Edited by
S. ISHII, T. HIRANO and M. WADA

HORMONES, ADAPTATION AND EVOLUTION

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Proceedings of the International Symposium on Hormones and Evolution in Honor of Professor Hideshi Kobayashi July 10 to 13, 1979, Tokyo

Edited by
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Preface

None of biological phenomena, such as heredity, development, metabolism, cellular electric activity, endocrine phenomenon, evolution, adaptation, can occur independently and they are interrelated. Among them, endocrine phenomena have an especially intimate relation with evolution and adaptation, as they occur only in multicellular organisms and are most highly developed in higher organisms such as vertebrates and arthropods. Accordingly, the comparative and evolutionary aspects are indispensable for endocrinologists.

This volume consists of all the papers and abstracts of posters presented at the International Symposium on Hormones and Evolution in honor of Dr. Hideshi Kobayashi. The Symposium was held in Tokyo, July 10 to 13, 1979, to commemorate the retirement of Dr. Kobayashi from the University of Tokyo. Dr. Hideshi Kobayashi, who is my teacher, coworker and friend, has dedicated years of his life to the University of Tokyo as a teacher and researcher. He has a wide comparative view of endocrinology and is always aware that his research objective is a result of evolution, resulting in research that is distinguished and brilliant. "Nothing but *Hormones and Evolution* can be considered as the title of the Symposium for Hideshi" was the unanimous opinion of the members of the International Program Committee of the Symposium. The committee selected speakers of the Symposium among distinguished comparative endocrinologists throughout the world, without considering

their relation to Kobayashi. Surprisingly, most of them have been collaborators of his. I believe that they are brave enough to discuss their own material in relation to evolution and adaptation, which are classic and also current problems in biology.

It was my pleasure that almost all the candidates of the plenary lectures responded so positively to my invitation to attend the Symposium, but it was my great regret that I had to eliminate all the names of Kobayashi's students from the list of the plenary lectures in order to limit the program to an appropriate length.

I would like to thank Professor Aubrey Gorbman and Professor Donald S. Farner of the University of Washington, Seattle, Professor Howard A. Bern of the University of California, Berkeley, and Professor Andreas Oksche of Justus Liebig Universität, Giessen for their kind and valuable suggestions concerning the Symposium program.

December 1979 *Susumu Ishii*

Abbreviations

A II	angiotension II
ABP	androgen-binding protein
ACTH	adrenocorticotropic hormone, adrenocorticotropin, corticotropin
AF	aldehyde fuchsin, paraldehyde fuchsin
AHP	adenohypophysis
APUD	amine precursor uptake and decarboxylation
AVP	arginine vasopressin
AVT	arginine vasotocin
b-	bovine
CCK	cholecystokinin
CLIP	corticotropin-like intermediate peptide
CNS	central nervous system
CRF	corticotropin(ACTH)-releasing factor
CSF	cerebrospinal fluid
DHT	dihydrotestosterone
DIT	diiodotyrosine
DOC	11-deoxycorticosterone
EDTA	ethylenediamine tetraacetic acid
EGF	epidermal growth factor

ER	endoplasmic reticulum
FFA	free fatty acid
FGF	fibroblast growth factor
FSH	follicle-stimulating hormone
GEP	gastro-entero-pancreatic
GH	growth hormone, somatotiopin, somatotropic hormone
GHIF	growth hormone-inhibiting factor
GHRF	growth hormone-releasing factor
GnIF	gonadotropin-inhibiting factor
GnRF	gonadotropin-releasing factor
GTH	gonadotropic hormone, gonadotropin
GVBD	germinal vesicle breakdown
h-	human
Hb	hemoglobin
HCG	human choronic gonadotropin, choriogonadotropin
HRP	horse radish peroxidase
HSD	hydroxysteroid dehydrogenase
5-HT	5-hydroxytryptamine
5-HTP	5-hydroxytryptophan
ir, IR	immunoreactive
LH	leuteinizing hormone
LHRH	LH-releasing hormone
LPH	lipotropic hormone
ME	median eminence
MRIF	MSH releasing inhibiting factor
MSF	multiplication-stimulating factor
MSH	melanophore-stimulating hormone, melanocyte-stimulating hormone
MTV	mammary tumor virus
NADPH	nicotinamide adenine dinucleotide phosphate (reduced form)
NGF	nerve growth factor
NHP	neurohypophysis
NIV	nucleous infundibularis
NLT	nucleus lateralis tuberis

NPO	nucleus preoptics
NRL	nucleous recessus lateralis
NRP	nucleous recessus posterioris
NPV	nucleus paraventricularis
NSILA	nonsuppressible insulin-like activity
o-	ovine
PD	pars distalis
PDGF	platelet-derived growth factor
PI	pars intermedia
PIF	prolactin-inhibiting factor
PMS, PMSG	pregnant mare serum gonadotropin
PP	pancreatic polypeptide
PRF	prolactin-releasing factor
PRL, Prl	prolactin
PTAH	phosphotungstic acid hematoxylin
PTH	parathyroid hormone, parathormone
PVP	polyvinyl pyrrolidone
r-	rat
RIA	radioimmunoassay
RRA	radioreceptor assay
Syn-	synthetic
T_3	triiodothyroxine
T_4	throxine
TG	triglyceride
TIF	thyrotropin-inhibiting factor
TRF	thyrotropin-releasing factor
TRH	thyrotropin-releasing hormone
TSH	thyrotropin, thyrotropic hormone, thyroid-stimulating hormone
VIP	vasoactive intestinal peptide

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Chapter 1

GENERAL ASPECTS

Hormones, Adaptation and Evolution (S. Ishii et al., eds.), 3–13
Japan Sci. Soc. Press, Tokyo / Springer-Verlag, Berlin (1980)

Hormones and Evolution: After 15 Years

E. J. W. BARRINGTON

In 1964 I published a little book called *Hormones and Evolution* (*1*), and I well remember how honoured I felt when I learned that it was to be translated into Japanese (*2*). So, when I was further honoured with an invitation to take part in this memorable tribute to Professor Kobayashi, I thought that it might be appropriate and useful to re-examine some of my earlier arguments in the light of 15 years of progress.

Those 15 years have seen the establishment of a widespread belief, governing much current research (not to mention the planning of this symposium), that the form, the functions and the distribution of hormones have been determined by Darwinian evolution. It is now commonly agreed that our analysis of endocrine systems is greatly helped by setting them in an evolutionary context. In the field of peptide endocrinology the atmosphere is positively euphoric, and understandably so. But it is no bad thing to counterbalance euphoria from time to time by asking ourselves how firm are the foundations of our current philosophy.

1. *Natural Selection and the Generation of Improbability*

Evolution can be defined as changes in the diversity and adaptation of populations (*3*). These changes are brought about by natural selection,

which acts upon pools of variation and promotes those variants that maximize reproductive success. The application of this definition raises important questions for endocrinologists, two of which questions, in the limited time available, will concentrate our minds and serve as a basis for my review: Are we now sufficiently convinced that endocrine systems can provide the pools of heritable variation which are required for the action of natural selection? And have we now adequate evidence that the diversification of endocrine systems and of their hormones has indeed been determined by adaptive advantage rather than by random processes?

Aldosterone provides a useful focus for attempting answers to these questions. In recent reviews of steroid endocrinology (*4*, *5*) to which I am much indebted, the authors explicitly set this hormone in an evolutionary context. But the evidence relating to the distribution of aldosterone, although much more extensive than in 1964, is still more limited than could be wished. It appears that only 3 species of elasmobranch fish have been investigated out of the existing 3,000, and only 11 species of teleost fish out of more than 20,000. So also with other groups: only 3 species of birds are listed, for example, out of a group estimated to contain some 420 breeding species in Europe alone. This limitation, however, is to some extent offset by the universally wide distribution and fundamental uniformity of steroid biosynthetic pathways, regulated by genes which must have provided from a very early stage of evolution the pools of variation for which we are seeking. We may thus expect that products of these ancient pathways would, from time to time, have been selected for new hormonal functions, even though the molecules concerned may not themselves have been evolutionary novelties.

Within this context we can accept a suggested proposition (*6*) that aldosterone production is a fundamental property of adrenocortical tissue. The emergence of this molecule as a hormone, however, is particularly characteristic of the tetrapod line, including the closely related lung-fish. Its physiological significance in the few teleosts in which it has been identified is open to question. Indeed, it has not been identified in some of the species studied, and it has not yet been found in elasmobranchs. What, then, were the selective forces that determined its full establishment as a tetrapod hormone?

It has been suggested that these forces can be correlated with the new stresses of terrestrial life, which could have made it advantageous for salt conservation to be mediated by a hormone which was not also involved in glucocorticoid functions. Differentiation was furthered by evolutionary