The body of evolutionary theory that currently occupies a dominant position in biological thought is neo-Darwinism. While this theory has considerable explanatory power, it is widely recognized as being incomplete in that it lacks a component dealing with individual development, or ontogeny. This lack is particularly conspicuous in relation to attempts to explain the evolutionary origin of the 35 or so animal body plans, and of the developmental trajectories that generate them.

This book examines both the origin of body plans in particular and the evolution of animal development in general. In doing so, it ranges widely, covering topics as diverse as comparative developmental genetics, selection theory and Vendian/Cambrian fossils. Particular emphasis is placed on gene duplication, changes in spatiotemporal gene-expression patterns, internal selection, coevolution of interacting genes, and coadaptation.

The book will be of particular interest to researchers and students in evolutionary biology, genetics, palaeontology and developmental biology.

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The Origin of Animal Body Plans

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A Study in Evolutionary Developmental Biology

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"We have seen that the members of the same class, independently of their habits of life, resemble each other in the general plan of their organisation. This resemblance is often expressed by the term 'unity of type'; or by saying that the several parts and organs in the different species of the class are homologous. The whole subject is included under the general name of Morphology. This is the most interesting department of natural history, and may be said to be its very soul."

Charles Darwin (1859, p. 434)

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Preface

A new discipline – *Evolutionary Developmental Biology* as Hall (1992) has called it – is in the process of being born. Its origins are scattered and heterogeneous: from von Baer and Haeckel, through D'Arcy Thompson, Garstang, de Beer and Waddington, to the many recent and current students of comparative developmental genetics and related topics whose work is examined herein. Its potential is enormous: essentially to build a bridge between the mechanisms of population genetics and evolutionary ecology on the one hand and the patterns of comparative anatomy and palaeontology on the other; and thereby to help unify evolutionary theory in general.

This book is intended to be a contribution to this new discipline. It has a focus, though not an exclusive one, on the origin of animal body plans. It probes the question of how the morphological 'designs' of the thirty-five or so animal phyla arose in a burst of creative evolutionary activity in the distant geological past. In particular, it asks the question: were the genetic, developmental and population-level processes involved the same as those occurring in present-day speciations? If not, then what was different about those key early evolutionary events? In attempting to answer these questions, the book ranges from molecules and cells through developing organisms and natural populations to cladograms and ancient fossils.

My own background is in evolutionary ecology and, to a lesser extent, in population genetics. However, to write this book I have had to divert time away from reading in my own field in order to cover all the areas mentioned above, and more besides. In consequence, I have doubtless become 'a jack of all trades and a master of none', with the emphasis firmly on the latter. But, while a position of being adrift in an interdisciplinary sea surrounded by vigorous, more tightly-focused endeavours on all sides feels somewhat vulnerable, I do not regret adopting it. New syntheses between established disciplines are catalysed by individuals adopting uncomfortable positions at interfaces. And the gradual emergence of evolutionary developmental biology as a discipline in its own right will decrease the discomfort as time goes on.

At the beginning of this endeavour, I rebelled against my neo-Darwinian background. By the time the first draft was three-quarters written, however, I had become clear that I was still a neo-Darwinian after all – albeit one who is highly critical of the extreme 'nondevelopmental fringe' of that tradition. Everything in this book is based on the view that key evolutionary changes take place in the context of mutation and selection occurring in localized populations. No 'higher order' or 'emergent' mechanisms are required. However, large-scale evolutionary patterns, such as von Baerian 'deviation', most certainly do occur within and between particular higher taxa; and their explanation in terms of the relative probabilities of different kinds of evolutionary change in developmental pathways represents a major challenge. Also, I argue that neo-Darwinism needs to take more fully on board the concepts of developmental constraint, internal selection and the coevolution of developmentally interacting genes.

With regard to the book's structure: it is designed to be read straight through, and to that end I have tried to keep it short. However, Chapters 2–6 (and Section 9.2) include background information necessary for the main argument of the book (the core of which occupies Chapters 5–11). Readers coming to the book from particular disciplinary bases may wish to omit those bits of background with which they are already familiar (e.g. Sections 2.2 on cladistic methods, 5.2 on some aspects of basic cell biology or 9.2 on simple population genetic models).

A word on style. I have deliberately varied the 'voice' throughout the book, interspersing 'we', 'I' and the passive. Overuse of 'I' can sound arrogant, while overuse of the passive is dull. My own preference is for the 'mathematician's we', representing as it does an author's attempt to meander through the arguments jointly with the reader. However, the 'we' style also has its limitations. At times it is simply inappropriate; and its overuse might be seen to indicate delusions of royalty. The mixed style that I have adopted will not appeal to everyone, especially advocates of the 'pan-passive' (Leather 1996); but then again, what style would be universally liked by all?

And now, some much-felt words of thanks. Draft chapters have been looked at, and critically commented on, by the following: Michael Akam, Helen Arthur, Simon Conway Morris, Gabby Dover, Richard Fortey, Scott Gilbert, Brian Hall, Philip Ingham, Alec Panchen, Linda Partridge, Colin Patterson, Keith Thomson, George Williams and Greg Wray. I have also benefited from discussions with Derek Briggs, Mark Davies, Paul Eady, Malcolm Farrow, Brian Goodwin, John Lazarus and Colin Scrutton. My visits to the geographically-distant of the above were funded through a Leverhulme Research Fellowship. This Fellowship also freed up much of my time for writing: without it, the book might never have come to fruition. I have had secretarial assistance second to none from Pam Giblin and Carolyn Stout. Access to the extensive library collections of both the Literary and Philosophical Society and the University of Newcastle upon Tyne has been invaluable. A special word of thanks goes to Alec Panchen for his help and encouragement throughout the book's gestation. Finally, the year of publication coincides with the year of retirement of my erstwhile PhD supervisor, Bryan Clarke, to whom I would like to say a belated 'thank you' for setting me off on a scientific trajectory which has never been easy but has usually been fun.

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November 1996

Preface to the Paperback Edition

Two years have elapsed since publication of the hardback edition, and many significant advances have been made during this period. I mention several of these below, ordered according to the first chapter on which they impact.

Molecular studies of the age of the animal kingdom, including attempts to date major divergences (e.g. protostome–deuterostome) have continued to proliferate (Ayala *et al.* 1998; Bromham *et al.* 1998; Wang *et al.* 1999). These have produced very varied estimates, and metazoan origins may yet lie anywhere between about 600 and 1200 *my* ago, as indicated in Chapters 1 and 3, or indeed somewhat earlier. Most of the molecular studies favor an early metazoan origin. However, the continuing lack of clear fossil evidence of undisputed metazoans in pre-Vendian times is still a powerful argument for a late origin.

Von Baer's proposed pattern of increasing phenotypic divergence through embryogenesis (Chapters 2, 4) continues to be challenged, yet continues to survive, albeit in modified form and in restricted numbers of taxa. The latest challenge has come from Richardson *et al.* (1997), who show that Haeckel's drawings, which ironically have provided part of the evidence for von Baer's 'laws', are somewhat inaccurate, and tend to gloss over some early embryonic differences. This acts to diminish, but not to eliminate, von Baerian divergence (see Chapters 2, 4 and 11).

There has been a major development in high-level animal phylogeny with the proposal of two new superphyletic groupings: Ecdysozoa and Lophotrochozoa (Aguinaldo *et al.* 1997; de Rosa *et al.* 1999; Ruiz Trillo *et al.* 1999). This is relevant to the phylogenies depicted in Chapters 3 and 7. In Section 3.2, I pose a series of questions regarding the structure of the Metazoa and the relationships between phyla. The last of these is 'What Other Superphyletic Clusters are Discernible?' (after protostomes and deuterostomes). Those pictured are conventional ones, including, for example, an arthropod/annelid/mollusc grouping. However, if the new proposal is correct, then arthropods are in Ecdysozoa along with nematodes and others, while annelids and molluscs are in Lophotrochozoa. It is not yet certain that these new groupings are correct, but the balance of probabilities is swinging in their favor.

Research into the genetic and cellular basis of development itself (Chapter 6) has continued at its characteristically rapid pace. One consequence of this is that the third body axis (left-right) is becoming much better understood (see review by Levin and Mercola 1998). It remains to be seen what evolutionary stories emerge as more types of organism are studied in relation to this axis. Recent work on the molecular developmental genetics of the anteroposterior and dorsoventral axes, and of the proximo-distal axis of limbs, has focused much attention on homology of genes, homology of structures, and the differences between them (Chapter 7; see also Abouheif *et al.* 1997; Panganiban *et al.* 1997; Shubin *et al.* 1997; Arthur *et al.* 1999).

There have been recent theoretical and empirical studies of the kinds of mutation that can occur in developmental genes (Chapter 8), and in particular the subset of these that can be incorporated into evolutionary change at the population level and beyond (Chapter 9). Orr's (1998) model of an inverse relationship between magnitude of phenotypic effect and frequency of contribution to evolutionary change adds rigor to one of the central proposals of the book. Orr's model is a development from the Fisher principle (Chapter 2), but it is a distinct step forward because it avoids Fisher's extreme 'micromutationist' view. It also looks at the time sequence of mutations fixed as the optimum is approached, which Fisher did not consider. On the empirical side, Stern (1998) has shown that small-effect mutations in *Hox* genes can contribute to interspecific divergence (between *Drosophila* species). This helps to refine our view of *Hox* genes as being not exclusively big-effect 'selector genes', but capable of a range of effects from very minor to very major (Akam 1998a,b).

So, two years on and there has been considerable progress on many fronts, but much remains to be done. The next couple of decades hold much promise as Evolutionary Developmental Biology continues to grow and to mature as a discipline. It is interesting that since publication of the hardback the number of journals dedicated to Evolutionary Developmental Biology, or 'evo-devo', has risen from one to three: to *Development, Genes and Evolution* have been added *Evolution and Development* and also *Molecular and Developmental Evolution* (a section of *Journal of Experimental Zoology*). Still a small drop in the ocean of biological journals, of course; but this 'proportional tininess' is more than compensated for by the huge conceptual excitement that characterizes the field. Long may it continue.

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