# Preface

Evolution is the most wonderful area of biology: not only does it have an overarching grandeur, but it provides a perspective that unifies everything that we know about life. In 1973, Theodosius Dobzhansky wrote that 'Nothing in biology makes sense except in the light of evolution.' He was right then and he is right now. The history of evolution is however hard to untangle because what we see today is a contemporary snapshot of a rich and complex biosphere of more than a million species, together with an equally rich and complex, but incomplete fossil record. This record extends back more than three billion years with ever-decreasing clarity to a very simple bacterium that was the first universal common ancestor of all subsequent species. Any author writing a book about evolution thus has the joint tasks of giving that long history together with its supporting evidence and of explaining how change happened and, as Darwin noted, is still happening.

As there are already many books about evolution, any potential reader naturally wonders what this one offers that others do not. It has four aims. The first is to be terse, focusing particularly on the principles of evolution – it assumes that readers know a fair amount about biology, and want neither secondary material repeated nor excessive amounts of detail. The second is to explain the two major themes of the scientific study of evolution, the evidence for evolution and the mechanism by which novel speciation happens – the problem that so interested Darwin. The third is to give the core features of the history of life. The final aim of the book, and one that particularly distinguishes it from others, is to consider the subject from the perspective of systems biology.

This systems biology approach to biological thinking is relatively recent and is based on two ideas. The first is that most activity in living organisms is driven by complex protein networks rather than by individual proteins. This realization particularly helps understand evolutionary developmental biology (evo-devo) and the origins of variation. The second is that causality in living organisms is widely distributed; this can be seen, for example, in considering the relationship between the genotype and the phenotype or in how selection operates. Systems biology provides a natural context for integrating such complex evolutionary knowledge. The systems approach also has a third use: its formal language is helpful in constructing and understanding phylogenetic trees, both cladograms and phylograms (Chapter 5).

The first section of the book gives some necessary background. Section two includes the evidence for evolution and the history of life (Chapters 4–11). This evidence comes from analysis of the fossil record, from phylogenetics, and from evo-devo, with each contributing its own insights. As a result, this history is distributed across the section and so has its own table of contents. The third section (Chapters 12–16) covers the core mechanism or theory of evolution: that new species arise from existing ones through selection acting on variants in small, reproductively isolated populations. The section concludes with a chapter on the evolution of *Homo sapiens*, partly because so much is known and partly because of its particular interest to us. The book ends with a series of appendices that cover some wider aspects of evolution; the fourth of these considers the different viewpoints of evolution and creationism.

There are two areas of evolution where the treatment is light. The first is plant evolution, and this is partly because of the thinness of the fossil evidence, partly because the genetic evidence is not simple, but mainly because of the limitations of the author. The second is the mathematical theory of evolutionary population genetics. This is because the theory mainly focuses on only a single step in the complex mechanism of speciation, how gene distributions in a population can change under random drift, mutation, and selection. There are other reasons: a proper treatment of the theory requires far more mathematics than most biologists have, while the amount of space needed to discuss the theory in adequate depth would have been disproportionate to its importance in the wider scheme of evolution. The solution that I have adopted for handling this theory is to use its important ideas and results where appropriate, particularly in the contexts of genetic inheritance within small groups, of selection, and of coalescent analysis, and to refer the interested reader to the relevant textbooks for mathematical detail.

There is also an interesting difficulty with the theory of evolutionary population genetics, and this is with its view of genes, which dates from the 1940s. Then, a gene was viewed as the heritable component of a phenotypic trait, a view that derived from Mendel's work on peas. He worked with traits that bred reliably, such as seed shape and color, and assumed that the organism had factors whose activity underpinned all such traits. Now, of course, we know that most such trait-defined genes rarely breed true and also have little molecular meaning. Genes are of course DNA sequences coding for particular functions, often detected through mutations that affect an organism's phenotype. Unravelling the complex relationship between trait-defined genes and DNA-sequence genes is not straightforward, but an attempt has been made in the last parts of Chapters 12 and 13 using the framework of systems biology.

Two areas that are treated in a more detailed and integrated way here than in other textbooks are evo-devo and the mutational basis of anatomical variation (Chapters 10–13). A systems-based introduction to the principles of development leads on to an analysis of the functional homologies across embryos (evo-devo). This is followed by detailed discussion about the origins of variation as reflected in changes to embryological development, which is of course where adult anatomical variation usually originates. For Darwin, variation was the most difficult evolutionary problem to solve and he just had to take its occurrence for granted. Now, of course, it is obvious that anatomical and physiological variants usually result from germline mutations, but the idea that a change in a DNA base has a simple or direct effect on the phenotype is rarely correct or even helpful. The view taken in this book is that many of the important and immediate effects of such mutations are on those proteins operating in the networks that drive embryogenesis. Such mutations lead to changes in the functional outputs of these networks, which in turn lead to the broad spectrum of heritable anatomical variants seen within the adult populations. It is on this distribution across a population that selection acts. Without variation there can be no selection: it is the origin of speciation.

**A note on the literature.** Only a small amount of the vast literature on evolution can be discussed here. A few core publications are given at the end of each chapter, but most are cited in the text and detailed in the final reference list. These many papers, books, and websites point readers to important experiments and areas that may only be briefly discussed. The level of the book is such that undergraduate students should be able to read it without needing to refer to these references, although I hope that they will want to. Final year undergraduate and graduate students are encouraged to read more deeply: one only gets to grips with the science of evolution by seeing in detail how nature has been made to yield its secrets.

**Timing convention.** There are several abbreviations for historic time in the literature. Those used here are By and Bya, My and Mya, and Ky and Kya for billions, millions, and thousand years, respectively, with the additional 'a' meaning 'ago.'

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