EVOLUTION

A DEVELOPMENTAL APPROACH

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WILEY-BLACKWELL

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A Developmental Approach

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"This book, written as an undergraduate text, is a really most impressive book. Given the burgeoning interest in the role of developmental change in evolution in recent times, this will be a very timely publication. The book is well structured and, like the author's other books, very well written. He communicates with a clear, lucid style and has the ability to explain even the more difficult concepts in an accessible manner."

Dr Kenneth McNamara, University of Cambridge

"There is much more to evolution than mere gene frequency changes in natural populations. Wallace Arthur was among the first to recognize fully the lack of a developmental dimension from the traditional view of evolution and is among the main actors who have been shaping the emerging agenda of evolutionary developmental biology.

From his research experience, the author has distilled in this book an original approach to the study of evolution, written in his uniquely attractive style where immediateness successfully mixes with conceptual clarity."

Professor Alessandro Minelli, University of Padova

COMPANION WEBSITE

This book has a companion website:

www.wiley.com/go/arthur/evolution

with Figures and Tables from the book for downloading

"a theory of evolution requires, as some part of it, a theory of development"

Conrad Hal Waddington, *The Evolution of an Evolutionist*, 1975

Preface

I have written this book first and foremost for students who are taking a course in evolution at a university or college. Although there are many evolution texts 'out there', there are none that cover the ground in the same way as this one. This book adopts a very specific approach to the evolution of animals and plants – an approach in which the central theme is how evolution works by altering the course of egg-to-adult development.

When I was a student, I bought a book that defined evolution as 'a change in the gene frequency of a population'. While evolution does indeed involve change at the population level, it involves changes at other levels too – most importantly at the level of the individual organism, like you and me. What makes us different from our closest living non-human relatives, chimpanzees, lies in our different structures and behavioural capabilities, as well as in the genetics of our populations.

The overly population-based approach to evolution is now giving way to a more integrative approach – one in which the process of development that turns fertilised eggs into adults is seen as being important to the evolutionary process in a variety of ways. However, it is seen as being important *as well as*, not instead of, changes in gene frequency caused by Darwinian natural selection. This is a crucial point, because some previous developmental approaches to evolution advocated a dismissal of population genetics and a denial that micro-evolutionary changes within species form the basis of most long-term evolution; this denial is now seen to be mistaken.

The recent resurgence of a developmental approach to evolution has several sources, all of them clustered into a short period of a few years around 1980. The most important of these was the discovery that the genetic basis of development in widely different animals is much more similar than was previously thought – a conclusion that was later extended to plants.

This discovery gave birth to the science of evolutionary developmental biology, or 'evo-devo' for short, in which comparisons of the developmental roles of homologous genes among different taxa became the focus of attention. But this is not a book devoted solely to evo-devo. There are some good such books already, and thus no need for another one just now. Rather, this is a book about how evo-devo can be integrated with other approaches to evolutionary biology, giving us a more complete view of evolution than has ever been available before.

I have tried to keep the book short and its level in the early chapters introductory, so that it will be useful to undergraduates taking their first university courses in

evolution. However, as is appropriate for educational books in general, the level of discussion rises as the book progresses. Some of the later chapters would thus work well as the subject of seminars and tutorials in more advanced courses. This is particularly true from Chapter 10 onwards.

I should now say a few words about the book's style and structure and, associated with those things, how best to use it.

This book, like other textbooks in science, represents a journey of exploration of a particular field, with the author leading the reader through a sequence of topics. Because of this, I have adopted the 'we' style of speech traditionally used by mathematicians but increasingly favoured in science too. So, instead of 'thus it can be seen that evolution is caused by ...,' the text reads 'thus we can see that evolution is caused by...' I hope that my chosen style will be perceived as it is intended: friendlier and less formal.

With regard to structure, the book's 20 chapters are grouped into four Parts. At the beginning of each of these, there is a cover-page giving a brief synopsis of what each chapter in the relevant Part deals with. So, while one way to read the book is from start to finish (and of course I would recommend that!), another is to read those four cover-pages first, and to choose a different route. This might be especially useful for readers with enough background in the subject to omit a few chapters, particularly some of the early ones.

At the end of each chapter are a few suggestions for further reading; and at the end of the book there is a list of references. In the text, readers are directed to this reference list (if they wish to be) by superscripts. The rationale behind this split in the pointers to additional reading is that the chapter-end lists are short and usually include only books and review articles, rather than the harder-to-penetrate 'primary literature'. The latter is grouped together at the end. This way, beginning students can ignore the superscripts in the text and the back-of-the-book reference list, and just look at the short chapter-end lists of more reader-friendly sources. More advanced students can do the opposite, or adopt an intermediate approach.

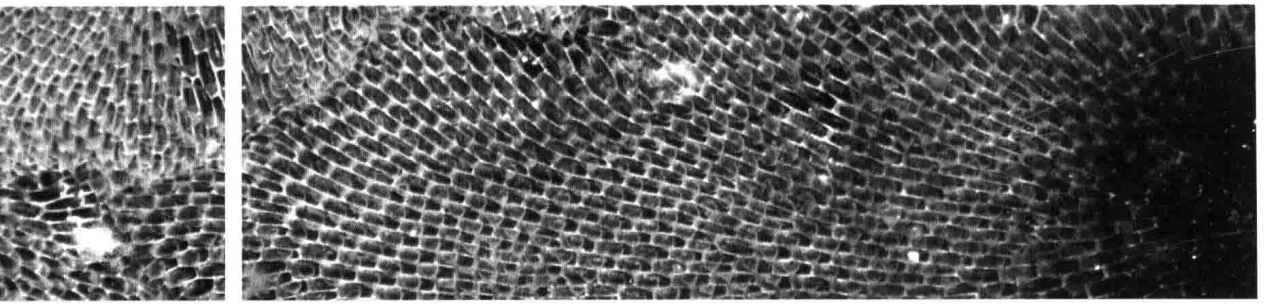
A word of caution on the references: because this is a student text, I have not attempted to give an exhaustive coverage of the literature. To do so, given the breadth of the field, would result in a reference list of perhaps 5000 publications, which would be inappropriate here. Instead, you will find about 250 publications, the aim being to provide just a *sample* of original research papers (and some historical texts) spread over the various topics that are covered.

At the back of the book, you will also find additional sources of information. There is a Glossary, which provides brief definitions of many scientific words that are used in the book. The first time a Glossary word is used in each chapter it is highlighted in bold. There are also four appendices: one that gives a little bit of history; one that deals with gene names, which can be inscrutable to newcomers; one that describes the geological time-scale, which is often used in the book to place major evolutionary events in the appropriate temporal context; and one that gives a very introductory account of how to infer patterns of relationship (evolutionary trees) from comparative data on different species.

Finally, a few words of thanks. I am grateful to all of the following for their help. Alec Panchen, Alessandro Minelli, Ken McNamara, and Patricia Moore kindly read and constructively criticised the entire draft manuscript. My sons Michael and Stephen

produced much of the original artwork. I am also very grateful to the many colleagues, authors and publishers who granted permission for the use of artwork that was reproduced (in some cases in modified form) from elsewhere. The editorial staff at Wiley-Blackwell have helped in many ways. I would especially like to thank Ward Cooper for his support throughout the project; also Rosie Hayden, Emily Tye, Delia Sandford, Revathy Kaliyamoorthy and Carla Hodge. Much of the writing was done while on sabbatical leave from my University; I am grateful to the University for granting this leave. I am also grateful to Darwin College Cambridge for giving me a Visiting Associate position during my sabbatical. Finally, I would like to thank the various friends, colleagues and students with whom I have discussed the subjects presented herein over many years: you are too numerous to name, but you know who you are! Discussion, including argument between the proponents of different points of view, is a key element of the progress of science.

Wallace Arthur
September 2010



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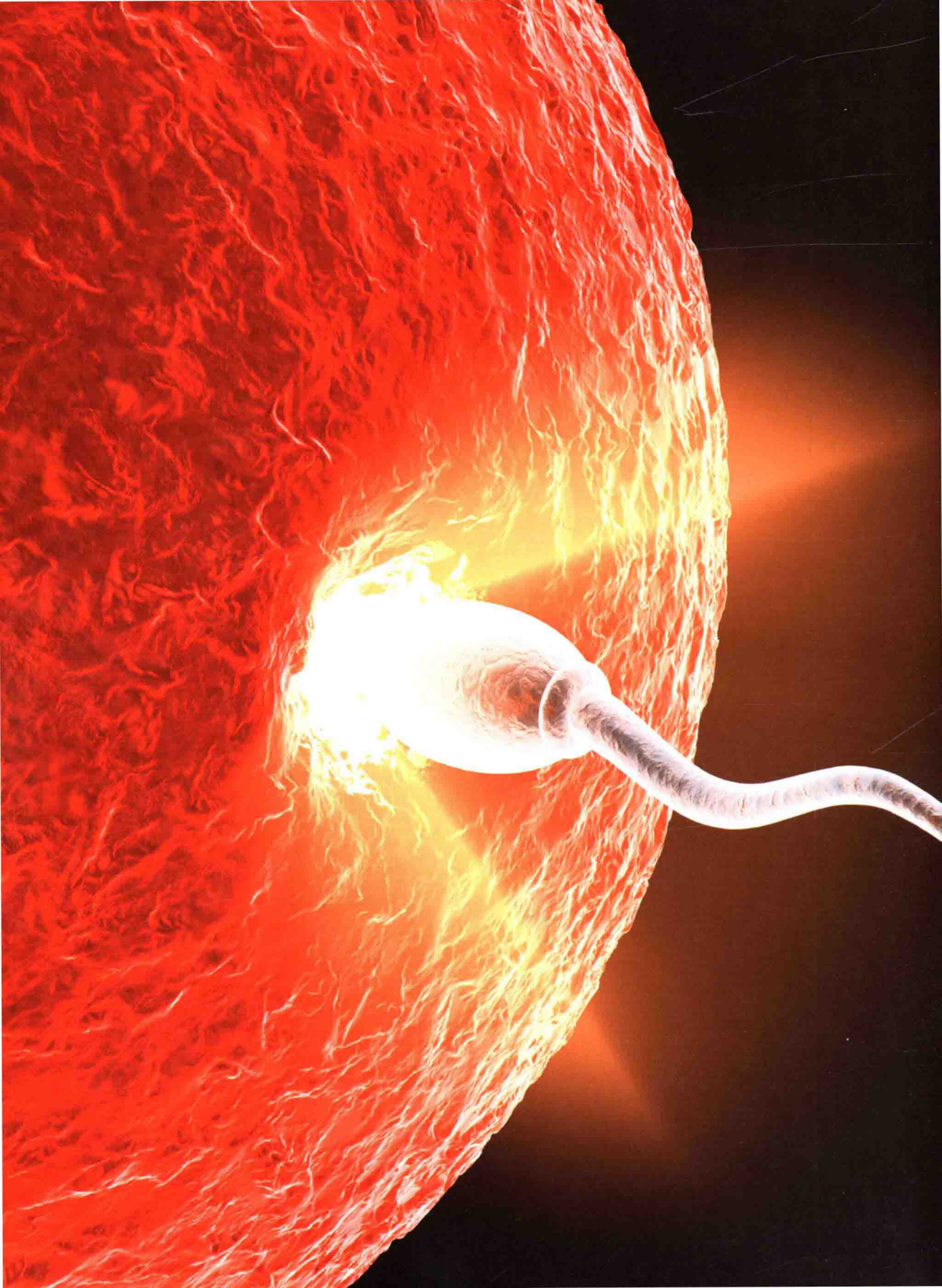


PART I

Foundations

'Science is, I believe, nothing but trained and organised common sense'.

Thomas Henry Huxley ('Darwin's bulldog') ***Collected Essays*****, vol. 3, 1893**

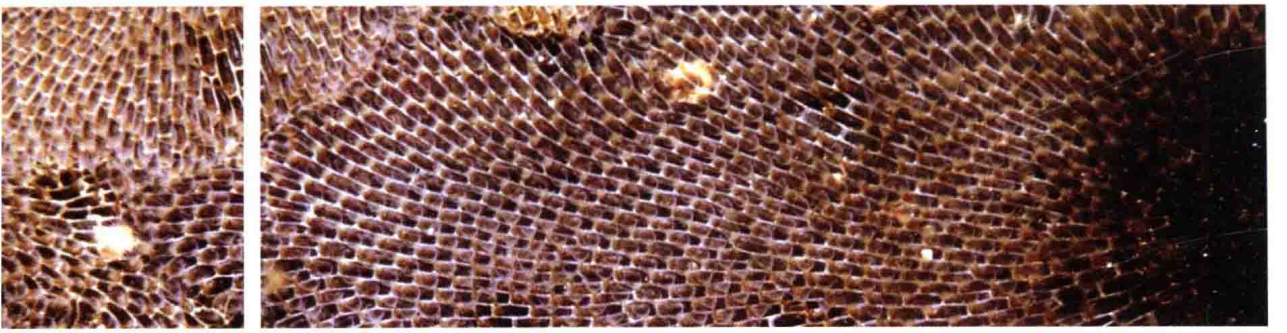
The exciting challenge that this book sets itself is to explain to you what is known about the ways in which the development of animals and plants evolves; and also, in the final chapter, to explain what is not yet known, and thus what are the key questions for future research. We begin to approach this challenge on the foundations provided by the first four chapters, as follows:

Chapter 1: We start by examining the reason why understanding egg-to-adult development is absolutely crucial for a complete picture of the evolution of multicellular creatures.

Chapter 2: This chapter deals with the forerunners of present-day evolutionary developmental biology (or evo-devo), the way in which evo-devo has arisen, and the nature of evo-devo today, including the range of approaches that can be included within it.

Chapter 3: Here, the focus is on the nature of the developmental process, in terms of the things cells do, which are the results of an interplay between genes, their products, an array of other molecules and, often, environmental effects.

Chapter 4: Our focus now shifts to the structure of natural populations, since it is in these that all evolution happens. We examine their spatial, age and genetic structure. We then look at ways in which the genetic structure of populations can be altered by natural selection.



CHAPTER 1

Introduction

1.1 From Darwin to Development

The theory of evolution, established by Charles Darwin more than 150 years ago, and still itself evolving, is one of the most impressive products of science. As Darwin said[1] in the closing paragraph of *The Origin of Species*: 'There is grandeur in this view of life' – a view in which many diverse creatures, both past and present (Fig. 1.1), have been brought into existence by natural processes, and in particular by the interplay between two such processes – heritable variation and natural selection.

Darwin marshalled a wide range of evidence in support of his theory. He drew on information from animal and plant breeding, fossils, behaviour, morphology, embryology and geography, among others. And he used all of these to build a sound basis for his key contribution to evolutionary theory: natural selection.

But evolution is, as noted above, the result of an *interplay* between two things – heritable variation and natural selection – it is not explicable by either of these on its own. The fact that Darwin was unable to enlighten us as much about the former as about the latter was hardly due to an oversight on his part; rather, it was due to limitations on what was generally known at the time in this area of 'heritable variation'.

It is worth dissecting this phrase, because it includes both the inheritance of genetic variation and the process of development through which **phenotypic** variation is produced. Darwin was aware of the problem that there was not, in the 1850s, a clear understanding of how inheritance worked, but proceeded as best he could regardless. He later tried to supply a theory of inheritance – 'pangenesis' – but got it wrong. He was doubtless also aware that there was not a clear understanding of how egg-to-adult development worked, in terms of causal mechanisms, but he proceeded to use











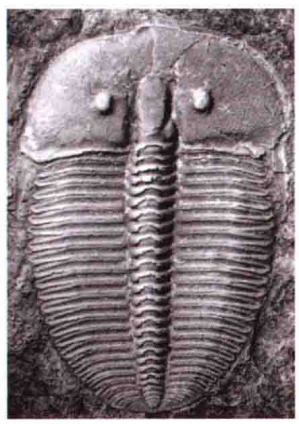



Figure 1.1 A sample of creatures, present and past. All these forms and countless others have been produced from earlier ancestral forms by evolutionary modification of the course of development. This process can in each case be traced back to one of the several origins of multicellularity in the distant evolutionary past. The organisms included here are all discussed as examples later in the book.