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978-0-521-38856-6 - From Gene to Animal: An Introduction to the Molecular Biology of
Animal Development: Second Edition

David de Pomerai

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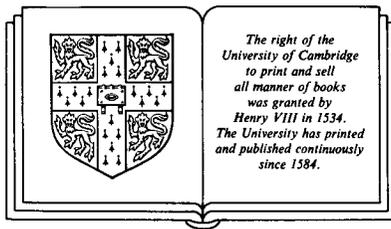
From gene to animal

An introduction to the molecular biology of animal development

SECOND EDITION

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*In memory of Valerie and Odile,
who would have wished to understand;
and for Lesley,
who will have to try!*

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Preface to the second edition

This is virtually a new book. Dedicated palaeontologists will find skeletons of the fourth, fifth and sixth chapters of the first edition discernible in chapters 2 and 3 of the present version, while a few faint traces of the old chapter 7 appear in the new chapter 5. Chapter 4 has sprung *de novo* from scattered mentions in the old text, and likewise the bulk of chapter 5 is completely new. Much of the molecular biology of animal systems, dealt with at length in chapters 1–3 of the first edition, has now been jettisoned; a brief summary of this material now appears as chapter 1. The present book is already substantially longer than its predecessor, and to update the molecular material thoroughly would demand a great deal more space. In some ways this is a pity; several reviewers particularly praised the opening chapters of the first edition, while others liked the linking of molecular and developmental biology in a single text. However, yet others criticised the book on these same grounds, pointing out that molecular biology is now taught in foundation courses as well as in specialist options, and that many excellent texts cover this area. Moreover, molecular studies of development have so burgeoned and borne fruit over the past five years that they are now established as a distinctive speciality; this much is evinced by a new journal title – *Genes and Development* – which has become indispensable within three years of its appearance.

This second edition aims to explain the progress achieved towards a molecular understanding of developmental processes. Inevitably it is selective in its coverage; both *Caenorhabditis elegans* and *Drosophila* receive chapters (4 and 5) to themselves, while aspects of vertebrate development are covered in chapter 3 and at the end of chapter 5. This plan owes much to Adam Wilkins' text *The Genetic Analysis of Animal Development*. Likewise, the organisation and coverage of chapter 2 is based on the third edition of Eric Davidson's classic *Gene Activity in Early Development*. Chapter 4 is modelled on *The Nematode*

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Caenorhabditis elegans edited by William Wood, which aims to become the bible of nematode molecular geneticists for many years to come. It is unfortunate that all three of these excellent books are priced way beyond the means of most students. As for *Drosophila*, brave indeed are they that venture into print concerning this creature, for surely their statements shall become outdated before they emerge from the printing press! I think this is a risk that simply has to be taken; chapter 7 in my first edition failed sadly on this score, since the whole subject began to change radically almost as soon as I had sent the manuscript to the printers, and only limited changes could be made at the proof stage. The unsatisfactory results of this were pointed out by a number of reviewers, and I can only hope that the present attempt withstands the test of time a little better. I make no apologies for devoting nearly half of this text to *Drosophila*, for it is here and in *C. elegans* that the cross-fertilisation between genetics, embryology and molecular biology has proved most fruitful. Some other topics have been excluded quite deliberately from this text, not because they are unimportant in animal development, but simply because the molecular information available is too limited. Thus embryonic fields and induction are mentioned only briefly; likewise the cell surface is given rather scant attention, except where genes of known developmental importance (e.g. *Notch*, *lin-12*) encode cell surface components. This is not to decry the recent molecular progress achieved in vertebrate systems involving the cadherins and CAM proteins, but we are still some way from understanding the genetic control of these molecules or their precise roles in development and differentiation.

Finally, I should like to thank a number of people who have contributed in various ways to this book. Firstly, I am grateful to the many reviewers of the first edition, both for their praise (which encouraged me to try again) and criticism (which showed me where improvements might be made next time). Several experts have provided detailed comments on parts of this second edition; it is a pleasure to thank John Sulston (chapter 4) and Mike Akam (chapter 5) for correcting my misapprehensions and broadening my knowledge of *C. elegans* and *Drosophila*, respectively, as well as Gary Morgan for comments on chapter 1. The errors that remain are my own; I hope they are not too numerous. I am very grateful to Mike Akam, Robb Krumlauf and Tom Kornberg for sending me material prior to publication. Special thanks are due to Mrs Marian Routledge for typing the enormous reference list with unflinching accuracy; the rest of the text was word processed on Amstrad 1512 and 1640 micros. Finally, I am indebted to my wife

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Lesley for her patience and forbearance throughout the long rewriting process. I am grateful to the publishers for the opportunity to update parts of this text during the course of 1989, so as to keep abreast of recent developments in key areas.

DAVID DE POMERAI

Nottingham, December 1989

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Abbreviations and definitions

rRNA	Ribosomal RNA.
tRNA	Transfer RNA.
mRNA	Messenger RNA.
pre-mRNA	Precursors of messenger RNA.
rDNA	Ribosomal DNA, i.e. DNA containing rRNA-coding genes.
S value	(As in 18S/5.8S/28S); a non-linear measurement of molecular size based on sedimentation rate.
kb	Kilobases (= 1000 bases); measurement of RNA chain length.
kbp	Kilobase pairs (= 1000 base pairs); measurement of gene or DNA-fragment length.
kd	Kilodalton (= 1000 daltons or molecular weight units); measurement of protein molecular size, e.g. 37 kd = 37 000 MW.
EM	Electron microscopy.
UV	Ultraviolet light.
pol I/II/III	Nuclear RNA polymerases I (A), II (B) and III (C).
Animal pole	Region of oocyte containing nucleus, from which polar bodies are extruded during meiosis. Also that region of early embryo derived from same.
Vegetal pole	Region of oocyte or early embryo opposite animal pole; often a yolk-rich part of the egg.
5', 3'	RNA chains are transcribed in a 5' to 3' direction. By convention, in DNA the 5' end of a gene denotes the transcriptional start (or cap) site, whereas the 3' end denotes the termination (or polyadenylation) site. Upstream or 5'-flanking sequences are those preceding the start of the gene, while downstream or 3'-flanking sequences lie beyond the end of the gene.

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Gene	This term is used throughout in a broad sense to describe any transcription unit (encoding an RNA or protein final product) plus its associated regulatory sequences (promoter, enhancers, etc.). Structural gene sequences denote the coding part of the gene as opposed to the regulatory sites, but in some cases these two may overlap. Although most genes encode a single protein or RNA product, there are instances where a single gene can encode several products via alternative splicing of multiple exons (see below) or cleavage of a large precursor protein/RNA.
Exon	Those parts of a transcription unit which are represented in the messenger RNA. Not all of these are necessarily translated into protein (e.g. untranslated 5' leader or 3' trailer sequences in many mRNAs).
Intron	Internal sequences of DNA within a transcription unit which are represented in the primary transcript (e.g. pre-mRNA) but which are absent from the cytoplasmic mRNA; intron transcripts are excised by splicing during RNA processing within the nucleus.

Genetic nomenclature: frequently the same set of initials is used to denote, on the one hand, mutations in a particular gene and the resultant mutant phenotype, and on the other, the wild-type gene and its RNA or protein products. To avoid confusion, the following conventions are adopted throughout this text (for a hypothetical gene *ex*):

<i>ex</i>	the wild-type gene itself, including its regulatory DNA (promoter, etc.).
<i>ex</i> ⁺	the wild-type RNA or protein products of that gene.
<i>ex</i> ⁻	recessive null or deficient mutants lacking <i>ex</i> ⁺ function.
<i>ex</i> ^D	dominant mutants which express <i>ex</i> ⁺ products constitutively or inappropriately.

In some cases, where a particular mutation has not yet been assigned to the – or D classes, a phrase such as ‘an *ex* mutant’ will be used; it should be clear from the context that this does not refer to the wild-type gene or its promoter.