

## Understanding Evo-Devo

Why do the best-known examples of evolutionary change involve the alteration of one kind of animal into another very similar one, like the evolution of a bigger beak in a bird? Wouldn't it be much more interesting to understand how beaks originated? Most people would agree, but until recently we didn't know much about such origins. That is now changing, with the growth of the interdisciplinary field of evo-devo, which deals with the relationship between how embryos develop in the short term and how they (and the adults they grow into) evolve in the long term. One of the key questions is: Can the origins of structures such as beaks, eyes, and shells be explained within a Darwinian framework? The answer seems to be yes, but only by expanding that framework. This book discusses the required expansion, and the current state of play regarding our understanding of evolutionary and developmental origins.

Wallace Arthur was one of the founders of the interdisciplinary field of evo-devo (evolutionary developmental biology) in the 1980s. He was a founding editor of the journal *Evolution & Development*. His interests are focused on the evolutionary origins of novel types of animal, and how these origins may differ from 'routine evolution'.

Cambridge University Press  
978-1-108-83693-7 — Understanding Evo-Devo  
Wallace Arthur  
Frontmatter  
[More Information](#)

---

‘Wallace Arthur treats his readers to an eminently readable but still deeply rooted introduction into one of the most significant achievements of evolutionary biology: how evolutionary developmental biology put the organism back into the centre of evolutionary thinking.’

Günter P. Wagner, Yale University, USA

‘Evo-devo deals with the multiple connections that exist between the biological processes of evolution and development. However, as an interface subject, there is a plurality of views on its content and its boundaries. In spite of that, Wallace Arthur has succeeded in writing an extremely clear and highly accessible guide to this fascinating, multifaceted discipline. Using the concept of “developmental repatterning” as a common thread, the book provides a balanced view of evo-devo, covering its main achievements and future challenges. This is an ideal entry point for the non-specialist, but also a stimulating read for the practitioner who wants to consider her/his research in a wider perspective.’

Giuseppe Fusco, University of Padova, Italy

‘Occasionally I feel that the field of Evolution and Development has lost its way, becoming submerged in myriad examples and details that don’t expand our understanding of life. Wallace’s book expounds the intellectual underpinnings of Evolution and Development, leads us through the key questions, and finally shows how the details and examples inform our future understanding. This book provides not just a guide to Evolution and Development, but also a spur to refocus and redouble our efforts to use development to help understand the evolution of life on Earth.’

Peter Dearden, University of Otago, New Zealand

Cambridge University Press  
978-1-108-83693-7 — Understanding Evo-Devo

Wallace Arthur

Frontmatter

[More Information](#)

The ***Understanding Life*** series is for anyone wanting an engaging and concise way into a key biological topic. Offering a multidisciplinary perspective, these accessible guides address common misconceptions and misunderstandings in a thoughtful way to help stimulate debate and encourage a more in-depth understanding. Written by leading thinkers in each field, these books are for anyone wanting an expert overview that will enable clearer thinking on each topic.

Series Editor: Kostas Kampourakis <http://kampourakis.com>

**Published titles:**

<i>Understanding Evolution</i>	Kostas Kampourakis	9781108746083
<i>Understanding Coronavirus</i>	Raul Rabadan	9781108826716
<i>Understanding Development</i>	Alessandro Minelli	9781108799232
<i>Understanding Evo-Devo</i>	Wallace Arthur	9781108819466

**Forthcoming:**

<i>Understanding Genes</i>	Kostas Kampourakis	9781108812825
<i>Understanding DNA Ancestry</i>	Sheldon Krinsky	9781108816038
<i>Understanding Intelligence</i>	Ken Richardson	9781108940368
<i>Understanding Metaphors in the Life Sciences</i>	Andrew S. Reynolds	9781108940498
<i>Understanding Creationism</i>	Glenn Branch	9781108927505
<i>Understanding Species</i>	John S. Wilkins	9781108987196
<i>Understanding the Nature–Nurture Debate</i>	Eric Turkheimer	9781108958165
<i>Understanding How Science Explains the World</i>	Kevin McCain	9781108995504
<i>Understanding Cancer</i>	Robin Hesketh	9781009005999
<i>Understanding Forensic DNA</i>	Suzanne Bell and John Butler	9781009044011
<i>Understanding Race</i>	Rob DeSalle and Ian Tattersall	9781009055581
<i>Understanding Fertility</i>	Gab Kovacs	9781009054164

CAMBRIDGE

Cambridge University Press  
978-1-108-83693-7 — Understanding Evo-Devo  
Wallace Arthur  
Frontmatter  
[More Information](#)

---

# Understanding Evo-Devo

WALLACE ARTHUR  
National University of Ireland, Galway



CAMBRIDGE  
UNIVERSITY PRESS

Cambridge University Press  
978-1-108-83693-7 — Understanding Evo-Devo  
Wallace Arthur  
Frontmatter  
[More Information](#)

---

## CAMBRIDGE UNIVERSITY PRESS

University Printing House, Cambridge CB2 8BS, United Kingdom

One Liberty Plaza, 20th Floor, New York, NY 10006, USA

477 Williamstown Road, Port Melbourne, VIC 3207, Australia

314–321, 3rd Floor, Plot 3, Splendor Forum, Jasola District Centre,  
New Delhi – 110025, India

79 Anson Road, #06–04/06, Singapore 079906

Cambridge University Press is part of the University of Cambridge.

It furthers the University's mission by disseminating knowledge in the pursuit of education, learning, and research at the highest international levels of excellence.

[www.cambridge.org](http://www.cambridge.org)

Information on this title: [www.cambridge.org/9781108836937](http://www.cambridge.org/9781108836937)

DOI: 10.1017/9781108873130

© Wallace Arthur 2021

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2021

Printed in the United Kingdom by TJ Books Limited, Padstow Cornwall

*A catalogue record for this publication is available from the British Library.*

ISBN 978-1-108-83693-7 Hardback

ISBN 978-1-108-81946-6 Paperback

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.

Cambridge University Press  
978-1-108-83693-7 — Understanding Evo-Devo  
Wallace Arthur  
Frontmatter  
[More Information](#)

---

**In memory of Rudolf Raff, evo-devo pioneer, 1941–2019**

# Contents

Foreword	<i>page</i> xiii
Preface	xv
Acknowledgements	xix
<b>1 What is Evo-Devo and Why is it Important?</b>	<b>1</b>
What is Evo-Devo?	1
Origins of Evo-Devo: the Homeobox	6
Origins of Evo-Devo: Other Factors	10
Evo-Devo and Darwinism	12
The Importance of Evo-Devo	15
<b>2 Antecedents of Evo-Devo</b>	<b>19</b>
Quasi-Distinct Stretches of Time	19
Nineteenth-Century Comparative Embryology	20
From Haeckel to Homeobox	25
Take-Home Messages From History	32
<b>3 Evolutionary and Developmental Essentials</b>	<b>37</b>
Evolutionary Pattern	37
Evolutionary Process	41
Development in the Context of Life Cycles	46
Model Organisms	49
The Nature of the Developmental Process	51

## x CONTENTS

<b>4</b>	<b>Evo-Devo Essentials</b>	58
	Developmental Repatterning	58
	Developmental Constraint, Bias, or Channelling	60
	Modularity and Evolvability	63
	The Evo-Devo Hourglass	65
	Body Plans and Evolutionary Novelties	67
	Genes for Building Bodies	70
<b>5</b>	<b>The Evolution of Variations on a Theme</b>	74
	Levels of Evolutionary Change	74
	Developmental Variation	76
	Artificial Selection and Developmental Bias	83
	Phenotypic Plasticity and Developmental Bias	85
	Natural Selection and Genetic Drift	88
	Natural Selection and Developmental Bias	91
<b>6</b>	<b>The Evolutionary Origins of Themes and Novelties</b>	96
	Developmental Bias versus Macromutation	96
	Evolution of Reversed Asymmetry	98
	The Nature of Novelty	103
	Type I Novelty: the Turtle's Shell	105
	Type II Novelty: the Centipede's Venom Claws	108
	From Case Studies to Generalizations	111
<b>7</b>	<b>The Evolutionary Origins of Body Plans</b>	114
	The Pattern of Animal Relatedness	114
	The Timescale of Body-Plan Origins	117
	Mechanisms of Body-Plan Origins	121
	Genes and Body-Plan Origins	129
<b>8</b>	<b>Body-Plan Features and Toolkit Genes</b>	131
	Homologous versus Convergent Features	131
	Genes and Generality	134
	Segments, Notch Signalling, and Hox Genes	137
	Limbs, <i>distal-less</i> , and Dlx Genes	139
	Eyes, <i>eyeless</i> , and Pax Genes	141
	Gene Co-option in Evolution	144

<b>9 Bringing It All Together</b>	149
A Combined View of Development	149
Towards a More Comprehensive Evolutionary Synthesis	150
Variation and its Interaction with Selection	153
Developmental Repatterning	156
Developmental Bias and the Direction of Evolution	158
The Origins of Novelty and Body Plans	160
The Pattern of Occupation of Morphospace	163
<b>Concluding Remarks</b>	166
<b>Summary of Common Misunderstandings</b>	169
References	173
Figure Credits	182
Index	183

## Foreword

*Understanding Evo-Devo*, by Wallace Arthur, takes readers on a fascinating voyage across the animal kingdom, and beyond. The author shows that, contrary to some representations, evolution and development are not two distinct processes but, rather, two entirely intertwined ones. Evo-devo, which is short for evolutionary developmental biology, studies evolution and development, and especially their interactions. In particular, it studies both the evolution of development – that is, how developmental processes evolve – and the developmental basis of evolution – that is, how development structures the evolution of the features of organisms.

Wallace Arthur has produced a concise and informative book, written with passion and clarity, which provides readers with a coherent understanding of how evolution occurs through changes in development, and of how the study of developmental processes reveals that distantly related organisms with very different body forms have deeper similarities than you might previously have thought. When you come to realize why and how the same genes are crucial for the developmental processes of morphologically very different organisms, you will likely be astonished by the unity of life. Also, evolution cannot be studied by looking at populations and genes alone; rather, individuals and their developmental trajectories must be taken into account too, as this book convincingly shows. This is a must-read for anyone interested in understanding life.

**Kostas Kampourakis, Series Editor**

## Preface

About 40 years ago, a new branch of science was born. Its nickname is evo-devo, and it is generally known by this, since its full name, evolutionary developmental biology, is a bit cumbersome. Its aim is to understand the ways in which the short-term process of biological development (including embryogenesis) is intertwined with the long-term process of evolution. Like any new branch of science, it has roots that extend back into the past – at least into the nineteenth century in this case. But the evo-devo of today is a far cry from the activities that characterized its deepest roots. Today both development and evolution can be explained in terms of genes – their interactions with each other and with various other players ranging from proteins and cells to environmental variables such as temperature and population density. A common language enables us to link evolution and development in a way that was impossible before the 1980s.

The aim of this book is to describe evo-devo, its historical roots, and its interactions with the flanking disciplines of evolutionary and developmental biology, in a way that is accessible to non-specialists. The anticipated readership thus includes students in all areas of the biological sciences, professional biologists who specialize in other fields, and the ‘educated layperson’. I have tried to keep this final category of reader firmly in mind while writing. I have assumed a high-school level of biological knowledge but no more. Thus I expect readers to know what the following things are, at least in general terms: DNA, proteins, cells, embryos, larvae, life cycles, inheritance, and natural selection. However, I do not expect readers to have come across more specifically evo-devo entities and concepts, and so I will explain these where they first arise, for example: developmental bias, evolutionary

xvi PREFACE

novelties, heterochrony, body plans, homeobox, toolkit genes, the evo-devo hourglass, and gene co-option.

A word about the figures. There are 20 of these in the book, spread through all the chapters. I have kept them as non-technical as possible. Some of them are only referred to in the chapter in which they occur, while others are referred to intermittently throughout the book. Of the latter, four are especially important as ways of locating things against a broad genetic, taxonomic, and palaeontological background. These four, and their locations in the book, are as follows: the broad structure of the living world (Figure 1.1, page 3); within this, the structure of the animal kingdom (Figure 7.1, page 116); a classification of types of genes, including the developmentally important toolkit genes (Figure 4.2, page 71); and the geological timescale (Figure 7.2, page 118).

Now, a word about the references. A book of this kind should not be cluttered with superscripts, footnotes, or other technical or overly prescriptive ways of linking the text to other sources of information. So what I have done is as follows. When there is a connection between an author mentioned in the text and a source listed at the end of the book, I give the year as well as the author's name in the relevant piece of text, though not in a fixed style. Thus wherever you see a name and a date that are reasonably close together, there is a source to look up at the end of the book if you feel like doing so. On the other hand, if there is a name and only a vague timespan, e.g. 'the 1980s' or 'the early twentieth century', then there is no corresponding entry in the reference list. References are grouped by chapter at the end of the book.

Finally, a word about the use of italics, which is more important than you might think. In evo-devo, there are two standard uses of italics, one that comes from taxonomy, and one from genetics. Regarding the taxonomic use, we always italicize the name of a species and the genus to which it belongs, as in *Homo sapiens* or our close relative *Gorilla gorilla* (the latter showing that on rare occasions the genus and species names are the same as each other). In contrast, we do not italicize the names of any of the higher-level taxa to which the species concerned belong – in this case, for example, Mammalia and Vertebrata. Regarding the genetic use, we always italicize gene names but not the names of the corresponding proteins, so that the two may be readily distinguished. For example, the gene *hedgehog*, which we will meet in the first chapter, makes a protein called Hedgehog. This gene and

Cambridge University Press  
978-1-108-83693-7 — Understanding Evo-Devo  
Wallace Arthur  
Frontmatter  
[More Information](#)

---

## PREFACE xvii

protein were first discovered in flies, but are found widely in many sorts of animals, including humans and, as it turns out, hedgehogs. The widespread occurrence of the same developmental genes across very different-looking animals is a key discovery of evo-devo. For more information on this and other discoveries, read on . . .

## Acknowledgements

Many people kindly agreed to read draft material – anything from a single chapter to the whole manuscript. Those who are subject specialists kept me on my toes regarding accuracy, and those who are not did likewise regarding accessibility. I am very grateful to everyone who helped in these complementary respects, and whose composite efforts thus considerably improved the book, namely: Michael Akam, Sean Carroll, Andy Cherrill, Ariel Chipman, Michael Coates, Katrina Halliday, Ronald Jenner, Kostas Kampourakis, Chris Klingenberg, Colin Lawton, and Sandro Minelli. I would also like to thank my son, Stephen Arthur, who produced all the final artwork and made a major contribution to the cover design.

My interactions with Cambridge University Press have been a pleasure, as always, and I would particularly like to thank Katrina Halliday for her invitation to write this book for the Understanding Life series. I was ably helped along the way by Olivia Boulton, and Sam Fearnley oversaw a very smooth path through the production process. I thank Chloe Bradley in advance for her help on the marketing side of things; I have every confidence that she will be as outstanding in that domain as she was with my previous book. Hugh Brazier improved the clarity of countless bits of writing at the copy-editing stage; this is the third book we have worked on together, and by now I feel that we have become e-friends as well as e-colleagues. Finally, I would like to thank the series editor, Kostas Kampourakis, for putting up with my robust defence of those sections of text that I felt didn't need to be changed, and for his kind comments about the book in the Foreword.