

Evolution

A Developmental Approach

Wallace Arthur

National University of Ireland, Galway



A John Wiley & Sons, Ltd., Publication

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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.”

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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.”

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“a theory of evolution requires, as some part of it, a theory of development”

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



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This book has a companion website: www.wiley.com/go/arthur/evolution



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.

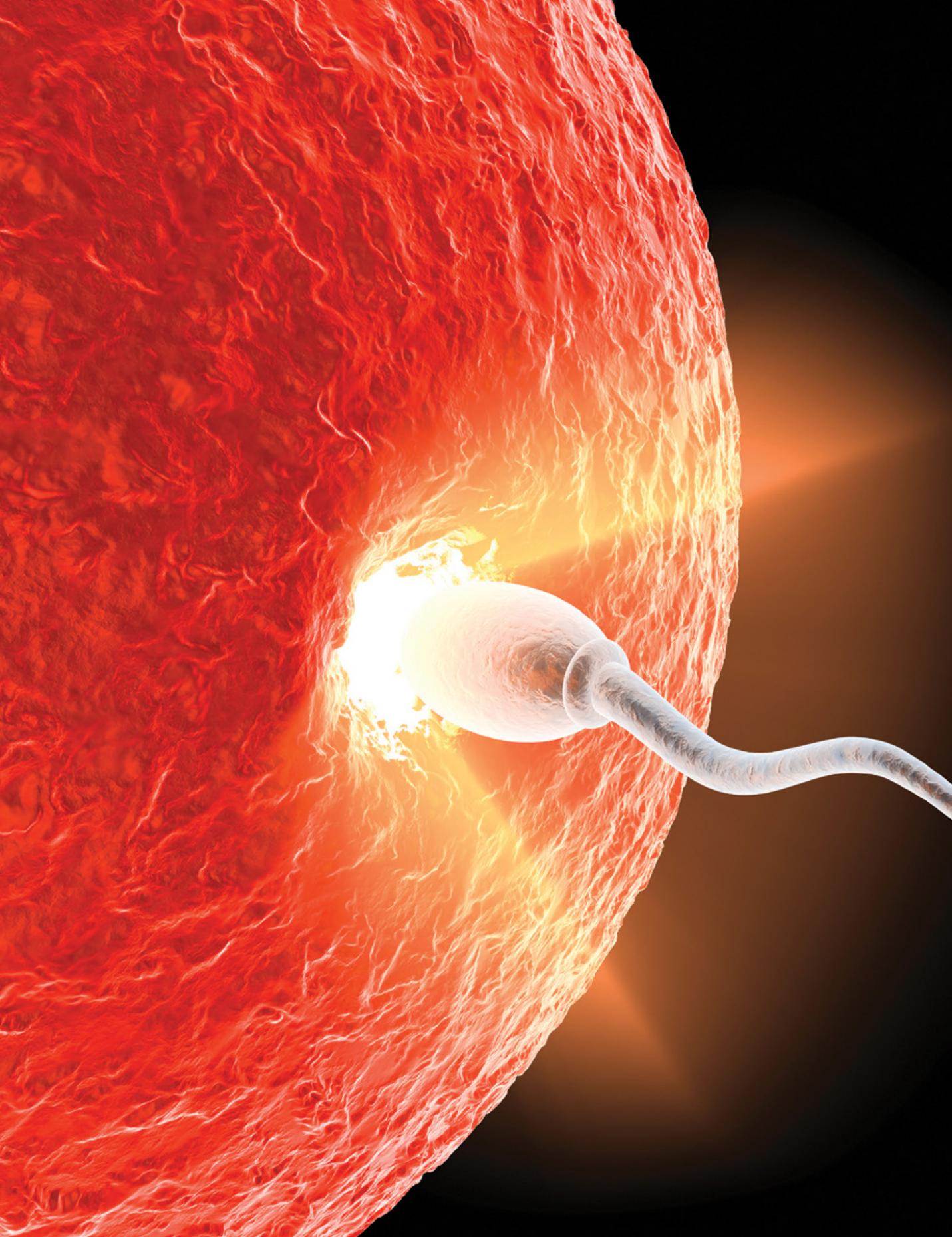
A word of caution on the references: because this is a student text, I have not attempted to give an exhaustive coverage of the literature. To do so, given the breadth of the field, would result in a reference list of perhaps 5000 publications, which would be inappropriate here. Instead, you will find 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*



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

1.2 Development; and Evolutionary Changes in Development

1.3 Development and the Realm of Multicellularity

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 said¹ 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

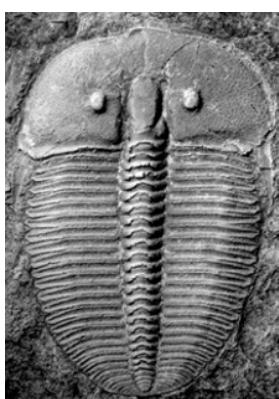


Figure 1.1 A sample of creatures, present and past. All these forms and countless others have been produced from earlier ancestral forms by evolutionary modification of the course of development. This process can in each case be traced back to one of the several origins of multicellularity in the distant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

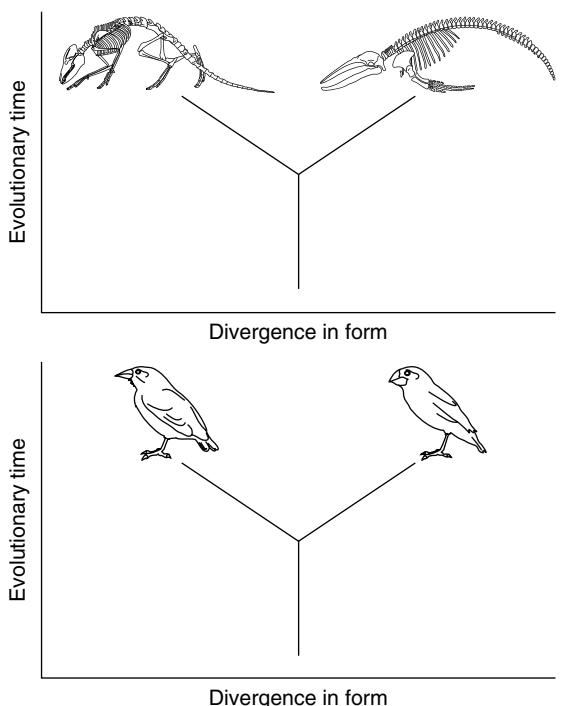


Figure 1.2 Two typical evolutionary trees, as often found in books, articles and posters on the subject. Top: a tree depicting divergence in general form between whales and their sister-group (the extinct mammal *Indohyus*). Bottom: a tree depicting divergence in a particular character – the depth of a bird's beak. Note that in the former case the top of the time axis cannot be the present because *Indohyus* is extinct. (*Indohyus* redrawn from Thewissen et al. 2007, *Nature*, **450**: 1190–1194.)

the information on descriptive and comparative embryology that did exist in the 1850s to good effect. As he remarked (Chapter 13), ‘community in embryonic structure reveals community of descent.’

The two most important things that have happened since Darwin’s synthesis of the evidence for evolution in 1859 have been the incorporation of genetics and developmental biology into the ‘big picture’, with the result that it has even more grandeur than before. The incorporation of genetics, which came first (Appendix 1), had both positive and negative effects on the incorporation of developmental biology that followed, is still in full swing, and is the subject of this book.

But why, actually, is development so important for evolutionary theory? There is a very specific and compelling answer to this question. It relates to the ways in which evolution *can* and *cannot* produce one type of animal or plant from another. This point is best made in relation to the type of evolutionary trees typically found in papers and books on the subject, two of which are shown in Fig. 1.2. Notice that in both trees the vertical axis is some measure of time, while the horizontal axis is some measure of difference in the morphology of the animal concerned, in one case ‘generalised’ and hard to quantify, in the other case a very specific measure of a particular structure (the depth of a bird’s beak).

In a very important sense, both of these trees represent impossible evolutionary transitions. They both employ the familiar shorthand method of representing an animal by one particular stage of its life-cycle – the adult. But evolution cannot make one kind of adult directly from another. Rather, it can only make a new kind of adult by altering, over a period of generations, the egg-to-adult **developmental trajectory** (Fig. 1.3).

So, an adequate theory of evolution must include not only an account of how **fitness** differences cause changes at the population level, but also an account of how the developmental differences that natural selection acts upon arise in the first place. And these latter differences cannot simply be written off as **mutations**, because a mutation is merely a change in the DNA sequence of a gene. If the gene that mutates causes the developmental trajectory to alter, then we need to know how this happens. Furthermore, developmental trajectories can in most cases be influenced by environmental factors as well as by genes. This is true not just of extreme cases, such as the production of male or female forms in turtles by egg incubation temperature, but also of more subtle cases, such as slight differences in the amount of left-right body asymmetry (often referred to as **fluctuating asymmetry**) that can be the result of variation in temperature and other environmental factors.

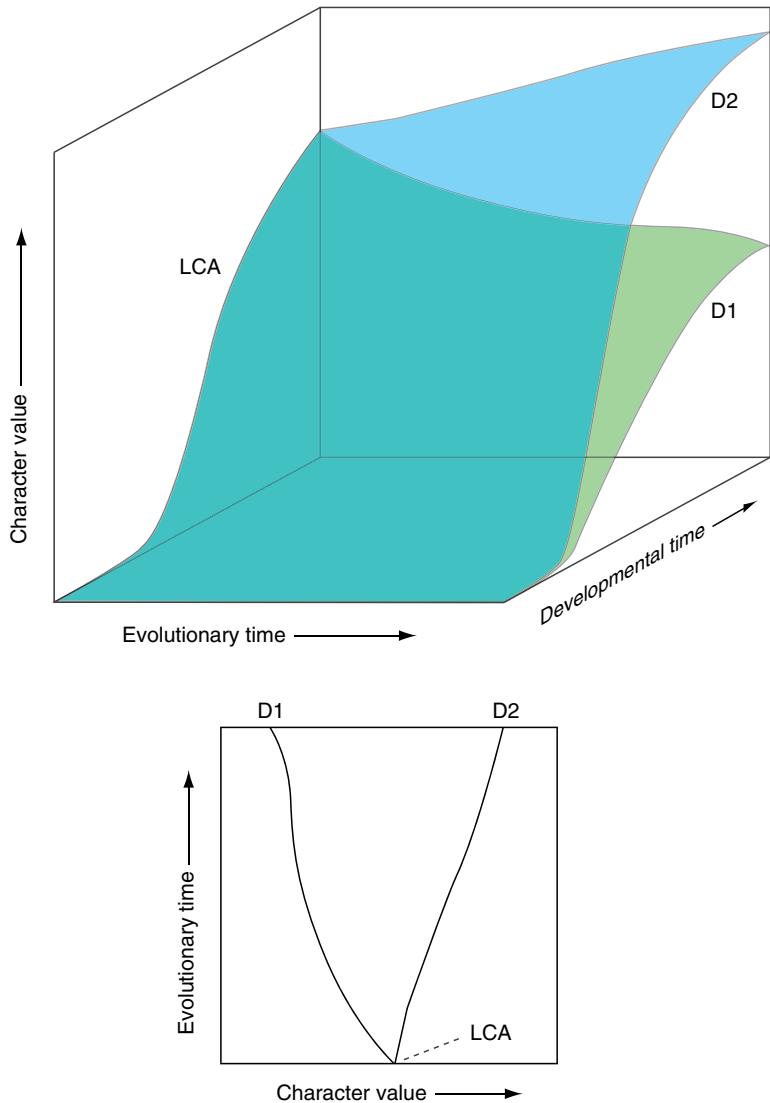


Figure 1.3 A three-dimensional evolutionary tree (top) including the extra dimension of developmental time. This shows how the value of a character (such as the bird's beak depth shown in Fig. 1.2) changes during development, and how this pattern of change itself changes in evolution. Note that the beak depth starts at zero because early bird embryos do not have beaks; and that if the developmental time axis is ignored, the tree reduces to two dimensions (bottom) and resembles that shown in Fig. 1.2 (bottom). LCA – last common ancestor; D1 – daughter species 1; D2 – daughter species 2.

Such considerations give the environment not just one role in evolution – that of selective ‘sieve’ – but rather two, with the other being a role in the production of the variation in the first place. Of course, non-heritable variation, or phenotypic **plasticity**, cannot itself contribute to evolution, precisely because of its non-heritable nature. But if different **genotypes** differ in their pattern of developmental response (or their developmental **reaction norm**) to environmental variation, as is now widely known to occur, then this provides material for evolutionary change. Indeed, all evolutionary theory that deals with phenotypes that are completely genetically determined can be regarded as a subset of more general evolutionary theory in which the determination of developmental trajectories, and hence of phenotypes, is more complex.

What evolve, therefore, are not just adult animals or plants, but rather complete life-cycles. Furthermore, we should not think of pre-adult stages as evolving ‘in order

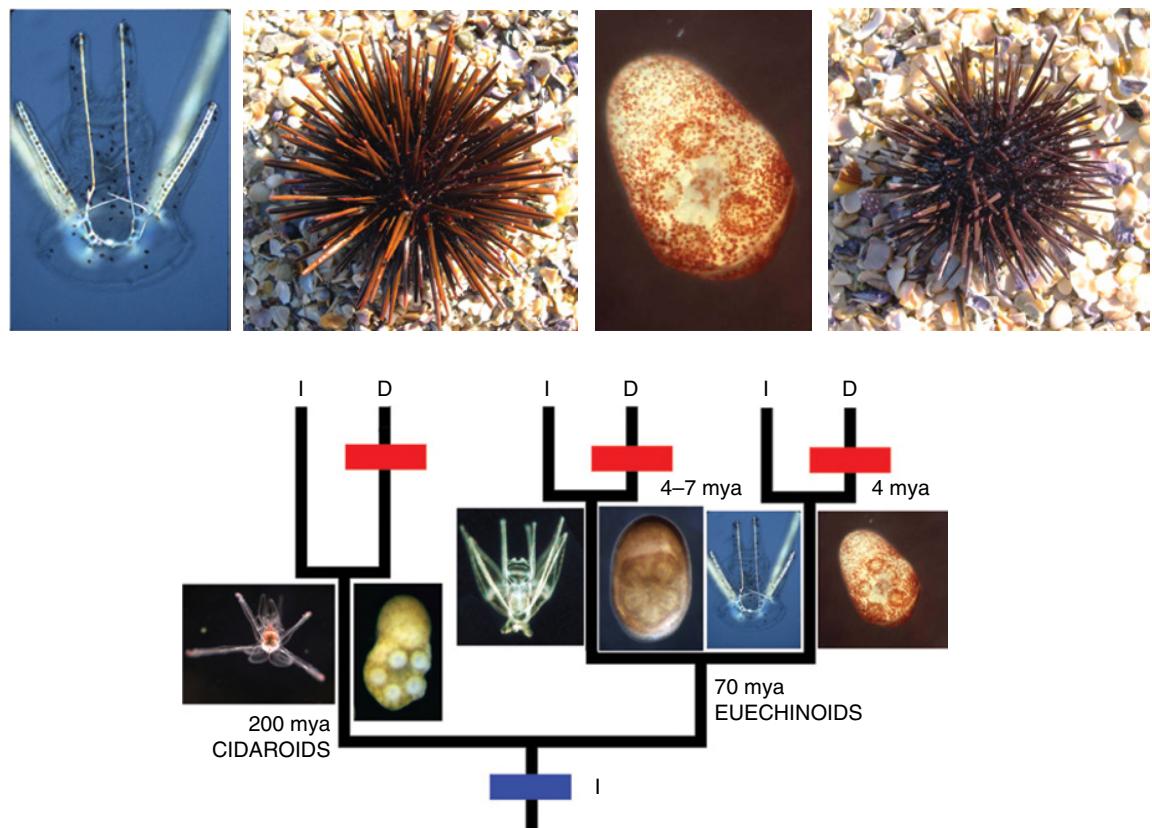


Figure 1.4 Evolution of early developmental stages, as exemplified by the evolutionary divergence of yolk-feeding and plankton-feeding echinoderm larvae. Top: Comparison of the larvae and adults of the congeneric species *Helicidaris tuberculata* and *H. erythrogramma* (photographs courtesy of E.C. Raff and R.A. Raff). Bottom: Phylogeny showing multiple origins of yolk-feeders (red bars) from ancestral plankton-feeders. I – indirect development; D – direct development. (See Appendix 4 for an introduction to the business of inferring phylogenetic trees from comparative data.) (Reproduced with permission from *Int. J. Dev. Biol.*, **47**: 623–632.)

to enable adult forms to evolve'. This overly 'adultocentric' view of things (as recently criticised by the Italian biologist Alessandro Minelli²) is misleading. Instead, what happens is that there are variations at *all* developmental stages. In each case, some variants may be fitter than others, *either* because of the advantages they possess at that stage *or* because of advantages that accrue further **downstream** in the developmental pathway or, of course, for both reasons. In some cases, particularly in animals with complex life-cycles (or 'indirect development' – i.e. development to adult via a **larval** form), evolution of larval stages may occur quasi-independently of evolution of the adult. This is true, for example, in the case of evolutionary switches between plankton feeding and yolk feeding in **echinoderm** larvae³, where the plankton-feeders have 'arms' that the yolk-feeders do not (Fig. 1.4), but this does not lead to a corresponding difference in the adults.

Having now seen that the case for the centrality of development in the evolutionary process is unassailable (but with a caveat to be discussed in Section 1.3), we need to examine development itself, and also to ask about the ways in which it can evolve. This approach (Section 1.2) will reveal several problems, some of which can be easily remedied at our current stage of knowledge, but some of which cannot. These problems include: the absence of some key terms; the previous over-emphasising of some processes (e.g. **heterochrony**); the need to connect organism-level observations with both molecular and populational ones; and the crucial issue of whether development in some sense guides evolution. This last issue is perhaps the most fascinating of all but is also the hardest to deal with and the most controversial. At stake here is the question of whether the structure of the developmental variation available to natural selection can influence the direction that evolution takes, rather than this direction being entirely set by selection alone; and if the former, then whether the role of development is merely negative ('constraint') or both positive and negative ('bias'). This will be discussed in detail in Chapter 13.

1.2 Development; and Evolutionary Changes in Development

The development of any animal or plant can be thought of as a time-sequence of more or less well-defined stages. The simplest kind of development is 'direct development', as in mammals. Indirect development, whether in echinoderms, insects or amphibians, is more complex in that the route to the adult takes what might be thought of as a 'detour' via immature stages that are radically different from the adult as opposed to miniature versions of it. Some plants, notably trees, and also some colonial animals, such as **bryozoans** ('moss animals'), are of a **modular** nature, which means that within one individual tree or one bryozoan colony, a major phase of development repeats itself multiple times. This is readily apparent to the casual observer of deciduous trees in successive springs, as the development of leaf modules occurs on a massive scale. It is also apparent, though only readily through a microscope, to observers of the growth of bryozoan colonies (Fig. 1.5), by the development of additional **zooid** modules around a colony's periphery.

In any animal or plant, both the overall developmental process, and any particular component of it, such as the developmental pathways leading to the appearance of segments, limbs or leaves, can be thought of as a trajectory. Each such trajectory represents a very specific route for a cell population that is different from other possible routes.



Figure 1.5 Modular development, as exemplified by a bryozoan colony. Each zooid is genetically identical to every other one in the colony, which is formed by the repeated asexual reproduction and development of zooids from the first one, which is referred to as the 'ancestrula'. A large colony may consist of many hundreds of zooids (photograph courtesy of Peter Wirtz).

But equally, each trajectory can vary, both within an individual (the leaves on a single maple tree are not all identical) and, more importantly from an evolutionary perspective, among the various individuals that make up an ecological population. It is here that we move from thinking about development itself to how altered development can arise in evolution.

This is an absolutely crucial moment in our approach to the whole subject of this book. We can now see the nature of what we are dealing with: a change in something that is itself a process of change. This is very different to the old ‘ecological genetics’ approach to evolution, the practitioners of which were usually observing evolutionary change in something that was the fixed outcome of development. An example of the latter is industrial **melanism** in moths, where the phenotype studied was the external pigmentation of the *adult* (Chapter 4). Development itself was ignored in most such studies.

Given the more recent ‘change in a process of change’ approach, we need to be very careful that we have a suitable language to use to deal with such a complex situation. The complexity was nicely described by the American developmental biologist Scott Gilbert⁴ in 2007, as follows: ‘For evolutionary developmental biology, the current challenge is producing a 5-dimensional representation: the four standard dimensions of space and time placed into the context of the paleontological temporal dimension.’

So, now to the issue of a suitable language. Biologists call a change in a gene ‘mutation’. Although this can be extended to the phenotypic level by talking of mutant phenotypes, this usage is not helpful. It connects better with the old ecological genetics approach of ignoring development and concentrating on the *adult* phenotype. What we need instead is a different term that indicates clearly that we are referring to a change in development. We can’t just call it ‘developmental change’, as that would be ambiguous and more likely to be interpreted just as going along one particular trajectory (in developmental time) rather than switching from one trajectory to another (in evolutionary time). But if ‘developmental change’ won’t do, what will?

One term that definitely will not do as an overall term for evolutionary change in **ontogeny** (i.e. development) is ‘heterochrony’, despite the book title by McKinney and McNamara⁵, *Heterochrony: The Evolution of Ontogeny*, with its implication that the two are synonymous. Rather, heterochrony (evolutionary change in developmental timing) is merely a subset of the overall evolution of development, as indicated by the chapter title ‘It’s not all heterochrony’ in Rudolf Raff’s book⁶ *The Shape of Life*.

Two phrases that have already been used in the context of evolutionary changes in development may be considered as candidate ‘umbrella-terms’ to cover *all* such changes, whether heterochronic or other. These are **developmental repatterning**⁷ (sometimes in the form ontogenetic repatterning⁸, which is synonymous) and developmental reprogramming⁹. There are two reasons why the former phrase is preferable. First, ‘developmental program(me)’, ‘programming’ and ‘reprogramming’ are too philosophically loaded, and are interpreted by some biologists as smacking of ‘genetic imperialism’ (Appendix 1). Second, ‘developmental reprogramming’ has become used in a different, and narrower, way¹⁰ in the last few years. So, developmental repatterning now seems the obvious choice as the umbrella-term for all evolutionary changes in development, and we will use it throughout this book.

Any developmental process can be thought of as a pattern in time, space or (usually) both. Already ‘pattern’ is part of the language at different levels of developmental

study. For example, at the molecular level we speak of the **expression pattern** of a gene in an embryo (Fig. 1.6); and at the tissue level we speak of **pattern formation**, to indicate, for example, the different developing patterns of the five digits of our hand.

If the development of one individual can be thought of as patterning (in a multitude of senses), then the evolution of development can be thought of as repatterning. Logically, considering any aspect of development – for example, the expression pattern of a gene – there are four types of repatterning that can occur: changes in time, place, amount or type. There are well-established terms for the former two – **heterochrony** and **heterotopy**; and there are more recently-introduced terms for the latter two – **heterometry** and **heterotypy**. This series of terms provides a broad categorisation of the types of evolutionary change that can occur in the developmental process. It will be useful to keep them in mind later (and so they are used as chapter titles in Part II) as the intricacies of particular **case studies** emerge.

1.3 Development and the Realm of Multicellularity

There is a restriction to the importance of development in evolution that does not apply to the importance of genes; specifically, development is only a necessary part of evolutionary theory when the creatures that are evolving are multicellular. This is because creatures that are unicellular throughout their life-cycle lack ‘development’, at least in the sense in which the word is normally used. Thus evo-devo deals mainly or wholly with what we will call here the realm of multicellularity.

Note that this term – realm – is not part of the taxonomic hierarchy (in the way that **domain**, **kingdom** and **phylum** are). The reason for adopting such a term is that if we take as a group all multicellular creatures, they do not form a

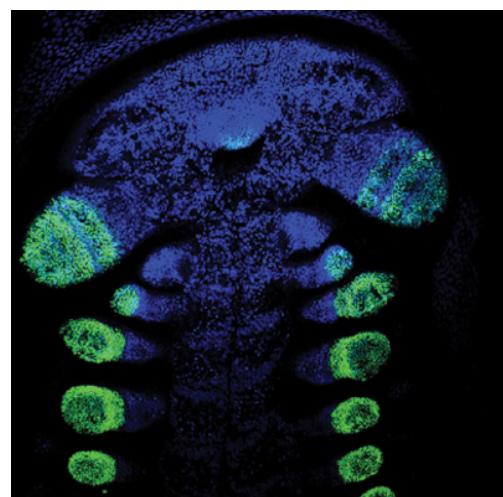


Figure 1.6 The expression pattern of a gene in embryos. The example shown is the expression of a gene called *distal-less* (see Appendix 2 for information on gene names) in insect (top) and centipede (*Strigamia*) embryos. In the insect the red staining reveals expression of the gene in developing appendages in early-stage (left) and later-stage (right) embryos (photograph courtesy of Nipam Patel); in the centipede (*Strigamia*) the expression of the gene is shown in green (photograph courtesy of Cornelius Eibner).

single **clade**. Indeed, far from it: multicellularity has arisen at least five times in evolution, and probably much more often.

The five major origins of multicellularity – in animals, plants, fungi, brown algae and cellular slime moulds – are shown in Fig. 1.7. More minor origins, in the sense that they have led to more restricted invasions of multicellular **morphospace**, have occurred (*inter alia*) as follows: in the cyanobacteria (strings and mats of cells); in the diatoms (which have some multicellular forms, despite being very largely a clade of unicells); and in other groups of ‘slime moulds’ unrelated to the group shown in Fig. 1.7. It should be noted that the deep divisions of the living world shown in the figure are different from those that can be seen in comparable trees produced a mere decade ago; and our picture of deep **phylogeny** may well yet change further. Despite this, the conclusion that multicellularity has arisen several times in evolution is likely to be robust.

How did multicellularity originate? A recent clue has come from the study of **choanoflagellates** – a clade of unicells that appears to be the **sister-group** of the animal kingdom. The first choanoflagellate genome project¹¹ has revealed that these creatures possess many genes previously known only from animals and associated with multicellularity, such as genes that make cell adhesion and cell-cell signalling molecules. These proteins may have been used in the unicellular ancestors of animals (and in present-day choanoflagellates) to interact with the environment, including **conspecifics** (potential mates) and other unicells (potential prey). If so, this would represent an example of **exaptation**, in which something initially evolved for one selective reason later becomes useful (and hence selected) for another. This fascinating topic will be discussed further in Chapter 12.

As ever, there is a caveat. One main strand of the evidence for a sister-group relationship between choanoflagellates and animals is the similarity in the form of

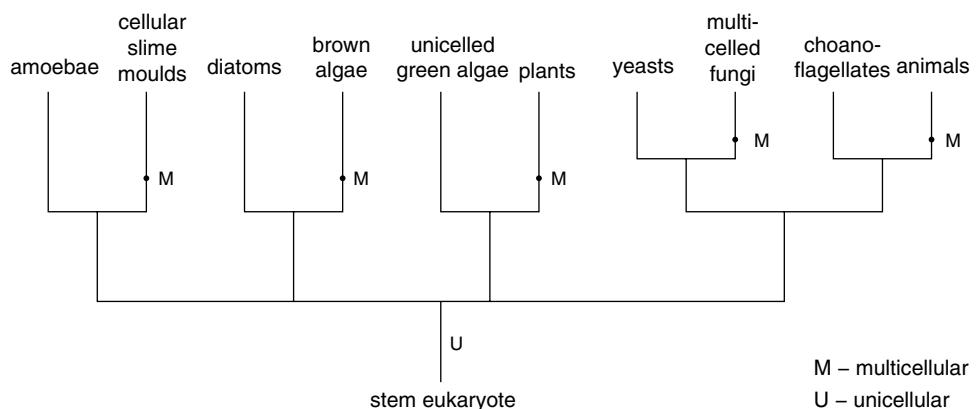


Figure 1.7 The five ‘main’ evolutionary origins of multicellularity, each marked with an M on the lineage concerned. In each case the probable sister-group is also indicated. Note that in a typical multicellular creature there is also a *developmental* origin of its multicellular state in each generation. In some branches, what is shown is ‘exact’ – for example, there was probably only a single origin of multicellularity in animals; but in other cases, for example fungi, what is shown may be a simplification.

the typical choanoflagellate cell (possessing a collar) and the collar-cells of sponges (Porifera), which have long been regarded as the most primitive animals. But if a recent molecular phylogeny of the animal kingdom¹² is to be believed, the **ctenophores** (comb jellies) are more basal than sponges. However, the authors concerned admit that their placing of the ctenophores as basal should only be regarded as a hypothesis for now. Figure 1.8 shows this hypothesis and its main alternative, along with pictures of collar cells. A complication to both hypotheses is that the sponge group Porifera may be **paraphyletic** or even **polyphyletic**.

An important general point emerges from this recent dispute about the relationships among the most **basal** animals. In general, it is best to have an agreed phylogeny of

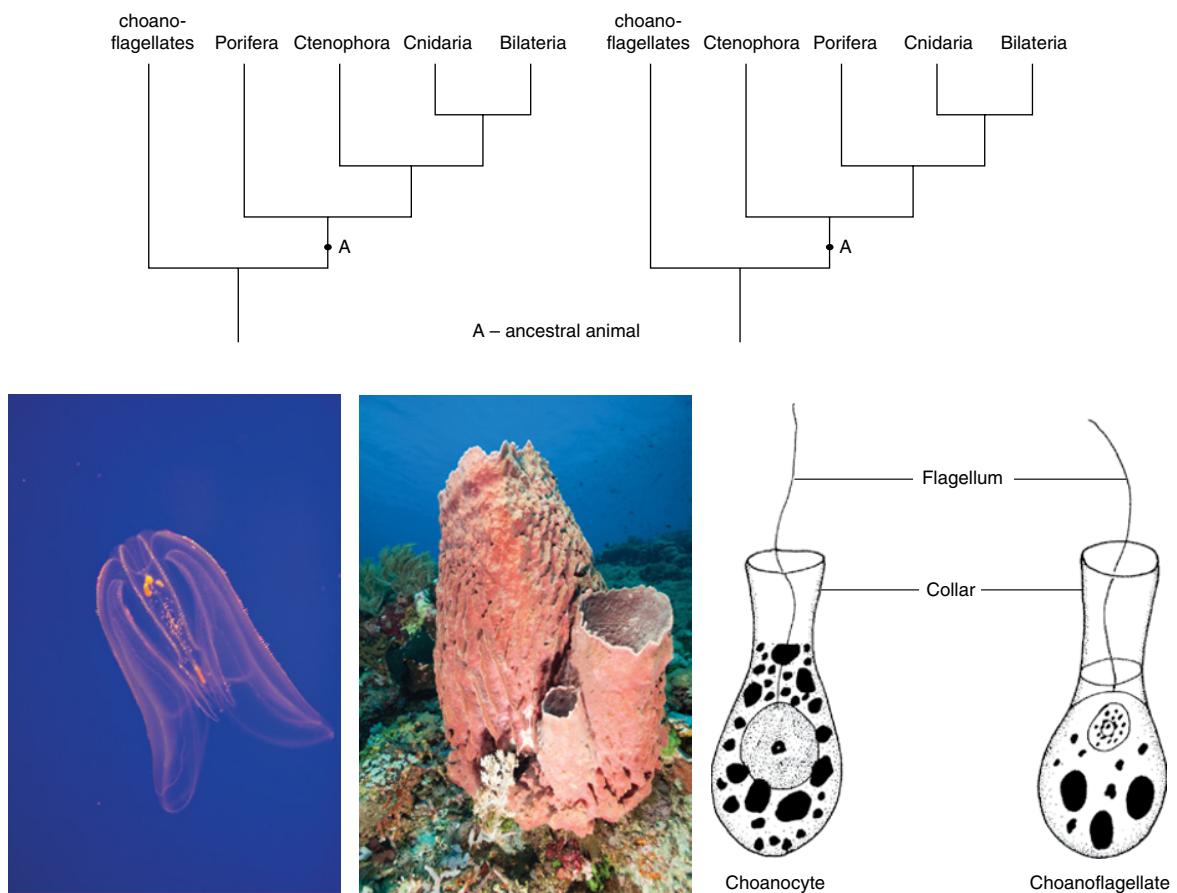


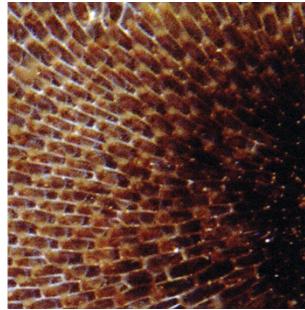
Figure 1.8 Our understanding of the pattern of relationships among the most basal animal groups is still very imperfect. Top: Conflicting hypotheses as represented by alternative trees. Bottom: Pictures of a ctenophore, a sponge, a collar-cell (choanocyte) of a sponge and a choanoflagellate.

any group of animals or plants before mapping onto it (as in Chapter 11) evolutionary changes in development. For some groups, this is not a problem; but for others, our current view of phylogeny may alter radically in the future. If it does indeed alter, then so too must our views on the nature and temporal sequence of evolutionary changes in development – that is, of developmental repatterning.

SUGGESTIONS FOR FURTHER READING

Two good, but very different, introductory books on the ‘new science of evo-devo’ and on developmental approaches to evolution more generally are:

- Minelli, A. 2009 *Forms of Becoming: The Evolutionary Biology of Development*. Princeton University Press, Princeton, NJ.
Carroll, S. 2005 *Endless Forms Most Beautiful: The New Science of Evo-Devo and the Making of the Animal Kingdom*.
Norton, New York.



CHAPTER 2

What is Evo-Devo?

- 2.1** Forerunners of Evo-Devo
- 2.2** Nineteenth-Century Comparative Embryology
- 2.3** Diverse Antecedents—1900–1980
- 2.4** Conclusions from History; Messages for the Present
- 2.5** The Advent of Evo-Devo in the 1980s
- 2.6** Broad and Narrow Views of Evo-Devo
- 2.7** Too Few Laws, Too Many Facts?

2.1 Forerunners of Evo-Devo

As Winston Churchill said: ‘The farther backward you can look, the farther forward you are likely to see.’ This was intended as a comment on history in general, but it can be applied just as well to the history of science. Any branch of science can only be thoroughly understood in the context of how it has progressed over time.

A good example of how an understanding of present-day evo-devo is informed by a study of its forerunners is the proposed **recapitulation** by embryos of their evolutionary past. Initially regarded (wrongly) as a law of how development evolves, it was later completely rejected (wrongly) and then eventually regarded (correctly) as one of several possible patterns, all of which we need to be able to explain.

So, looking at the historical background of present-day evo-devo is not optional – it is essential. If you are seriously history-averse, you can skip to the skeletal version in Section 2.4 – but I would advise against doing so.

2.2 Nineteenth-Century Comparative Embryology

In the decades following publication of Darwin's classic text in 1859, the leading evolutionary embryologist was Ernst Haeckel, whose publications included three major books. While English translations of the first two have never been undertaken (a project for the future, perhaps), the last – a more popular account of Haeckel's views – was translated¹³ into English in 1896 as *The Evolution of Man*. This translation is important because it allows the many English-speaking biologists who cannot read German (alas a large number, and including myself) to understand Haeckel's key points.

Haeckel's work has frequently been misunderstood, as has the relationship between his 'law' and the 'laws' of the pre-Darwinian comparative embryologist Karl Ernst von Baer, whose principle of embryonic divergence is shown in Fig. 2.1. Some leading figures have been guilty of such misunderstanding, including the English biologist Gavin de Beer (see below and Section 2.3). It is important to clarify this matter here, because the evo-devo of today must build on the comparative embryology of the past – but only on those parts of it that we believe to be correct.

Von Baerian divergence, as can be seen from Fig. 2.1, is a pattern of early similarity giving way to later differences. Von Baer¹⁴ gave four laws to describe this pattern; but it can adequately be described by the first of these: 'The general features of a large group of animals appear earlier in the embryo than the special features.' (Source: Alec Panchen's¹⁵ *Classification, Evolution and the Nature of Biology*).

Haeckel famously produced the 'biogenetic law' or 'law of recapitulation'. 'This fundamental law...', writes Haeckel (1896: p. 7) states:

that Ontogeny is a recapitulation of Phylogeny; or, somewhat more explicitly: that the series of forms through which the Individual Organism passes during its progress from the egg cell to its fully developed state, is a brief, compressed reproduction of the long series of forms through which the animal ancestors of that organism (or the ancestral forms of its species) have passed from the earliest periods of so-called organic creation down to the present time.

Now, two very important questions arise. First, did Haeckel mean that the **ontogenies** of descendant species went through stages similar to the *adult* forms of their ancestors? Second, and related to that, is Haeckel's law compatible or incompatible with von Baer's laws?

Regarding the first question, here is the answer provided by de Beer¹⁶, who interprets Haeckel's law as follows (p. 5): 'The *adult* stages of the ancestors are repeated during the development of the descendants' [my italics]. De Beer's next section is entitled 'The rejection of the theory of recapitulation'. But should we accept that a thorough student of embryology, such as Haeckel, really believed this? Probably not. Here, again, is Haeckel (1896: p. 18):