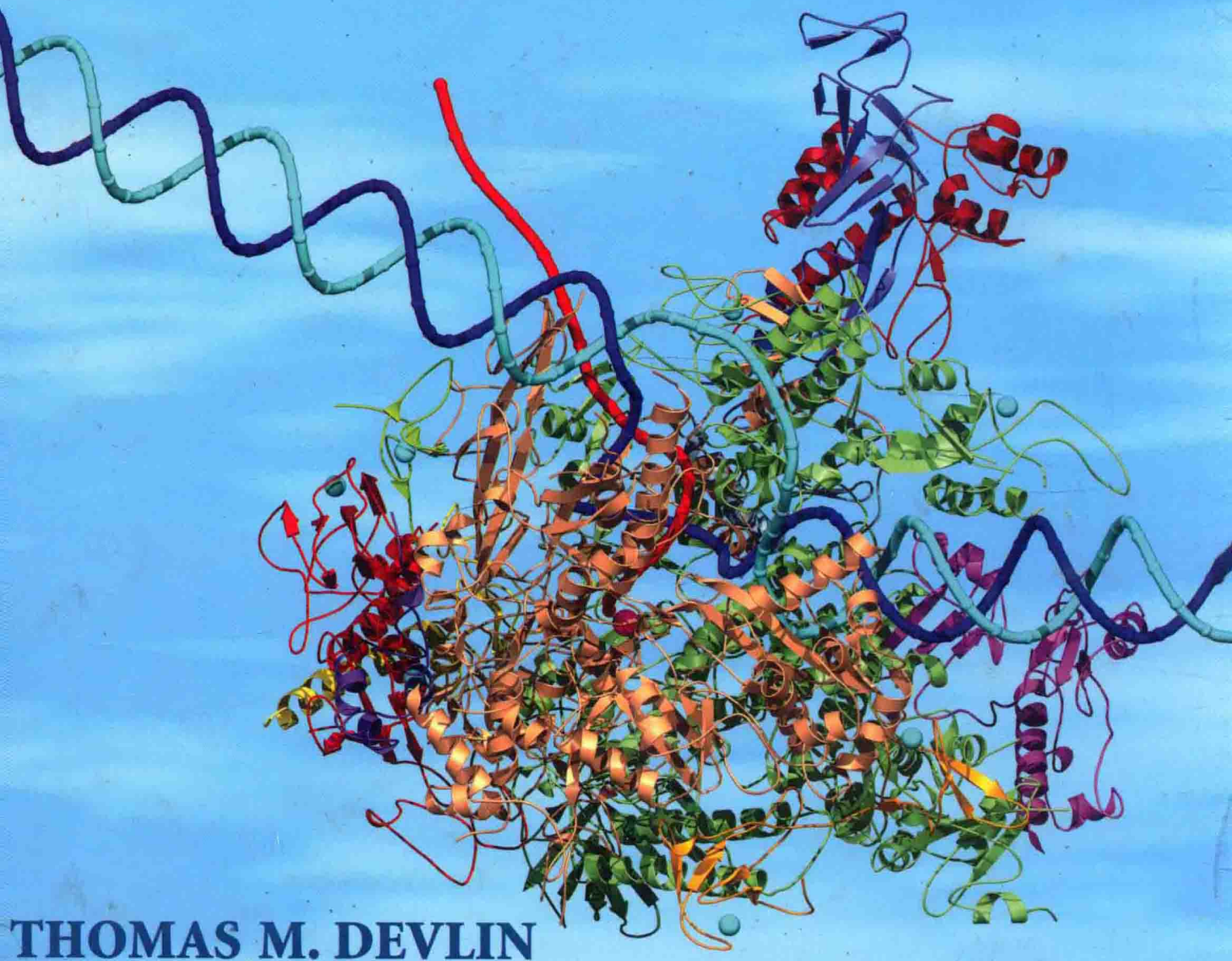
TEXTBOOK OF BIOCHEMISTRY

With Clinical Correlations

SIXTH EDITION



THOMAS M. DEVLIN
Editor

Textbook of BIOCHEMISTRY

With Clinical Correlations

Sixth Edition

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Cover Illustration: The front and back covers contain two views of the complete structure of the yeast RNA polymerase II elongation complex. The views are a ribbon model of the twelve polymerase subunits and nucleic acids. The polymerase subunits Rpb1-Rpb12 are colored silver, gold, red, light red, magenta, cyan, blue, green, orange, dark blue, yellow, and light green, for Rpb1, Rpb2, Rpb3, Rpb4, Rpb5, Rpb6, Rpb7, Rpb8, Rpb9, Rpb10, Rpb11, and Rpb12, respectively. Template DNA, nontemplate DNA, and product RNA are in dark blue, light blue and red, respectively. See page 184 for discussion of RNA polymerase II. Figures were adapted from Kettenberger, H., Armache, K.-J., and Cramer, P. Molecular Cell 16: 955, 2004, and kindly supplied by Dr. H. Kettenberger, Dr. K. Armache, and Dr. Patrick Cramer, Managing Director, Gene Center, Ludwig-Maximilians-University of Munich, Feodor-Lynen-Str. 25, 81377, Munich, Germany.

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ABBREVIATIONS IN BIOCHEMISTRY

A (or Ade)	adenine
Ab	Antibody
ABC	ATP-binding cassette
ACP	acyl carrier protein
ACTH	adrenocorticotropic hormone
ACP	acyl carrier protein
acyl CoA	acyl derivative of CoA
ADH	antidiuretic hormone
AdoMet	S-adenosylmethionine
ADP	adenosine diphosphate
Ag	antigen
Ala	alanine
ALA	δ-aminolevulinic acid
AMP	adenosine monophosphate
cAMP (cyclic AMP)	adenosine 3′,5′-cyclic monophosphate
Arg	arginine
ARS	autonomously replicating sequence
Asn	asparagine
Asp	aspartate
ATP	adenosine trisphosphate
ATPase	adenosine trisphosphatase
BMR	basal metabolic rate
bp	base pair
BPG	D-2,3 bisphosphoglycerate
C (or Cyt)	cytosine
CaM	calmodulin
CAP	catabolite gene activator protein
CBC	cap binding complex
CDK	cyclin dependent kinase
CDP	cytidine diphosphate
CMP	cytidine monophosphate
CoA or CoASH	coenzyme A
CoQ	coenzyme Q (ubiquinone)
CTP	cytidine trisphosphate
cyclic AMP	adenosine 3′,5′-cyclic monophosphate
cyclic GMP	guanosine 3′,5′-cyclic monophosphate
Cys	cysteine
d	2′-deoxyribo
dd	dideoxy
Da	Dalton
DHF	dihydrofolate
DNA	deoxyribonucleic acid
cDNA	complementary DNA
Dol	dolichol
dopa	3,4-dihydroxyphenylalanine
dTDP	thymidine diphosphate
dTMP	thymidine monophosphate
dTTP	thymidine trisphosphate
EcoR1	EcoR1 restriction endonuclease
EF	elongation factor
ER	endoplasmic reticulum
FAD	oxidized flavin adenine dinucleotide
$FADH_2$	reduced flavin adenine dinucleotide
fMet	formylmethionine
FMN	flavin mononucleotide (oxidized form)
$FMNH_2$	flavin mononucleotide (reduced form)
Fp	flavoprotein
G	Gibbs free energy
G (or Gua)	guanine
GABA	γ-aminobutyric acid
Gal	galactose
G_i	inhibitory G protein
Glc	glucose
Gln	glutamine
Glu	glutamate
Gly	glycine
GDP	guanosine diphosphate
GMP	guanosine monophosphate
GTP	guanosine trisphosphate
G_s	stimulatory G protein
GSH	glutathione
Hb	hemoglobin
HbCO	carbon monoxide hemoglobin
HbO_2	oxyhemoglobin
HDL	high density lipoprotein
HMG CoA	β-hydroxy-β-methylglutaryl CoA
hnRNA	heterogeneous nuclear RNA
HSP	heat shock protein
HX	hypoxanthine
Hyp	hydroxyproline
IDL	intermediate density lipoprotein
IF	initiation factor
IF	intermediate filament
IgG	immunoglobulin G
Ile	isoleucine
IP_3 ($InsP_3$)	inositol 1,4,5 trisphosphate
IDP	inosine diphosphate
IMP	inosine monophosphate
IS	insertion sequence
ITP	inosine trisphosphate
Km	Michaelis-Menten constant
kb	kilo base pair
LDL	low density lipoprotein
Leu	leucine
Lys	lysine
m	milli (10^{-3})
M	molar
Mb	myoglobin
MbO_2	oxymyoglobin
Met	methionine
MetHb	methemoglobin
mol	mole
NAD^+	oxidized nicotinamide adenine dinucleotide
NADH	reduced nicotinamide adenine dinucleotide
$NADP^+$	oxidized nicotinamide adenine dinucleotide phosphate
NADPH	reduced nicotinamide adenine dinucleotide phosphate
NANA	N-acetylneuraminic acid
PC	phosphatidylcholine
PCR	polymerase chain reaction
PE	phosphatidylethanolamine
PEP	phosphoenolpyruvate
PG	prostaglandin
Phe	phenylalanine
Pi	inorganic orthophosphate
PI	phosphatidylinositol
PLP	pyridoxal 5-phosphate
PPi	inorganic pyrophosphate
Pro	proline
PRPP	phosphoribosylpyrophosphate
Q	ubiquinone (CoQ)
RER	rough endoplasmic reticulum
RF	release factor
RFLP	restriction fragment length polymorphism
RNA	ribonucleic acid
mRNA	messenger RNA
rRNA	ribosomal RNA
tRNA	transfer RNA
RNase	ribonuclease
RQ	respiratory quotient (CO_2 production/O_2 consumption)

S	Svedberg unit
SAM	S-adenosylmethionine
Ser	serine
SH	sulfhydryl
SNARE	synaptosome-associated protein receptor
snRNA	small nuclear RNA
snRNP	small nuclear ribonucleoprotein
SSB	single-strand binding protein
T (or Thy)	thymine
TCA	tricarboxylic acid cycle
TF	transcription factor
TG	triacylglycerol
THF	tetrahydrofolate
Thr	threonine
TPP	thiamin pyrophosphate
Trp	tryptophan
TTP	thymidine trisphosphate
Tyr	tyrosine
U (or Ura)	uracil
UDP	uridine diphosphate
UDP-galactose	uridine diphosphate galactose
UDP-glucose	uridine diphosphate glucose
UMP	uridine monophosphate
UTP	uridine trisphosphate
Val	valine
VLDL	very low density lipoprotein
YAC	yeast artificial chromosome

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NORMAL CLINICAL VALUES: BLOOD*

INORGANIC SUBSTANCES

Ammonia	10–80 µg/dl
Bicarbonate	22–26 mEq/L
Calcium	9.0–10.5 mg/dl
Carbon dioxide	21–30 mEq/L
Chloride	98–106 mEq/L
Copper	70–140 µg/dl
Iron	50–150 µg/dl
Lead	<10–20 µg/dl
Magnesium	1.8–3.0 mg/dl
P_{CO2}	35–45 mmHg 4.7–5.9 kPa
pH	7.38–7.44
Phosphorus	3.0–4.5 mg/dl
P_{O2}	80–100 mmHg 11.0–13.0 kPa
Potassium	3.5–5.0 mEq/L
Sodium	136–145 mEq/L

ORGANIC MOLECULES

Acetoacetate	<1 mg/dl
Ascorbic acid	0.4–1.0 mg/dl
Bilirubin Direct	0.1–0.3 mg/dl
Indirect	0.2–0.7 mg/dl
Carotenoids	0.8–4.0 mg/ml
Creatinine	<1.5 mg/dl
Glucose	75–115 mg/dl
Lactic acid	0.6–1.7 mEq/L
Lipids Cholesterol	120–200 mg/dl
HDL cholesterol	>40 mg/dl
LDL cholesterol	<100 mg/dl
Free fatty acids	8–25 mg/dl
Triglycerides	<160 mg/dl
Phenylalanine	0–2 mg/dl
Pyruvic acid	60–170 µEq/L
Urea nitrogen (BUN)	10–20 mg/dl
Uric acid Female	1.5–6.0 mg/dl
Male	2.5–8.0 mg/dl
Vitamin A	20–100 µg/dl

PROTEINS

Total	5.5–8.0 g/dl
Albumin	3.5–5.5 g/dl
Ceruloplasmin	27–37 mg/dl
Globulin	2.0–3.5 g/dl
Glucagon	20–100 pg/ml
Hemoglobin (whole blood)	
Female	12–16 g/dl
Male	13.5–17.5 g/dl
Insulin	0–20 µU/ml
Transferrin	230–390 mg/dl

ENZYMES

Alanine aminotransferase	0–35 U/L
Aldolase	0–6 U/ml
Amylase	60–180 U/L
Aspartate aminotransferase	0–35 U/L
Cholinesterase	5–12 U/ml
Creatine kinase	
Female	40–150 U/L
Male	60–400 U/L
Lactic dehydrogenase	100–190 U/L
Lipase	0–160 U/L
Nucleotidase	1–11 U/L
Phosphatase (acid)	0–5.5 U/L
Phosphatase (alkaline)	30–120 U/L

PHYSICAL PROPERTIES

Blood pressure	120/80 mmHg
Blood volume	8.5–9.0% of body weight in kg
Osmolality	280–296 mOsm/kg H_2O
Hematocrit	37–52%

NORMAL CLINICAL VALUES: URINE*

Acetoacetate (acetone)	0
Amylase	4–400 U/L
Calcium	<300 mg/24 hr
Coproporphyrin	50–250 mg/24 hr
Creatine	<100 mg/24 hr
Creatinine	1.0–1.6 g/24 hr
Glucose	50–300 mg/24 hr
Nitrogen (urea)	6–17 g/24 hr
pH	5.0–9.0
Phosphorus (inorganic)	varies; average 1 g/24 hr
Porphobilinogen	0
Protein (quantitative)	<150 mg/24 hr
Titratable acidity	20–40 mEq/24 hr
Urobilinogen	up to 1.0 Ehrlich U
Uroporphyrin	0–30 mg/24 hr

*Selected values are taken from normal reference laboratory values in use at the Massachusetts General Hospital and published in the New England Journal of Medicine (Kratz A., Ferraro M., Sluss, P. M., and Lewandrowski, K. B. N. Engl. J. Med. 351:1548, 2004.) The reader is referred to the complete list of reference laboratory values in the literature citation for references to methods and units. Assays were conducted with either serum or plasma unless indicated otherwise. U, units as defined by specific assay for substance; p, pico; dl, deciliters (100 ml); L, liters; and hr, hours.

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TO ALL THE RESEARCH SCIENTISTS
whose contributions to our knowledge
are the source of the information presented here,

and

TO MARJORIE
for her enduring encouragement, support, and love.

PREFACE

The objectives of the sixth edition of the *Textbook of Biochemistry with Clinical Correlations* remain unchanged from those for the previous editions. They are: (1) to present a clear and precise discussion of the biochemistry of eukaryotic cells, particularly those of mammalian tissues; (2) to relate biochemical events at the cellular level to physiological processes in the whole animal; and (3) to cite examples of abnormal biochemical processes in human disease. The text continues to have an emphasis on the biochemistry of mammalian cells because of the importance of biochemistry in understanding human diseases. Information from biochemical investigations of prokaryotes and other eukaryotes, however, is presented when these studies are the primary source of knowledge about a topic. The unraveling of many biological and physiological processes at the molecular level is due in part to the multiplicity of new innovative techniques and research approaches from different disciplines. The differences and research approaches between biochemistry, molecular biology, cell biology, cell physiology, and molecular pharmacology are becoming indistinct. Thus as biochemistry has spread through other disciplines, so have these disciplines permeated biochemistry. The continuing expansion of information in the biological sciences and the integration of disciplines have had a significant impact on the content of biochemistry courses, requiring inclusion of many topics heretofore presented in a more general descriptive manner. It also has had an impact on the content of textbooks. In the preparation of this revision, every chapter was updated with inclusion of new information and deletion of some material. Totally new topics are included in some chapters, such as sections on the basal lamina protein complex, and molecular motors, and two new chapters, **Fundamentals of Signal Transduction**, and **Cell Cycle, Programmed Cell Death and Cancer**, have been added.

The scope and depth of presentation in this book should fulfill the requirements of most upper-level undergraduate, graduate-level, and especially professional school courses in biochemistry. Topics for inclusion were selected to cover the essential areas of both biochemistry and physiological chemistry. The textbook is organized and written such that any sequence of topics considered most appropriate by an instructor can be presented. The content of the sixth edition is divided into five major parts, in which related topics are grouped together. **Part I, Structure of Macromolecules**, contains an introductory chapter on cell structure, followed by chapters on nucleic acid and protein structure. **Part II, Transmission of Information**, describes the synthesis of the major cellular macromolecules, that is, DNA, RNA, and protein. A chapter on biotechnology is included because information from this area has had such a significant impact on the development of our current knowledge. Part II concludes with a chapter on the Regulation of Gene Expression in which mechanisms of both prokaryotes and eukaryotes are presented. **Part III, Functions of Proteins**, opens with a presentation of the structure-function relationship of four major families of proteins. This is followed by a discussion of enzymes, including a separate chapter on the cytochromes P450, then a chapter on membrane structure and transmembrane transport mechanisms. Part III concludes with a chapter covering the fundamentals of cellular signal transduction mechanisms. **Part IV, Metabolic Pathways and Their Control**, begins with a chapter on bioenergetics and oxidative metabolism, then separate chapters describing the synthesis and degradation of carbohydrates, lipids, amino acids, purine and pyrimidine nucleotides, and heme. Each chapter highlights the mechanism of control of the individual metabolic pathways. A chapter on the integration of these metabolic pathways in humans completes this part. **Part V, Physiological Processes**, covers those areas unique to mammalian cells and tissues beginning with a chapter on hormones that emphasizes their biochemical functions as messengers, and a chapter on molecular cell biology containing discussions of four major physiological signal transducing systems: the nervous system, the eye, muscle contraction and molecular motors, and blood coagulation. The textbook concludes with presentations of the biochemistry of digestion and absorption of basic nutritional constituents, and principles of human nutrition.

In each chapter, the relevancy of the topic being discussed to that of human life processes is presented in separate **Clinical Correlations**, which describe the aberrant biochemistry of disease states. A number of new correlations have been included because the genetic and biochemical bases of an ever increasing number of diseases have been described. There has been no attempt, however, to review all of the major diseases; rather the purpose of the Clinical Correlations is to present examples of disease processes where the ramifications of deviant biochemical processes are well established. References are included in the Clinical Correlations to facilitate exploration of the topic in more detail. In some instances, the same clinical condition is presented in different chapters, but each from a different perspective. All pertinent biochemical information is presented in the main text, and an understanding of the material does not require a reading of the Clinical Correlations. In some cases, clinical conditions are discussed as part of the primary text because of the significance of the medical condition to an understanding of the biochemical process.

Every chapter contains a **Bibliography** that serves as an entry point to the research literature; references are generally to review articles and seminal publications. A set of **Questions and Answers** concludes each chapter. They include multiple choice questions, some with clinical vignettes as they are the type used in national medical examinations, and problem solving questions. Brief annotated answers are given.

Illustrations were updated and new figures added including a number of protein structures. The adage "A picture is worth a thousand words" is appropriate and the reader is encouraged to study the illustrations because they are meant to clarify confusing aspects of a topic.

The Appendix, **Review of Organic Chemistry**, is designed as a ready reference for the nomenclature and structures of organic molecules encountered in biochemistry; it is not intended as a comprehensive review of organic chemistry. The material is presented in the Appendix rather than at the beginning of chapters dealing with the different biologically important molecules. The reader should become familiar with the content of the Appendix and then use it as a ready reference when reading related sections in the main text. A **Glossary** has been compiled for the sixth edition; the ever expanding language of the biochemical sciences indicated a need for a ready reference to the most common words. Pertinent **Biochemical Abbreviations** and **Normal Clinical Laboratory Values for Blood and Urine** are presented on the inside of the front and back covers, respectively.

We still believe that a **multi-contributor textbook** is the best approach to achieve an accurate and up-to-date presentation of biochemistry. Each contributor is involved actively in teaching biochemistry in a medical and/or graduate school, and has an active research interest in the field in which he or she has written. Thus, each has the perspective of the classroom instructor, with the experience to select the topics and determine the emphasis required for students in a biochemistry course. Every contributor, however, brings to the book an individual approach, leading to some differences in presentation. Every chapter, however, was edited to have a consistent writing style and to eliminate unnecessary repetitions and redundancies. A few topics are presented in two different places in the book in order to make the individual discussions complete and self contained. This repetition should facilitate the learning process.

The contributors prepared their chapters for a **teaching book**, selecting the important and relevant information in their subject matter. The textbook is not intended as a compendium of biochemical facts or a review of the current literature, but each chapter, however, contains sufficient detail on the subject to make it useful as a resource. Contributors were requested not to reference individual researchers and not to dwell on the historical aspects of their topic; our apologies to the many scientists who deserve recognition for their outstanding research contributions.

One person must accept the responsibility for the final product in any project. The decisions concerning the selection of topics and format, reviewing the drafts, and responsibility for the final checking of the book were entirely mine. I welcome comments, criticisms, and suggestions from students, faculty, and professionals. It is our hope that this work will be of value to those embarking on the exciting experience of learning biochemistry for the first time as well as those returning to a topic in which the information is expanding so rapidly.

THOMAS M. DEVLIN

Berwyn, Pennsylvania
September, 2005

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The efforts and encouragement of many people have made possible the publication of this sixth edition of the Textbook of Biochemistry. As in the past, I am personally indebted to each of the contributors for accepting the challenge of preparing the chapters, sharing their ideas to improve the book, accepting so readily suggestions to modify their contributions, and cooperating throughout the period of preparation. To each I extend my deepest appreciation for a job well done. The individual contributors have received the support of colleagues and students in the preparation of their chapters. Thus, to everyone who gave unselfishly of their time and shared in the objective and critical evaluation of the text, we extend a sincere thank you. In addition, every contributor has been influenced by former teachers and colleagues, various reference resources, and, of course, the scientific literature. We are very indebted to these many sources of inspiration.

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