Compartive Vertebrate Endocrinology

The long-awaited third edition of this popular textbook retains the successful format of previous editions, dealing with the nature, actions and roles of hormones among vertebrate animals. Special emphasis is placed on the evolution and origins of hormones and their receptors, on the role of hormones in the physiological coordination of vetebrates, and on dealing with each endocrine process in the context of the organism's physiology, ecology and evolution.

Comparative Vertebrate Endocrinology discusses the intimate physiology of the endocrine system and the pivotal role of hormones in coordinating basic body processes such as nutrition, reproduction, calcium metabolism and osmoregulation, as well as their contributions to animal coloration, molting and development. The species included range from lower chordates through to mammals, including marsupials.

Peter Bentley graduated from the University of Western Australia where his first degree was in Zoology and his PhD in Physiology.

In a distinguished career which has seen the publication of over 200 original research articles and five books, Professor Bentley has held academic positions at University College London, the University of Western Australia, University of Bristol, Duke University, and the Mt Sinai School of Medicine of the City University of New York. Prior to returning to Australia, he was Burroughs Wellcome Distinguished Professor of Pharmacology in the College of Veterinary Medicine, North Carolina State University.

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THIRD EDITION

P.J. BENTLEY

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Dedicated to the memory of Hans Heller and Harry Waring,
who introduced me to comparative endocrinology

Contents

Preface to the third edition

This edition has been extensively revised and contains nearly 1000 new references and over 60 new or modified figures. This proliferation reflects advances in our knowledge of hormones and their actions, and a persistent interest in the application of this knowledge to the domain of comparative endocrinology. Both of the dedicatees of this book are now deceased. When they first became interested in this subject over 60 years ago they utilized contemporary pharmacology to help to lay the foundations of the discipline. Its recent propagation largely reflects the use of the techniques of molecular biology and the unravelling of the genome to decipher the interrelationships of hormones in both vertebrates and their invertebrate progenitors.

It would not have been possible for me to prepare this edition without the collaboration of The University of Western Australia, particularly the Physiology Department and Professor Trevor Redgrave. All members of the department helped by making me feel welcome there. The Biological Sciences Library is the principal repository of the new information that I have used. Its comprehensive collection and helpful staff provided a pleasant venue for many hours of searching.

Peter Bentley
The University of Western Australia
December 1997

Preface to the second edition

It is over 6 years since the first edition of this book went to press. Interest in comparative endocrinology has not wanted in that time, as shown by the steady stream of papers and the organization of meetings and symposia on this subject. Several new hormones have been identified and described in the interim. Information about the synthesis of proteins that act as prohormones has provided enlightenment about the existence of more "hormone families" with consequent speculation about their evolution. An increased utilization of radioimmunoassays and immunohistochemistry has promoted many of these advances. There has also been an increased appreciation of commonalities of the endocrine and nervous systems, as described in the discipline of neuro-endocrinology. However, because the basic information about the endocrine system has not really changed, it has been unnecessary to alter significantly the conclusions at the end of each chapter.

In view of the great expansion of the literature, the preparation of this edition has been especially challenging. I have generally refrained from substituting new references for old ones, a practice that would ignore the seniority of discoveries and distort the historical perspective of the subject. There are thus many more references in the text. I hope that this does not distract the students for whom this book is primarily intended. They should "read around" the references and use them as a source if necessary. More senior readers may find the expanded bibliography more useful. Finally, I would like to apologize to the many endocrinologists whom it has not been possible to quote but without whose discoveries our knowledge of this subject would be much poorer.

P. J. Bentley
New York
February 1982

Preface to the first edition

This book has been written primarily for use as a textbook by undergraduate, as well as graduate, students. It is hoped that it may serve as a basis for course work in comparative endocrinology and also as an auxiliary text to aid in the teaching of comparative animal physiology. In order to gain the most from this book, the reader should have a basic knowledge of zoology and animal physiology. I have nevertheless attempted to put the endocrinology that is described into a broader biological framework by relating it to the animal's physiology, ecology, and evolutionary background. This is one of the reasons why I have departed from the more usual format of previous textbooks in this area, which generally deal with each endocrine gland in succession, chapter by chapter. Instead, I have attempted to describe certain broad and basic biological processes, the functioning of which is often coordinated by the secretion from several endocrine glands.

No attempt has been made to describe invertebrate endocrinology, as the rapid growth of this area really justifies a separate textbook. The book by K. G. Highnam and L. Hill (*Comparative Endocrinology of the Invertebrates*, Elsevier: Amsterdam, 1970) deals admirably with this subject.

It has not been possible in a book of this nature to give a complete list of original references. There are far too many of these, and many of the earlier observations are already a part of the "classical literature". Instead, I have attempted to refer the reader to more recent papers and reviews that contain references to the material described and can act as useful "starting points" for the students who wish to study the subject further. In order to keep abreast of developments in the various subject areas described, the current literature should be consulted. The principal journals where papers on these subjects are published are *General and Comparative Endocrinology, Journal of Endocrinology, Endocrinology*, and *Comparative Biochemistry and Physiology*. In addition, many papers appear in the standard physiological journals, especially *Journal of Physiology* and *American Journal of Physiology*.

P.J.B.
Mount Sinai School of Medicine of The City University of New York
September 1974

Some abbreviations used in endocrinology

ACTH	corticotropin (adrenocorticotropic hormone)
ADH	antidiuretic hormone
AMH	antimullerian hormone
ANP	atrial natriuretic peptide (s)
AVP	arginine-vasopressin
cyclic AMP	cyclic adenosine-3'5'-monophosphate (cAMP)
CaBP	calcium-binding protein
CBG	corticosteroid (cortisol)-binding globulin
CCK	cholecystokinin
cDNA	complementary DNA
CG	chorionic gonadotropin
CGRP	calcitonin gene-related peptide
CRE	cyclic AMP response (or regulatory) element
CREB	cyclic AMP response element binding protein
CRF	corticotropin-releasing factor
CRH	corticotropin-releasing hormone
CT	calcitonin
DAG	diacylglycerol
DHEA	dehydroepiandrosterone
DHT	dihydrotestosterone
EDLF	endogenous digitalis-like factor
ER	estrogen receptor
FSH	follicle-stimulating hormone
GABA	γ-aminobutyric acid
GH	growth hormone (somatotropin)
GH-RF (or -RH)	growth hormone-releasing factor (or hormone)
GIP	gastric inhibitory polypeptide (glucose-dependent insulinotropic polypeptide)
GLP-I, GLP-II	glucagon-like peptide I, II
GMP	guanosine 5'-monophosphate
GnRH	gonadotropin-releasing hormone (LHRH)
GR	glucocorticoid receptor
GSD	genotype sex determination
GTH-I, GTH-II	gonadotropic hormone (in fish) I, II
hCG	human chorionic gonadotropin

hCS	human chorionic somatomammotropin (hPL)
hPL	human placental lactogen
HRE	hormone-response element
5-HT	5-hydroxytryptamine (serotonin)
-IF	-inhibiting factor
IGF-I, IGF-II	insulin-like growth factor (s) I, II
-IH	-inhibiting hormone
IP_3	inositol-1,4,5-trisphosphate
IT	isotocin
JAK	janus kinase
KT	ketotestosterone
LH	luteinizing hormone
LVP	lysine-vasopressin
MAO	monoamine oxidase
MCH	melanin-concentrating hormone
MIP	molluscan insulin-related peptide
mRNA	messenger RNA
MR	mineralocorticoid receptor
MSH	melanocyte-stimulating hormone (melanotropin)
MT	mesotocin
NHP	nasohypophysial protein
NPY	neuropeptide Y (or neuropeptide tryosine)
OT	oxytocin
PACAP	pituitary adenylate cyclase activating protein
PG	prostaglandin
PIP_2	phosphatidylinositol-4,5-bisphosphate
PKA	protein kinase A
PKC	protein kinase C
PL	placental lactogen
PLC	phospholipase C
PMSG	pregnant mare's serum gonadotropin
PMY	peptide MY (methionine–tyrosine)
PNMT	phenolethanolamine-*N*-methyltransferase
POMC	proopiomelanocortin
PP	pancreatic polypeptide
PR	progesterone receptor
PRL	prolactin
PTH	parathyroid hormone
PTHrP	parathyroid hormone-related protein
PYY	peptide YY (or peptide tyrosine–tyrosine)
-R	receptor (suffix)
RAS	renin–angiotensin system
-RF	-releasing factor
-RH	-releasing hormone
-R-IH	-release-inhibiting hormone
rT_3	reverse T_3

SHBG	sex hormone-binding globulin
SRIF	somatotropin release-inhibiting factor (somatostatin)
STC	stanniocalcin
T_3	triiodothyronine
T_4	thyroxine
TBG	thyroid hormone-binding globulin
TDF	testis-determining factor
TGF	transforming growth factor
TNF	tumor necrosis factor
TR	thyroid hormone receptor
TRH	thyrotropin-releasing hormone
TSD	temperature-dependent sex determination
TSH	thyroid-stimulating hormone (thyrotropin)
VIP	vasoactive intestinal peptide
VNP	ventricular natriuretic peptide
VP	vasopressin