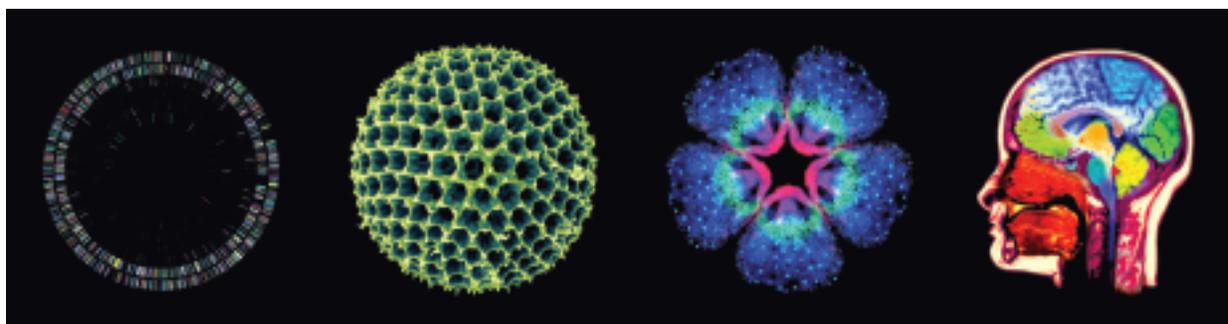


Publication Information For

# EVOLUTION



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## Advance Praise

The scope of Barton et al's new Evolution manuscript is magnificent. This is by far the best textbook on the subject yet and is much like another wonderful textbook *The Molecular Biology of the Cell*.

Well-written and the level of sophistication is pretty equivalent across chapters despite having multiple authors. Figures are, in general, excellent. In its coverage of Evolutionary Processes (Section 3), the analytical and conceptual tools of the field are presented in early chapters (genetic drift, population structure, quantitative genetics) and integrated to understand more complex problems in later chapters (i.e. the interaction between selection and other forces).

*Andrew Martin, Professor of Biology, University of Colorado*

It is the most comprehensive book out there, with an admirable and clear presentation of the facts. In section 2, which deals with the history of life and in many texts makes for tedious reading, there was remarkable clarity and conciseness, and a focus on the best case studies. I personally learnt a great deal from reading these chapters, and the book as a whole would be useful for workers in the field as a source of reference and to give them breadth.

*Trevor Price, Professor of Biology, University of Chicago*

It's really a fascinating new textbook . . . a brand-new approach . . . especially the novel examples, which are completely appealing and refreshing. It is certainly unique . . . an excuse to replace the emphasis on molecular and cell biology parts-list-type courses with an integrated evolutionary approach to teaching upper-level biology.

*David Fitch, Professor of Biology, New York University*

. . . very modern and up-to-date, it does an excellent job integrating molecular biology and evolution, bringing in areas such as evolutionary genomics, biochemistry, and developmental biology that tend to be under-represented in older textbooks.

*Artym Kopp, Professor of Biology, University of California, Davis*

. . . written by people who are involved in the cutting edge of many evolutionary fields. The examples are numerous, well-chosen and up-to-date. This gives each professor the option of picking and choosing among a number of excellent case studies, regardless of the emphasis of that particular professor's course. This is by far the most complete textbook currently on the market, with thorough and expert coverage of the very latest molecular findings.

*Christopher Wills, Professor of Biological Sciences, University of California, San Diego*

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# Book Description

*Evolution* elegantly synthesizes traditional evolutionary theories with contemporary concepts from genomics, developmental biology, human genetics, and other areas of molecular biology. As an innovative, interdisciplinary, and thoroughly integrated book on evolutionary biology with world-renowned authors, *Evolution* thoroughly illuminates this major paradigm of modern science. Evolutionary principles are introduced with examples from across the spectrum of life—from “jumping genes” and RNA molecules, to populations of yeast and *E. coli* reared in the laboratory, to dung flies, lizards, and deer in their natural habitats. A section is also devoted to human evolution and diversity, merging recent insights from molecular techniques with paleontological evidence. *Evolution* is recommended as a primary textbook for undergraduate courses in evolution and well as for biologists seeking a clear, current and comprehensive account of evolutionary theory and mechanisms.

## Book Specifications

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## About the Publisher

Cold Spring Harbor Laboratory Press is an internationally renowned publisher of books, journals, and electronic media located on Long Island, New York. Since 1933, it has furthered the advance and spread of scientific knowledge in all areas of genetics and molecular biology, including cancer biology, plant science, bioinformatics, and neurobiology. It is a division of Cold Spring Harbor Laboratory, an innovator in life science research and the education of scientists, students, and the public.

## Contact and Ordering Information

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For other inquiries or to order an individual copy of the book, please contact Liz Powers at Cold Spring Harbor Laboratory Press. Email: [powerse@cshl.edu](mailto:powerse@cshl.edu) Tel: (516) 422-4101.

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The *Evolution* Web site is an invaluable supplement to the textbook, including two web-only chapters, a resource for the teacher that contains downloadable figures and tables (for PowerPoint or overhead display), author notes, and chapter problems, and other material. Visit the Web site and request a detailed Table of Contents, Sample Chapters, and Exam Copies. *Evolution* will be available for Fall 2007 classes.

[www.evolution-textbook.org](http://www.evolution-textbook.org)

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# About the Authors

**NICHOLAS H. BARTON'S** early research was on narrow zones of hybridization that subdivide many populations; this involved work on a variety of species, including grasshoppers, butterflies, and toads. More recently, his research has been mainly theoretical and aimed at understanding the influence of selection on complex traits, models of speciation, the evolution of sex and recombination, and the coalescent process. He is Professor of Evolutionary Genetics at the Institute of Evolutionary Biology, University of Edinburgh.

**DEREK E.G. BRIGGS** has worked on the extraordinary fossils of the Cambrian Burgess Shale of British Columbia. His current research focuses on the preservation and evolutionary significance of exceptionally preserved fossil biotas. He is Professor in the Department of Geology and Geophysics at Yale University and Director of the Yale Institute for Biospheric Studies.

**JONATHAN A. EISEN** has worked on the evolution of hydrothermal vent symbioses in marine invertebrates and has studied the evolution of DNA repair processes in halophilic archaea. His current research focuses on the evolutionary diversification and genome sequencing of microbes—especially those from extreme environments—as well as the development of phylogenomic methods. He is Professor in the Department of Medical Microbiology and Immunology and the Department of Evolution and Ecology at the University of California, Davis.

**DAVID B. GOLDSTEIN'S** principal interests include human genetic diversity, the genetics of neurological disease, population genomics, and pharmacogenetics. His laboratory currently investigates how human genetic variation influences the response to drug treatments for common neurological and cardiovascular disorders. He is Director of the Center for Population Genomics and Pharmacogenetics at the Duke University Medical Center.

**NIPAM H. PATEL** has studied the molecular basis of *Drosophila* neuron specification and axon pathfinding, as well as the evolution of insect segmentation and embryo pattern formation. His research group continues to study arthropods with a focus on the evolution of development, including the formation of the central nervous system, changes in gene expression patterns and regulatory elements, and the evolution of segmentation and body morphology. He is Professor of Integrative Biology, Genetics, and Development at the University of California, Berkeley.

# Preface

**E**VOLUTIONARY BIOLOGY IS ONE OF THE CORNERSTONES of modern science. The publication of *On the Origin of Species*, by Charles Darwin in 1859, changed forever the way that people view life on our small planet. Over the 150 years since, the study of evolution has itself evolved, taking a quantum leap in the past 20 years through the exciting discoveries that have occurred at the interface of molecular and evolutionary biology. The powerful tools available through the use of molecular markers, genome sequences, and genetic manipulation have provided extraordinary insights into how evolution works. In addition, a fascinating new realm of natural history has opened up, revealing a remarkable variety of molecular adaptations and an array of fundamental molecular mechanisms that are unexpectedly conserved throughout the living world.

Yet, these remarkable developments are scarcely reflected in the way that evolutionary biology is taught. Recent advances in topics such as molecular evolution and developmental evolution are often relegated to minor chapters in other textbooks. Our aim here is to integrate these and other modern breakthroughs into a complete evolutionary perspective that forms the central theme of the book.

Fundamental principles are illustrated repeatedly across all levels of organization (from molecular to organismal) and the entire diversity of life (from microbial to human). We illustrate the basics of natural selection using *in vitro* selection on RNA molecules and using the Galapagos finches (Chapter 17). We show how selection can be measured in laboratory populations of yeast and in natural populations of deer (Chapter 19). We illustrate evolutionary optimization using mating behavior in dung flies and metabolic flux in *Escherichia coli*, and we illustrate evolutionary games using production of toxins by bacteria and mating behavior in lizards (Chapter 20). We show how evolutionary conflicts occur between transposable elements and their host genomes and also between bees in a hive (Chapter 21).

The interdisciplinary approach that we adopt will be valuable to students from a whole-organism background (the majority of students now taking evolution courses), because it will widen their perspective on the scope of evolutionary biology and show them the new methods that are so important in current research. The integration of molecular and evolutionary biology also will be attractive to students whose background and interests are primarily molecular and to faculty in molecular biology departments who develop modern evolution courses.



## Structure of the Book

The book is divided into four parts. In Part I, we summarize the history of evolutionary and molecular biology and the evidence for evolution by natural selection. As well as giving a historical overview, this provides a compact summary of our current understanding, which guides the reader through the rest of the book. Part II describes the origin and diversification of life, including biochemical as well as morphological complexity, and gives a balanced treatment of bacterial, archaeal, and eukaryotic diversity. This section includes some of the most exciting recent discoveries in biology, such as the identification and characterization of particular genes and genetic pathways that play key roles in the development of plants and animals. In Part III, we explain the fundamental processes of evolution: mutation, random drift, recombination, gene flow, and, most importantly, natural selection. We then bring this understanding of the evolutionary process to bear on major questions: Why do organisms age? How can conflicts between organisms be resolved? How do new species originate? Why is sexual reproduction widespread? How do novelties evolve? In the final two chapters (Part IV), we turn to our own species, describing our evolutionary history and discussing the implications of evolution for humanity today.

This book provides the basis for a full course on evolutionary biology: building from a historical overview of evolutionary and molecular biology, through an account of the origin and diversification of life, to an explanation of the processes of evolution and how they interact, and ending with a discussion of human evolution. Parts of the book can also be used as a text for smaller courses.

- Chapters 1–3 give a concise overview of the subject.
- Part II provides material for a course on the origin and diversity of life. More specifically, Chapters 5–8 form the foundation for a course on microbial evolution.
- Part III treats the topics found in standard texts on the processes of evolution but with a strong molecular emphasis. Ideally, this would follow from a course based on Part II.
- Chapters 14, 17, 19, and 26 provide a course in quantitative genetics that goes further, and is more up-to-date, than any other textbook at this level.

## Web Resources

Our book is accompanied by an extensive Web site, which will be especially valuable for instructors and advanced students.

- Many of the illustrations and tables are available in a form that can be used in teaching.
- The glossary, which is included in the printed book, is also available online. All glossary terms are highlighted in **bold** at their first appearance within a chapter. The glossary possesses a search function.
- Each chapter is accompanied by discussion topics, which will allow the student to review ideas and should stimulate further thought.
- Chapters in Part III are accompanied by problems. It is important that the student work through these, so as to reinforce the quantitative material in these chapters. Some of the problems are more advanced and will require knowledge of the material in the online chapters (see next bullet).
- The main text describes the basics of quantitative and population genetics. The Web site includes two supplementary chapters, which allow students to build on the basics and explore more quantitative aspects of the subject. Chapter 27 explains

methods for inferring phylogenetic relationships, and Chapter 28 shows how the evolutionary process can be modeled. (These chapters are not indexed, but they can be searched, and are accompanied by Web Notes, as explained below.)

## Exploring the Literature

It is important that the reader can use this book as a platform to explore the literature of evolutionary biology. The success of science depends on being able to trace the evidence and arguments that support each statement and on this web of knowledge being open to all. We have not cluttered the main text with references to our sources, but have provided several routes into the literature. At the most basic level, each chapter ends with a Further Reading section, which lists reviews that cover the material. On the Web site, we include a section that describes the most useful journals in the field and explains how online databases such as the ISI Web of Knowledge and Google Scholar can best be used to search the literature. Each section of the book is accompanied by Web Notes, which give the primary sources for the material in the main text and expand on some points. Together, the Web resources make it straightforward for the reader to go beyond the introduction that we provide in the main text and to explore the subject in depth.

Evolutionary biology is an active and thriving field. Much is well established, but there are many open questions, and new discoveries are continually opening up new questions, which are highlighted throughout the book. We aim to set out clearly what *is* known, but also to lay out the evidence and arguments upon which this knowledge is based and to show how we can set about answering new questions. Our book is unique in integrating molecular biology with evolutionary biology—an approach that reflects the convergence of these fields in recent years.

## Acknowledgments

First, we would like to thank Jim Watson, who conceived the idea of a textbook that would integrate molecular and evolutionary biology. Cold Spring Harbor Laboratory Press has given outstanding support to the project throughout its long gestation: John Inglis and Alex Gann, in particular, showed exceptional skill in guiding their sometimes troublesome authors through to completion of the book. During the development and production of the book, Michael Zierler, Judy Cuddihy, and Hans Neuhart have shaped the writing and artwork into a coherent and attractive text. We also thank Jan Argentine, Elizabeth Powers, Maryliz Dickerson, Carol Brown, Mary Cozza, Maria Fairchild, Nora McNerny, Denise Weiss, Susan Schaefer, and Kathleen Bubbeo for their help throughout production of the book. Thanks are also due to Mila Pollock, Director of Cold Spring Harbor Laboratory Library and Archives and her staff, especially Clare Clark, Gail Sherman, Claudia Zago, and Rhonda Veros.

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Derek E.G. Briggs  
Jonathan A. Eisen  
David B. Goldstein  
Nipam H. Patel

# Aim and Scope of the Book

*“Nothing in biology makes sense except in the light of evolution”*

—Teodosius Dobzhansky

## EVOLUTIONARY BIOLOGY DESCRIBES THE HISTORY OF LIFE AND EXPLAINS WHY ORGANISMS ARE THE WAY THEY ARE

**O**UR WORLD IS FILLED WITH AN extraordinary diversity of living organisms (Fig. A&S.1). The Sun’s light is harvested by bacteria, algae, and plants, and every feasible source of chemical energy, from hydrogen gas to carbon monoxide, is exploited by some microbe. Life thrives in the most extreme environments, from Antarctic rocks to scalding undersea vents to crevices miles beneath the Earth’s crust. Organisms are sensitive to the slightest variations in their environment: Bacteria find their way by sensing the Earth’s magnetic field, moths find their mates from a few molecules’ scent, and owls see their prey from afar on a moonless night. Birds can use specialized tools to help them extract food, bees coordinate the activity of their hive, and human societies use language and technology to overcome the limitations of their biology.

All of these diverse functions are achieved by the same fundamental biochemical system. Genetic information stored in the sequence of bases in DNA is **transcribed** into RNA and then **translated** into sequences of amino acids that construct and maintain the organism. The engineering of organisms is as remarkable as its consequences. DNA sequences can be replicated with less than one error in a billion bases. Proteins at ambient temperatures can catalyze reactions that human chemists can achieve only under extreme conditions and with much coarser specificity. Interactions between DNA and proteins regulate precise patterns of gene expression that allow the reliable construction of complex organs, including, most impressively, the human brain, which generates and controls elaborate behavior. All of this is determined by a remarkably compact genome; the human DNA sequence, for example, encodes less information than is stored in a personal computer.

We know, at least in outline, how the DNA sequence is translated into proteins, how these proteins affect metabolism and regulate gene expression, and how multicellular organisms develop reliably from a single cell. We also know, at least in outline, how the diverse organisms now living came to be. All of them (including us) descended from one “universal ancestor” that lived about 3.5 billion years ago. That ancestor itself descended from a much simpler organism in which RNA carried out the present roles of both DNA and protein. Thus, all the biochemical, morphological, and behavioral diversity around us descended from a few original genes.

The exquisite biological devices that we now see appear as though carefully designed



**FIGURE A&S.1.** Diversity of adaptation. *Top row:* Life in extreme environments. Organisms can live in the very cold environment of Antarctic dry valleys (*left*) or in hydrothermal vents deep within the sea (tube worm community; *right*). *Middle row:* Diversity of morphological adaptation. The fine structure of moth antennae (*left*) allows the detection of just a few molecules of pheromone. The large eyes of the vermiculated screech owl (*Otus guatemalae*; *right*) allow it to find prey at night. *Bottom row:* Behavioral adaptation. The New Caledonia crow (*Corvus moneduloides*; *left*) fashions tools for specific purposes, here to extract insects from holes in a tree branch. Honey bees (*Apis mellifera*; *right*) live and work in an organized “society” with specific tasks assigned to maintain the hive.

for their present purposes, and this appearance of design was long taken as evidence of an intelligent creator. We now know that biological function is constructed and maintained by natural selection: the gradual accumulation of variations that arise by chance and that are preserved because they aid the survival and reproduction of their carriers. The theory of evolution is a synthesis of Darwinian natural selection and Mendelian genetics. It allows us to ask not just how life evolved, but why it is as it is: Why do organisms develop from a single cell?; Why is the genetic code as it is?; and Why is there sexual reproduction?

## EVOLUTIONARY BIOLOGY IS A VALUABLE TOOL

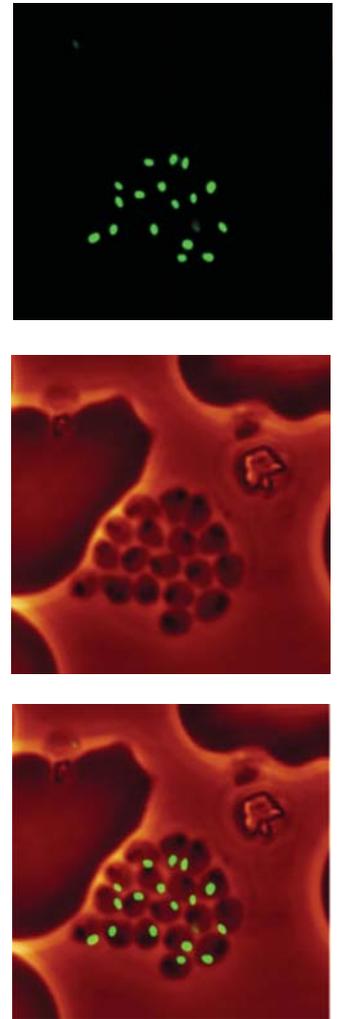
Our understanding of the history of life and the mechanism by which life has evolved has influenced virtually every aspect of human society from literature to medicine. However, evolutionary biology is not simply a historical science. Information on evolution and the application of principles learned from the study of evolution also have many practical uses in fields as diverse as geology, computer science, and epidemiology. We give here three examples.

Because closely related organisms tend to have similar features, evolutionary classification can help predict the biology of an organism through comparison with its relatives. Traditionally, microorganisms are studied by isolating them in culture. However, the great majority of microbes cannot at present be grown in the laboratory. By combining tools from molecular and evolutionary biology, genes from unculturable species can be cloned and analyzed to provide the information that places them into the tree of life. This allows scientists to infer much about these unculturable microbes, such as details of their metabolic processes or their interactions with other organisms.

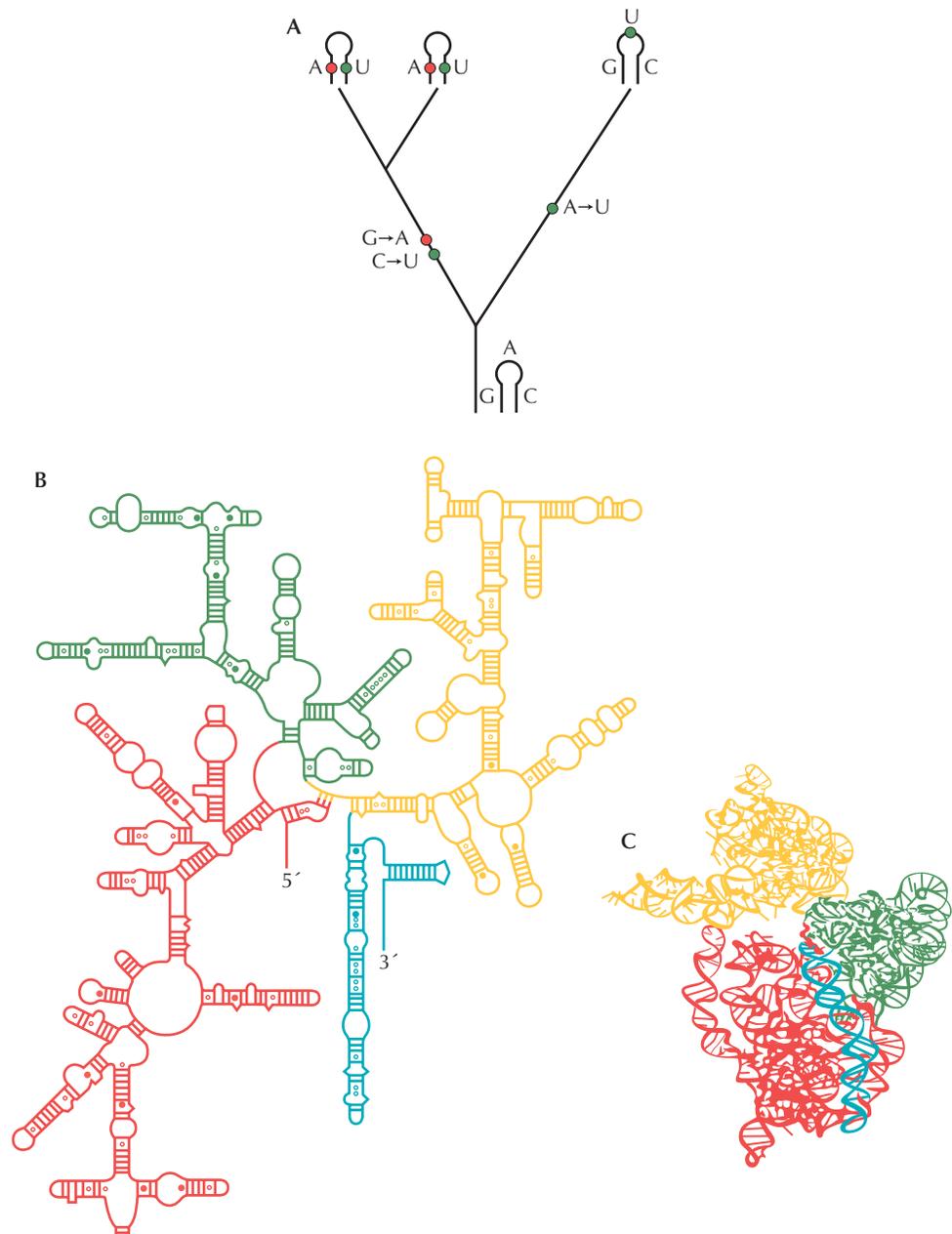
This approach has led to the development of new drugs for treating malaria and related diseases. Malaria is caused by the infectious parasite *Plasmodium falciparum*. Traditional antimalaria drugs that kill *P. falciparum* are frequently quite toxic to humans, because they attack pathways common to eukaryotes. In the 1970s, scientists found an unusual **organelle** in *P. falciparum* that contained its own DNA. Much to their surprise, evolutionary trees based on genes in this DNA indicated that this organelle (the apicoplast) was closely related to plant **chloroplasts** (Fig. A&S.2). Plant chloroplasts originated from an **endosymbiosis** between ancestors of plants and a bacterium related to modern day **cyanobacteria** (**Chapter 8**). Evolutionary analysis has shown that the *Plasmodium* lineage obtained this plastid by entering into a symbiosis with another eukaryote (most likely an alga) that contained a plastid. Although many of the features of this algal-like symbiont have since been lost, the plastid was maintained, and although *Plasmodium* does not carry out photosynthesis, the metabolic functions of the apicoplast are essential for its survival. The absence of the apicoplast metabolic pathways in mammals has suggested new targets for antiparasite medications. A variety of antibiotics, enzyme inhibitors, and herbicides that target the apicoplast show promise at killing *P. falciparum* and relatives that cause toxoplasmosis and cryptosporidiosis.

Evolutionary biology has also been very useful in enhancing our understanding of macromolecular structure. This is perhaps best shown through studies of **ribosomal RNA** (rRNA). In all organisms, rRNA is involved in the translation of messenger RNA into proteins. rRNA molecules form intricate structures, driven in part through internal base pairing, much like the base pairing that forms the DNA double helix (Fig. A&S.3). Biochemical analysis of rRNA molecules has been unsuccessful in solving the rRNA folding problem, partly because there are simply too many base-pair combinations to test. Until recently, structural studies have also been unsuccessful, because rRNA molecules do not readily form the crystals needed to solve structures by X-ray diffraction. However, the base pairings within rRNA molecules have been determined by tracing the evolutionary history of nucleotide changes and identifying cases in which changes occurred in two separate parts of the molecule at the same time. By identifying thousands of these correlated changes, researchers have been able to determine which nucleotides base pair with each other (**Chapter 19.21**).

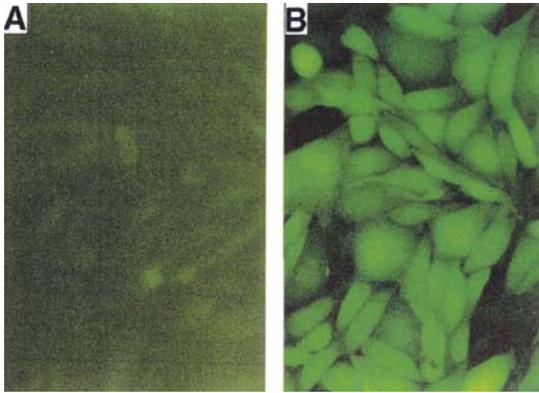
Numerous human endeavors have benefited from our understanding of how evolution works. Animal and plant breeding programs are continually improved through the application of principles of population genetics. Similar approaches are being used in biotechnology, through the use of so-called molecular breeding (**Chapter 17.1.1**). One example is the creation of designer proteins that have new or en-



**FIGURE A&S.2.** Apicoplasts are visible through the use of green fluorescent protein (*top*); round balls in center are malaria parasites (*middle*); and green apicoplasts inside parasites (*bottom*).



**FIGURE A&S.3.** The pattern of evolutionary change in an RNA molecule can be used to determine its structure. (A) Where two parts of the RNA molecule pair, a change in one base must be accompanied by a change in its partner if pairing is to be maintained (e.g., G→A [red] and C→U [blue]). This maintains the pairing between these bases. In contrast, changes in unpaired regions can occur independently (e.g., the single change A→U [green]). (B) The secondary structure of the 16S ribosomal RNA molecule was inferred using this method, based on comparisons between more than 7000 sequences from different bacterial species. Ladders indicate paired helices. (C) The full three-dimensional structure of crystals of the molecule was determined directly in 2000 and confirms the inference made by the comparative method: More than 97% of the predicted pairs were found in the crystal structure. Different colored regions in B and C correspond to different domains of the molecule.



**FIGURE A&S.4.** Molecular evolution can be used to solve a complex practical problem. Here in vitro selection of a synthetic green fluorescent protein (GFP) gene (*B*) was used to increase its signal over wild type (*A*).

hanced functions. Fluorescent proteins are very useful tools in biological research (e.g., Fig. A&S.2). They are detected using fluorescence microscopy and other light-sensitive instruments through the light emitted by the proteins when placed under the proper conditions. To make the best use of fluorescent proteins, it is helpful to have different forms that emit different colored light. The original green fluorescent protein was isolated from a jellyfish species, *Aequorea victoria*. Using in vitro molecular breeding methods, scientists have altered the green fluorescent protein, creating new versions that fluoresce at other wavelengths. Molecular breeding methods rely on our understanding of the mechanisms of evolution to enable designer macromolecules to be created (Fig. A&S.4). In nature, the evolution of new functions for, say, a protein may be limited by the likelihood that the appropriate genes carry the necessary combination of mutations. **Recombination** (which is used deliberately in molecular breeding) brings together different mutations and greatly increases the efficiency of in vitro selection (see **Chapter 23.x**).

### MOLECULAR BIOLOGY AND EVOLUTIONARY BIOLOGY ARE OVERLAPPING FIELDS OF STUDY

Molecular biology and evolutionary biology are both thriving fields. Over the last half-century, however, they have largely developed independently of each other. Of course, evolutionary biology uses many molecular techniques and investigates molecular as well as morphological and behavioral variation. Conversely, molecular biology uses (at least implicitly) evolutionary methods to establish relationships between organisms and between genes and to distinguish functional sequences. Nevertheless, the two fields remain as largely separate communities and ask rather different questions. Our aim in this book is to explain evolutionary biology in a way that will be accessible—and interesting—to molecular biologists and to show how evolutionary methods bear on some of the most recent molecular discoveries.

Part I provides a historical discussion of the two fields, outlining key advances and concepts. The overwhelming evidence for evolution is presented, including arguments supporting natural selection as its central mechanism. Part II presents an overview of the diversification of life. Beginning with the origins of life more than 3 billion years ago, this part shows how the three domains of life—bacteria, archaea, and eukaryotes—have diversified. We describe the evolution of multicellular organisms, both as seen in the fossil record and through our recent understanding of developmental programs. Part II lays the groundwork for Part III, which explains the nature of genetic variation, the mechanisms of evolution, and their consequences. Almost all popula-

tions contain abundant variation, which is generated by mutation and recombination. This variation is seen both at the level of DNA and protein sequence and in the morphology and behavior of the whole organism—traits that depend on the interaction between large numbers of genes. Natural selection acts on this variation and is responsible for the remarkable adaptations that we see in the living world. We show how the various evolutionary mechanisms interact with each other to generate these adaptations, to produce diverse species, and to shape the genetic system itself. Part IV closes the book with a discussion of the evolution of our own species and the role that evolution and evolutionary biology now play in human endeavors.

This textbook is supported by a comprehensive Web site, which includes two chapters on the quantitative methods that are used to study evolution. The first presents tools used to reconstruct phylogenies; the second is a detailed introduction to evolutionary modeling. The Web site also includes notes that give full references, expands on some of the arguments in the main text, and provides links to other useful Web sites. Combined with the recommended reading list found at the end of every book chapter, this will guide the student into the extensive literature of evolutionary biology and will provide useful background material for the instructor. Finally, the Web site includes problems and worked examples that are associated with the chapters in Part III.

We hope that, as well as providing a clear explanation of biological evolution, our book will help to bring molecular and evolutionary biology closer together. The past century has seen extraordinary advances in both branches of biology, and the coming decades promise to be still more exciting.

<http://evonet.org> is a Web site that provides a good overview of evolutionary biology.  
Meagher T.R. and Futuyma D. 2001. Evolution, science, and society.

*Am. Nat.* **158**: 1–46.  
Examples of how evolutionary biology can be applied in diverse ways. Also available from <http://evonet.sdsc.edu.evoscisociety/>.

## Evidence for Evolution

**E**VOLUTIONARY BIOLOGY HAS PROFOUNDLY altered our view of nature and of ourselves. At the beginning of this book, we showed the practical application of evolutionary biology to agriculture, biotechnology, and medicine. More broadly, evolutionary theory underpins all our knowledge of biology, explains how organisms came to be (both describing their history and identifying the processes that acted), and explains why they are as they are (why organisms reproduce sexually, why they age, and so on). However, arguably its most important influence has been on how we view ourselves and our place in the world. The radical scope of evolutionary biology has for many been hard to accept, and this has led to much misunderstanding and many objections. In this chapter, we summarize the evidence for evolution, clarify some common misunderstandings, and discuss the wider implications of evolution by natural selection.

Biological evolution was widely accepted soon after the publication of *On the Origin of Species* in 1859 (**Chapter 1.x**). Charles Darwin set out “one long argument” for the “descent with modification” of all living organisms, from one or a few common ancestors. He marshaled evidence from classification of organisms, from the fossil record, from geographic distribution of organisms, and by analogy with artificial selection. As we saw in **Chapter 1**, the detailed processes that cause evolution remained obscure until after the laws of heredity were established in the early 20th century. By the time of the **Evolutionary Synthesis**, in the mid-20th century, these processes were well understood and, crucially, it was established that adaptation is due to **natural selection** (**Chapter 1.x**). Now, evolution is accepted as a fact, and active research is extending our understanding of the processes responsible for it.

Despite this strong scientific consensus, many people do not accept that living organisms have evolved by purely natural processes. This skepticism has several roots. For some, it may arise from a conflict with prior religious beliefs. In others, it may come from doubts that the astonishing diversity of the living world could descend from one simple ancestral organism, or that complex adaptations—especially, the human mind—could be built up by natural selection acting on random variation. The conflict with religious belief is most sharply focused for those who believe in the literal truth of their sacred texts. Such believers must reject much of science—physics, astronomy, and geology, as well as biology—and, indeed, must reject the very methodology of science.

There is a continuous range of beliefs about the origin of life, from a literal belief in one of the creation myths in Genesis through to the purely material account given



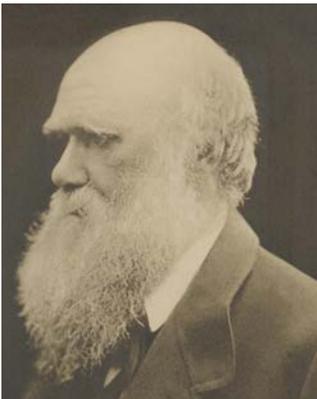
in this book. Some hold that each of the 6 days of the biblical account corresponds to many millions of years. Thus, they accept an old Earth, but still hold that species (or at least, higher taxa) were separately created. Others accept evolution, but invoke an “intelligent designer” to explain complex adaptation. The predominant position of the main Christian churches is **theistic evolution**, in which God works through natural laws, with little or no direct intervention. The Catholic Church accepts physical evolution via natural selection and other evolutionary processes, but invokes a supernatural introduction of the human soul. Most of the clashes between evolutionary biology and religion have come from people who believe in a single divine creator. Religions that do not assume such a deity, for example, Buddhism and Hinduism, have generally seen evolutionary ideas as compatible with their belief in a world that is in continual transformation.

Later in this book, we will set out the detailed history of evolution (**Chapters 4–11**); explain the mechanisms of natural selection and other evolutionary processes (**Chapters 12–17**); and explain how this accounts for adaptation, speciation, and the emergence of novel features (**Chapters 18–24**). We also devote considerable discussion specifically to human evolution (**Chapters 25 and 26**). In this chapter, we summarize the evidence that natural selection is responsible for the appearance of design. We discuss how the scientific process works and its relationship with the religious and moral beliefs that fuel much of the opposition to evolution by natural selection. Many of the points we make about the nature of evolutionary thinking will be considered in more detail later in the book. This chapter serves as a concise summary of the key arguments.

## EVIDENCE FOR EVOLUTION

### Patterns of Relationship Provide the Most Powerful Evidence for Evolution

Although direct observation and the fossil record each provide powerful support, the most compelling evidence for evolution comes from the patterns of similarity between present-day organisms, which reveal features that are shared across all organisms: a nested pattern of groups within groups, consistent across many different traits; and a correspondence between biological relationship, geological history, and geographical distribution.

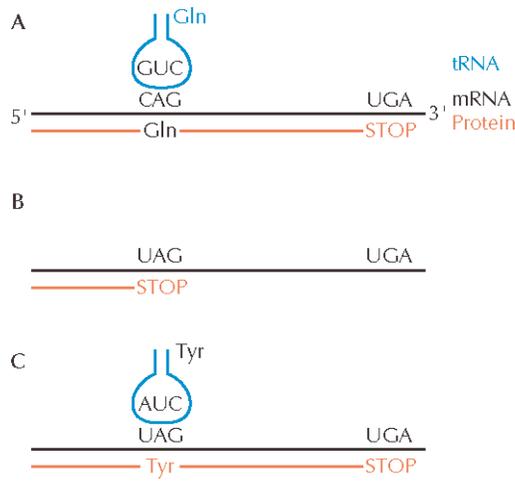


**FIGURE 3.1.** Charles Darwin. “There is grandeur in this view of life, with its several powers, having originally been breathed by the Creator into a few forms or into one” (from conclusion to *On The Origin of Species*).

#### *Universally Shared Features*

Even in Darwin’s time, the similarity of all living organisms was clear enough for him to suppose that all life descended from one or at most a few ancestors (Fig. 3.1). However, the full extent of this similarity was revealed when the universal principles of molecular biology were discovered in the middle of the last century. Almost all organisms use DNA to encode their genetic information, which is transcribed into RNA and then translated by a single universal genetic code into protein sequence. (Some viruses are based on RNA, not DNA, and there are slight variations in the genetic code [**Chapter 4.x**]*—*but these are minor exceptions.) Many molecular functions have been conserved across widely different taxa. For example, yeast that are defective in genes that control the cell cycle can be rescued by human genes that carry out the same function. Indeed, the basic machinery of replication, transcription, and translation is conserved across all living organisms. The success of molecular biology lies in the essential universality of its mechanisms (**Chapter 2.x**).

This shared biochemistry is largely arbitrary: These universal features are not constrained to be the way they are by physics or chemistry. For example, proteins are always made from L-amino acids, and never from their mirror-image D-stereoisomers



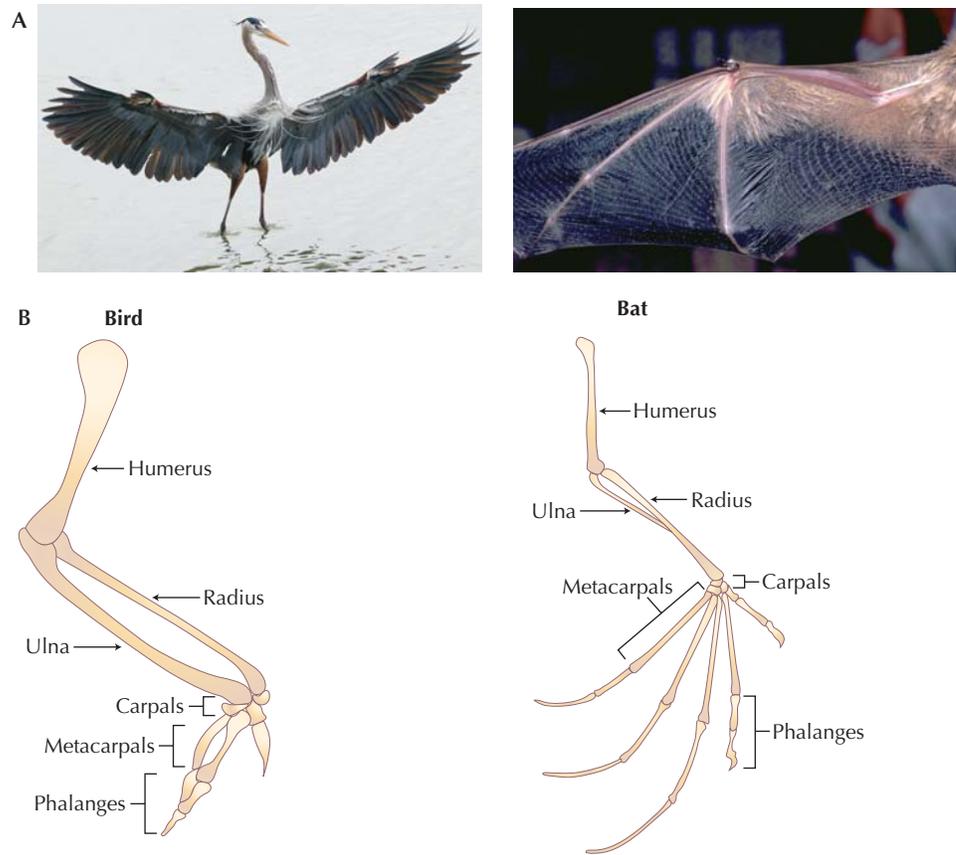
**FIGURE 3.2. Suppressor mutations** show that the universal genetic code is not constrained to be exactly as it is. **Nonsense mutations** generate stop codons that prematurely terminate translation of the protein. They can be suppressed by mutations in a transfer RNA that enables the tRNA to recognize the stop codon as an amino acid and so allow translation of the protein to be completed. In effect, these mutations have changed the genetic code. (A) Translation of the wild-type sequence is terminated by a UGA stop codon. (B) A mutation changes CAG (which coded for glutamine, Gln) to a stop codon, UAG, causing premature termination of translation. (C) A mutation in one of the transfer RNAs that codes for tyrosine (Tyr) changes the anticodon to AUC. This recognizes the UAG nonsense mutation, and so a full-length protein is produced, with tyrosine substituted for glutamine. (Recall that U in RNA corresponds to T in DNA.)

(**Chapter 2.x**)—even though a left- or a right-handed biochemistry would function equally well. This universal handedness is readily explained by descent from a single common ancestor. The genetic code is to a large extent a “frozen accident”: Any code that maps the 64 possible triplet codons onto the 20 amino acids would work and could be implemented just as easily by an appropriate set of transfer RNAs. This point is illustrated by occasional natural variants to the code (**Chapter 4.x**) and by laboratory mutations that alter the code (Fig. 3.2). (Later, we will discuss some regularities in the genetic code that indicate that it is not *entirely* random; **Chapter 4.x**.) As a final example, we saw in **Chapter 2.x** that RNA molecules carry out key catalytic functions—most notably, the joining of amino acids by peptide bonds to form a protein. These are explained as relics of an **RNA world**, in which RNA molecules instead of proteins were responsible for the chemical work of the cell, as well as for carrying hereditary information (**Chapter 4.x**).

### Hierarchical Classification

The naturally hierarchical classification of organisms into groups within groups, reflected in the Linnaean system of species, genera, and families, is immediately explained by “descent with modification”; the classification directly reflects shared ancestry. Moreover, the characteristics that are most useful in classification are not those that adapt species to their individual way of life, but rather those that retain their ancestral state throughout a group. This distinction between **analogy** and **homology** was appreciated before Darwin (Fig. 3.3). For example, the streamlined shape of fish and whales is an **analogous** feature: In other words, it is a consequence of their convergent ways of life. In contrast, the structure of the mammalian limb has remained the same, even though it is used for very different purposes in bats, humans, and porpoises. Such **homologous** structures are readily explained by common descent. Certain embryonic stages tend to be similar, even between species that have very different adult forms (Fig. 3.4). Darwin explained this pattern by pointing out that selection would diversify the adult form, but would act against potentially disruptive changes in the embryo. We will discuss this argument further in **Chapter 9**.

This pattern of groups within groups leads to a nested classification, with each group defined by sharing a unique set of characters. For example, vertebrates (the



**FIGURE 3.3.** (A) The wings of birds and bats are *analogous*, because they carry out the same function, but are not descended from a common ancestral structure having that function (*left*, great blue heron; *right*, male red bat) (B) The skeletal forelimbs of birds and bats are *homologous*, because they descend from the same structure in their common ancestor.

subphylum Vertebrata) have a backbone and limbs built to the same five-fingered plan. Within the Vertebrata are mammals (class Mammalia), who produce milk and are covered in hair. Ruminants (e.g., antelope, sheep, and cattle; a suborder of Mammalia) share cloven hooves and a specialized digestive system. This method of classifying nested groups of organisms continues down to the level of individual species, such as *Bos taurus* (the domesticated cow) (Fig. 3.5).

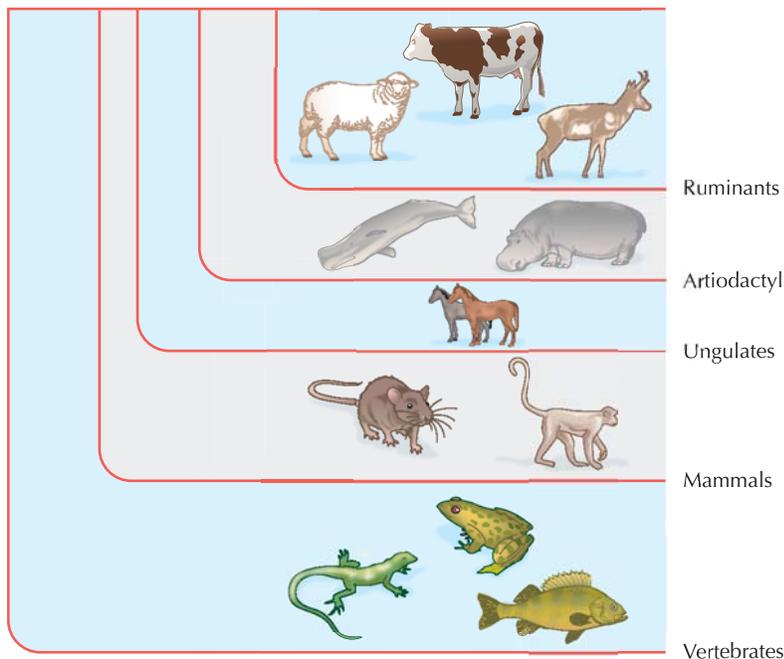
Notably, molecular characteristics support the same classification. For example, vertebrates share a particular arrangement of *Hox* genes, and classifications based on multiple DNA or protein sequences yield the same nested pattern. This nested classification of groups within groups, and its consistency across traits, is most easily explained as a reflection of the tree-like pattern of descent from a common ancestor. It is quite different from the pattern seen in designed artifacts. For example, although cars of the same brand share some superficial resemblance, different features are scattered across different makes wherever they are found useful.

As we explain in **Chapter 27 (online)**, the trees inferred from any one set of characters cannot be identified with certainty; rather, they are statistical estimates of the actual relationship and so will usually not be perfectly accurate. Nevertheless, the consistency across entirely unconnected traits—both molecular and morphological—is striking and is strong evidence for common descent (see **Chapter 9.x**).

The frequent difficulty in deciding whether two forms rank as species or mere



**FIGURE 3.4.** Similarity of embryos during early stages of development. Embryos of a grasshopper (insect; *A*), spider (chelicerate; *B*), and centipede (myriapod; *C*) are juxtaposed with their adult forms. Despite the differences between the adults of these three arthropods, the embryos are remarkably similar at this stage of development. (The embryos are stained for a gene product that highlights their conserved segmental nature.)



**FIGURE 3.5.** The vertebrates can be classified in a series of nested groups-within-groups, each group sharing a set of unique features. This pattern is explained by the underlying phylogeny that connects each species (see **Fig. 9.x**). The artiodactyls (even-toed ungulates) are a diverse group that includes the ruminants (shown here), but also highly modified groups such as the whales.

varieties was seen by Darwin as further support for “descent with modification.” Varieties are incipient species and a clear dividing line between them is not expected (see **Chapter 22.x**). In *On the Origin of Species*, Darwin wrote:

Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. This I feel sure, and I speak after experience, will be no slight relief.

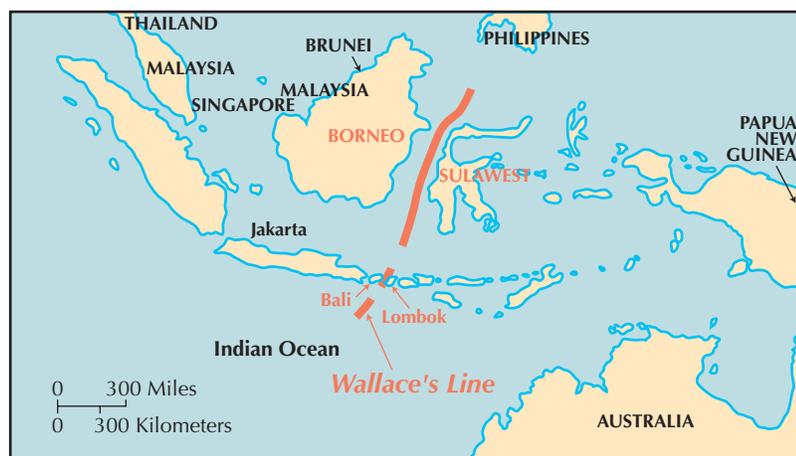
### *Geographic Distribution*

Darwin’s most compelling evidence for evolution came from the geographic distribution of myriad plants and animals that he saw during his travels on the *Beagle* (**Fig. 1.24**). Wherever he looked, Darwin found that organisms were related by their proximity to one another, even across diverse habitats. The marsupials in Australia and the toothless mammals in South America are but two of the many examples that led to Darwin to write:

. . . the naturalist in travelling, for instance, from north to south never fails to be struck by the manner in which successive groups of beings, specifically distinct, yet clearly related, replace each other. He hears from closely allied, yet distinct kinds of birds, notes nearly similar, and sees their nests similarly constructed, but not quite alike, with eggs coloured in nearly the same manner.

This pattern is especially striking on oceanic islands. For example, the mockingbirds that Darwin found in the Galapagos Islands differ between islands, but share an underlying resemblance with each other and, to a lesser extent, with the mainland birds from which they are derived. We now have many such examples of dramatic **adaptive radiations** on oceanic islands, including many species found on the Hawaiian Islands, and the cichlid fishes within the African Great Lakes (**Chapter 22.x**). Darwin explained the presence of the same species, or closely allied species, of alpine plants on different mountaintops across Europe and North America as a consequence of the retreat of glaciers, which stranded these organisms on isolated peaks. Without invoking evolution, such distributions cannot be explained except through an arbitrary number of separate creations.

Some of the most striking support for evolution comes from the correspondence between geographical distribution and geological history. Alfred Russel Wallace identified a sharp boundary between distinct fauna and flora that runs across the East Indies in an apparently arbitrary location (**Fig. 3.6**). We now know that this is an an-



**FIGURE 3.6.** Wallace’s Line (thick red line) separates two distinct present-day land faunas.

cient deep-water passage between two former land masses, which were connected when sea levels were about 100 m lower, during the Pleistocene (**Chapter 10.x**). A still more striking example is the distribution of species such as marsupials, lungfishes, and the southern beech (*Nothofagus*) across the southern continents. Although now widely separated, these were all part of the supercontinent of Gondwana, 120 Mya (see **Fig. 10.5**). Such patterns are immediately explained in terms of evolution, if species gradually disperse away from their point of origin.

### Evolutionary Processes Can Be Observed Directly

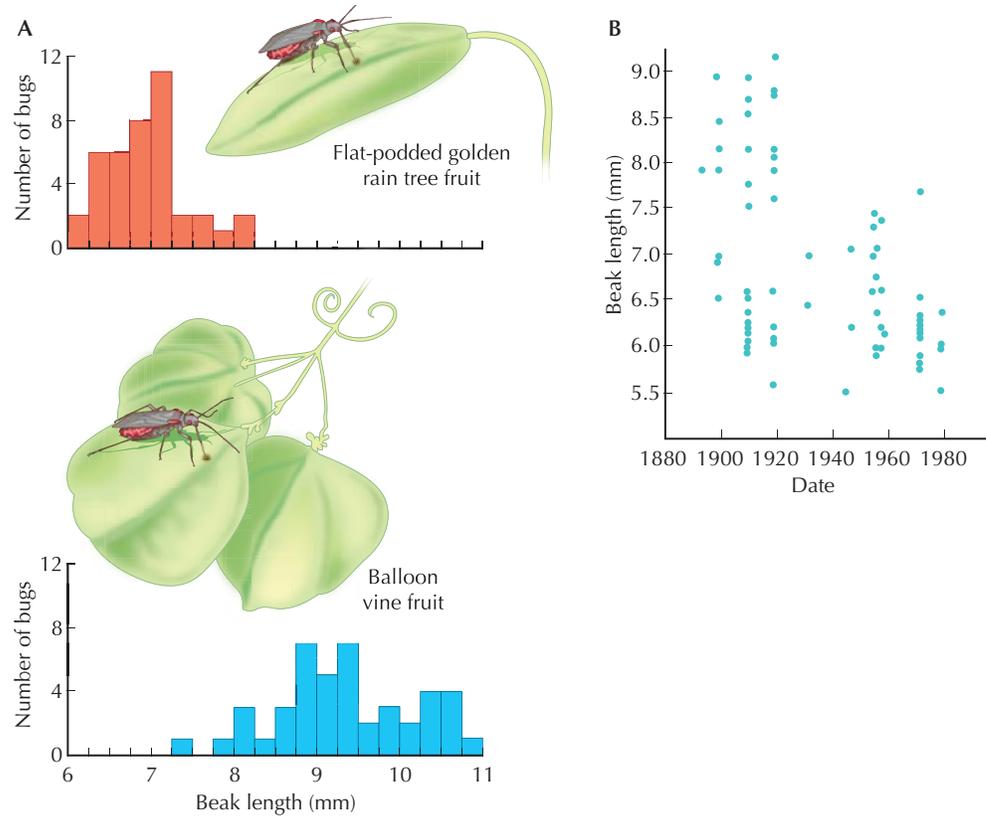
The astonishing success of artificial selection played a large part in shaping Darwin's ideas on evolution (**Chapter 1.x**). Agriculture relies on an extraordinary variety of domesticated animals and plants, which have been shaped simply through the continued selection of those individuals with desirable characteristics. Often, one species has yielded radically different varieties. The different breeds of dog differ much more in morphology and behavior than do typical mammalian species. Similarly, one plant species has been selected to produce apparently quite different crops (**Fig. 3.7**).

Rapid evolutionary change is also seen in nature. Good examples are the change in morphology of sparrows as they spread across North America since their introduction in 1852 or the response of soapberry bugs to the introduction of a new host plant in the 1920s (**Fig. 3.8**). On a quite different scale, when people infected by the human immunodeficiency virus (HIV) are treated with antiviral drugs, the HIV population evolves multiple amino acid substitutions that confer resistance. These evolutionary changes are consistently seen across different infections (**Fig. 3.9**).

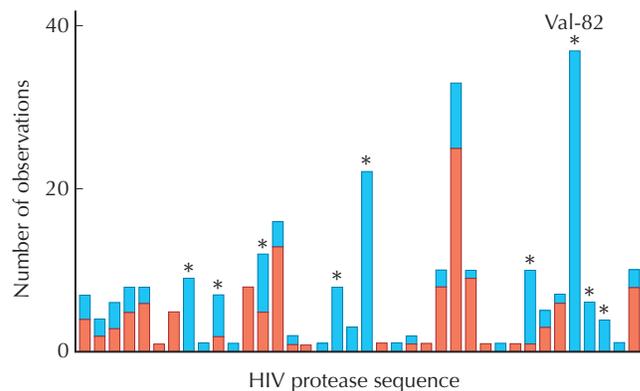
The origin of new species is usually too slow to be seen directly, but we do have several striking examples. There are cases where insects have been seen to shift to use a new host plant, thus producing populations that are on their way to becoming fully



**FIGURE 3.7.** Diverse varieties of *Brassica oleracea* include (A) cabbage; (B) broccoli; (C) cauliflower; (D) brussels sprouts; and (E) flowering kale.



**FIGURE 3.8.** Soapberry bugs in Florida originally fed on the native balloon vine (*A*, lower), using their sharp beaks to penetrate the fruit. In the 1920s, the flat-podded golden rain tree (*A*, upper) was introduced from Asia. This has thinner-skinned fruit and, correspondingly, soapberry bugs evolved shorter beaks after they switched to feed on this new host plant. (*B*) Each dot in the scatter plot shows the beak length of an individual bug taken from museum collections.



**FIGURE 3.9.** HIV evolves resistance to the antiviral drug ritonavir through multiple substitutions in the drug's target, HIV protease. The evolution of this enzyme was followed in 42 patients. The *red bars* show the variants observed in the base population. The *blue bars* show variants that emerged after drug treatment, most of them on multiple occasions. The nine variants marked by \* contributed to resistance, but significant resistance required several substitutions. For example, a change to valine at position 82 appeared first in most patients, but does not give resistance by itself.



**FIGURE 3.10.** *Primula kewensis* (left) was created artificially by crossing *Primula verticillata* (middle) and *Primula floribunda* (right). It has twice as many chromosomes as its parent species and so can interbreed with neither.

separate species; we discuss such examples in **Chapter 22.x**. Most striking is the rapid origin of new species following hybridization. An  $F_1$  individual occasionally doubles up its genome to produce a new **polyploid** species that cannot interbreed with either parental species. A substantial proportion of plant species have formed in this way; in many cases, their hybrid origin has been confirmed by artificially crossing the presumed parents, and generating the hybrid species anew (**Chapter 22.x**; Fig. 3.10). Indeed, this process is used routinely to generate new horticultural varieties, especially in orchids (Fig. 3.11).

As we will see later in this book, we now have abundant and detailed observations of just how the various evolutionary processes work both in the laboratory and in nature.

### The Fossil Record Provides Several Lines of Evidence for Evolution

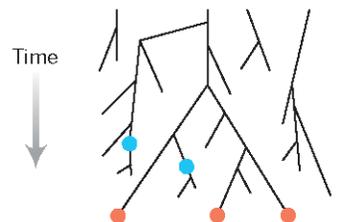
Although our knowledge of the fossil record is much fuller than it was in Darwin's time, there are still gaps—as is to be expected. The chance that any individual will be preserved and discovered is extremely small, and species that are soft-bodied or that lived in restricted areas may be lost entirely. In addition, the chance that a particular fossil will be found is remote—the world is a very large place. Even those fossils that are found are unlikely to be on the direct line of descent to living species, which makes reconstruction of phylogenetic relationships difficult (Fig. 3.12). Few species, and few individuals within species, are actually ancestors of today's organisms (**Chapter 15.x**). We now have many examples where more or less continuous evolutionary change can be traced (e.g., Fig. 3.13), but these are exceptional. Fossils do provide strong evidence for evolution, but for the most part, this is not through direct observation of evolutionary change.

As we saw in **Chapter 1**, arguments in the 19th century that the Earth is only a few million years old seemed among the strongest objections to evolution. The discovery of radioactivity resolved these arguments by permitting the age of fossils and geological samples to be measured using radiometric techniques. We now know, through multiple lines of evidence, that our planet formed 4.65 billion years ago and that conditions suitable for life were present relatively soon afterward (**Box 4.1**). Both morphological and molecular change (seen directly and in the fossil record, and inferred from comparisons between living species) can be rapid, and so there has been ample time for evolution to occur.

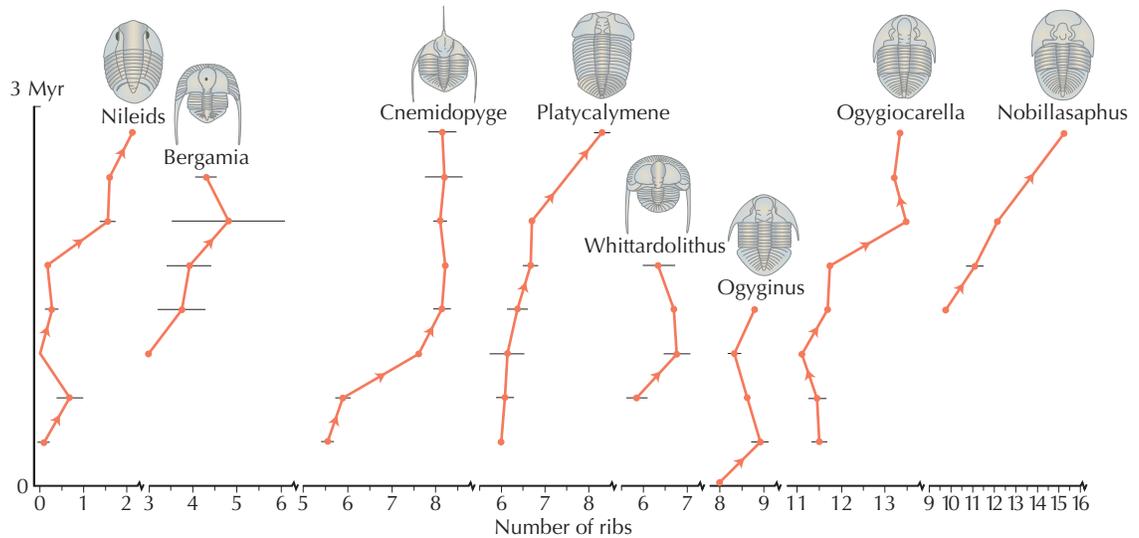
We would predict that groups that have diverged more recently should appear later in the fossil record—just as is observed (recall Fig. 3.5). Thus, the first chordates and fishes appear approximately 525 Mya, the first amphibians approximately 247



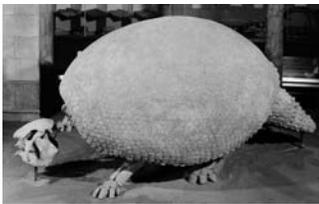
**FIGURE 3.11.** Orchids made by hybridization and polyploidy. (Top) Hybrid lady slipper orchids. (Bottom) Polyploid orchid *Ionocidium* Popcorn.



**FIGURE 3.12.** Fossils (blue) will rarely be on the direct line of descent to present-day species (red).



**FIGURE 3.13.** These eight lineages of Ordovician trilobites show gradual, rather than punctuated, change. The plot shows the mean number of ribs, with standard error.



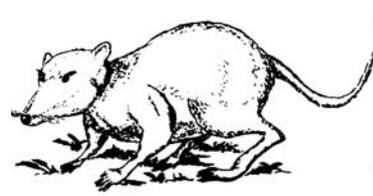
**FIGURE 3.14.** Darwin collected fossils of the extinct *Glyptodon* (top), a giant edentate (toothless mammal), and realized that it is related to armadillos (bottom), which live in the same region of South America.

Mya, and the first mammals approximately 225 Mya. It is important to realize that this prediction is made from comparisons between present-day species, which tell us the phylogenetic relationships and hence the order of appearance that we expect to see in the fossil record. J.B.S. Haldane made this point in a characteristically pithy way. When asked what observation might refute evolution, he replied “a pre-Cambrian rabbit.”

Another pattern that supports evolution is what Darwin called the “Law of Succession,” that is, fossils in any one region are related to that region’s present-day inhabitants (e.g., Fig. 3.14). The positions of the continents and their climates change over time, and so this pattern holds only for relatively recent fossils. Over longer periods of time, we must take account of geological changes. For example, fossils of marsupials have been found in Antarctica, just as predicted from their distribution across the southern continents (Fig. 3.15; also Fig. 10.5).

### Natural Selection Causes the Appearance of Design

The cumulative selection of slight variations has an astonishing power to create complex adaptations. The HIV virus evolves resistance through multiple changes in the proteins that are targets for drugs (Fig. 3.8), and bacteria acquire antibiotic resistance from plasmids that carry multiple resistance genes (Chapter 7.x). Artificial selection



**FIGURE 3.15.** Marsupial fossils in Antarctica. This upper Eocene fossil example of a lower jaw of a polydolopid was found on Seymour Island of the Antarctic Peninsula. An artist’s reconstruction of this 20-cm-long marsupial is shown at right.

among molecules *in vitro* is used to produce efficient functions that we could not design from first principles (recall the example of fluorescent proteins in **Fig. A&S.4**). Most obviously, the extraordinary range of domesticated plants and animals has been shaped by selection over the past few thousand years (e.g., **Fig. 3.9**). In computing, evolving programs often produce novel solutions to difficult problems. We will examine these and other examples of selection later in the book (especially in **Chapters 17** and **24**).

Of course, a sufficiently intelligent designer would find all these solutions directly. Such an ideal mechanism for adaptation would avoid the **genetic load** that accompanies natural selection. If one type of gene is to replace another, very many individuals must die or fail to reproduce over the many generations that such a replacement requires. We discuss the limits to natural selection further in **Chapter 19**. Here, we simply note that natural selection is an imperfect mechanism. Thus, evidence that natural selection is responsible for the appearance of design in the living world comes from characteristic imperfections in adaptation.

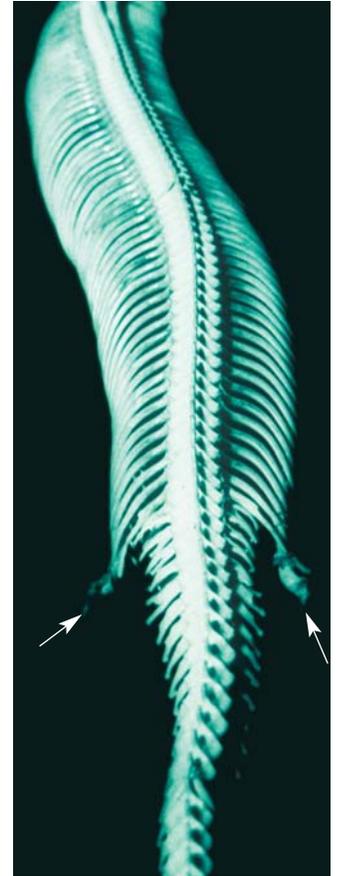
Vestigial structures, such as the rudimentary pelvis of snakes and whales (**Fig. 3.16**; also see **Fig. 3.18**, below), teeth that remain hidden under the gum in the upper jaws of calves, or the remnant eyes of blind cave fish, are extremely puzzling if organisms are rationally designed or are constructed according to some universal law. However, they are to be expected if the structures are relics that functioned in the ancestors. At the molecular level, extra copies of genes are generated by random mutation; these almost always accumulate deleterious mutations and lose their function. These **pseudogenes** are functionless by-products of a process that occasionally leads to the evolution of new functional genes (**Chapter 24.x**).

Natural selection must act on existing variation, and so adaptations are based on co-option of structures that evolved for other purposes. For example, vertebrates have employed the basic pentadactyl (five-fingered) limb for a variety of purposes (e.g., **Fig. 3.3**). In *On the Origin of Species*, Darwin discussed this example along with several others:

How inexplicable are these facts on the ordinary view of creation! Why should the brain be enclosed in a box composed of such numerous and such extraordinarily shaped pieces of bone? . . . Why should similar bones have been created in the formation of the wing and leg of a bat, used as they are for such totally different purposes? Why should one crustacean, which has an extremely complex mouth formed of many parts, consequently always have fewer legs; or conversely, those with many legs have simpler mouths? Why should the sepals, petals, stamens, and pistils in any individual flower, though fitted for such widely different purposes, be all constructed on the same pattern?

Molecular examples include the use of a metabolic enzyme, lactose dehydrogenase, as the transparent material in the lens of the vertebrate eye (see **Chapter 24.x**); and the use of the same basic set of *Hox* genes to direct early development in all animals (see **Chapter 9.x**). In Jacques Monod’s memorable phrase, these are examples of “evolution by tinkering.”

Natural selection acts through competition between individuals. As we shall see in **Chapter 21**, this conflict drives much of evolution. Some of the most striking examples involve **sexual selection**, in which males compete with each other to fertilize females. For example, many male insects produce a “mating plug” to prevent their mate being fertilized by other males (**Chapter 20.x**). Most known examples of rapid molecular evolution involve sexual selection, the spread of selfish genetic elements, or the struggle between host and parasite. Evolutionary conflicts such as these are to be expected from natural selection, but not if adaptations are designed in some optimal way.



**FIGURE 3.16.** Python skeleton showing vestigial pelvic limbs (arrows).

## OBJECTIONS TO EVOLUTION

### Objections to the Fact of Evolution

In this section and the next, we list some of the objections that have been made to evolution by natural selection and give a brief summary of the arguments that refute them. We do not include those that are directly and immediately refuted by science—for example, claims that the Earth is only a few thousand years old—because these imply rejection of science as a whole. Also, we do not consider here objections based on the supposedly pernicious social effects of belief in human evolution; we discuss such objections at the end of this chapter. Here, we refute arguments against evolution; in the next section, we refute arguments against natural selection as its chief mechanism.

*Argument: Evolution cannot be observed and so cannot be proved.*

*Rebuttal:* Just as in other areas of science, evolutionary biology does not for the most part rely on direct observation. In physics, we do not observe the gravitational attraction between Earth and Moon directly (how could we?), but instead bring together diverse lines of evidence—both in the laboratory and from astronomy—to build a simple and satisfying explanation. Similarly, in geology, we can observe the slow action of processes such as erosion and continental drift directly, but must then extrapolate to produce a consistent account of large-scale change. In just the same way, evolutionary biologists use direct observation to thoroughly understand the underlying processes, but rely on many lines of indirect evidence to explain evolution on a larger scale.

No hypothesis can be “proved” with absolute certainty. Indeed, a productive theory suggests new investigations that lead to its revision and modification. For example, Newton’s laws of gravitation make extraordinarily accurate predictions about the motions of celestial bodies, but slight deviations from them support Einstein’s general theory of relativity—a still more accurate theory, and one that brings a more profound understanding of space and time. Mendel’s laws of heredity were refined to include phenomena such as linkage after their rediscovery in 1900; half a century later, the discovery of their physical basis in DNA led to further refinements in our understanding of the gene. Evolutionary biology has developed in just the same way as the rest of science—changing and becoming richer as an ever-wider range of phenomena become understood.

*Argument: Evolutionary theory is not testable.*

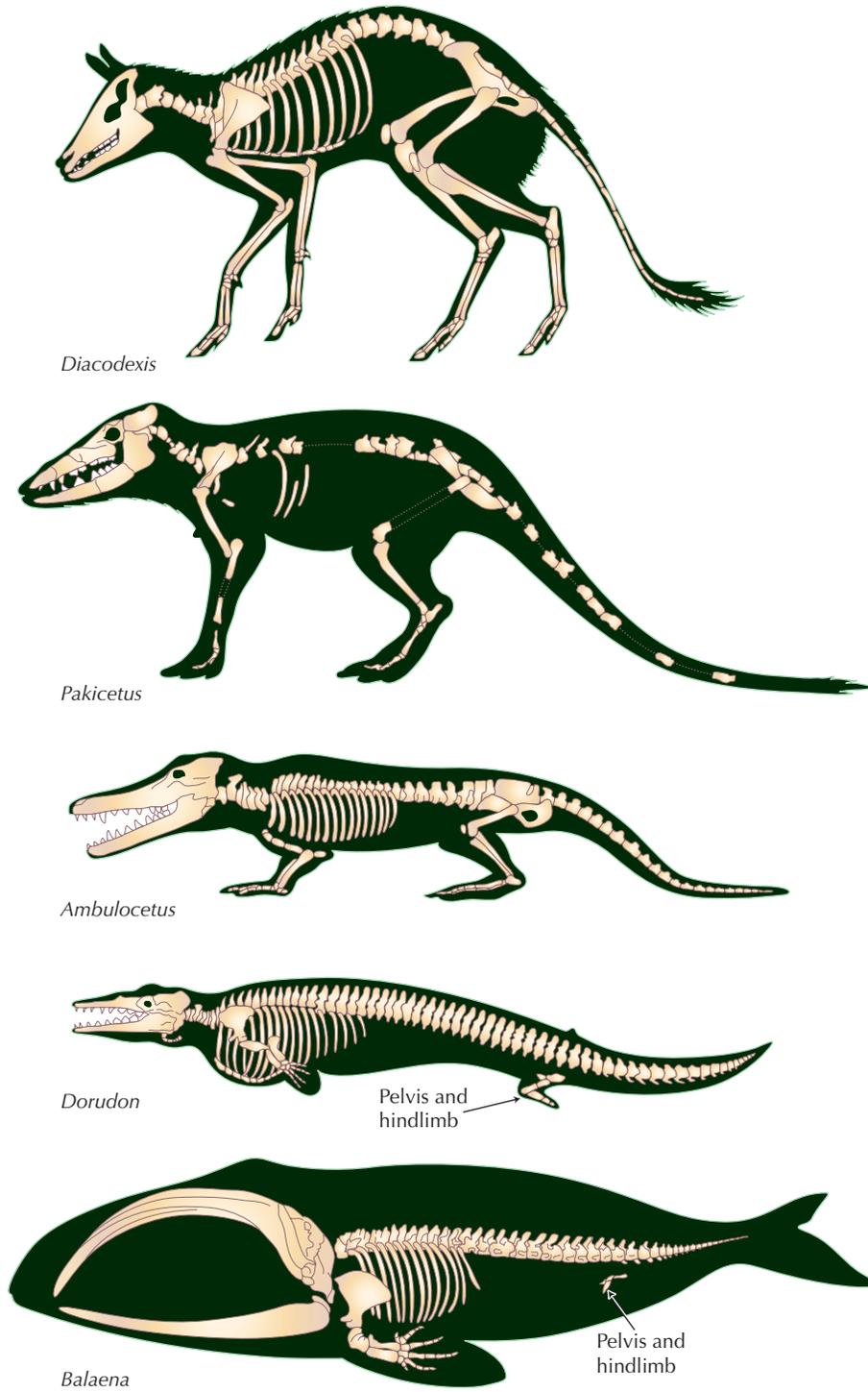
*Rebuttal:* A scientific theory is successful if many predictions are made based on the theory, those predictions are tested, and the theory survives those tests. These tests need not involve laboratory experiments. In evolutionary biology they more often involve predictions about patterns across living species, in the fossil record, or in the structure of the genome. We have already noted several key tests of evolution: the consistency of phylogenies inferred from different characters, the order of appearance of taxa in the fossil record, and patterns of geographic distribution. We will see much more evidence of this sort in the rest of the book.

*Argument: There are no transitional forms.*

*Rebuttal:* Continuous transitions can be seen only in the most favorable cases (e.g., Fig. 3.13). However, there are many striking examples of intermediate forms, which carry ancestral combinations of characters that had been predicted to exist from reconstructed phylogenies. Among the most striking examples are feathered dinosaurs, discovered in China in 1996 (Fig. 3.17), and the series of intermediates between whales and hippos that show how mammals adapted to life in the sea (Fig. 3.18). Fossils show



**FIGURE 3.17.** Feathered dinosaurs. These fossilized vertebrae of a tyrannosauroid from the Early Cretaceous show filamentous structures (*upper* portion of rock) thought to represent protofeathers.



**FIGURE 3.18.** A series of fossils from the Eocene (~50 Mya) hippo-like artiodactyl (*Diacodexis*, top) to a skeleton of the modern whale (e.g., *Balaena*, bottom) shows how mammals adapted to life in the sea. Among the most important changes, the pelvis and hindlimbs were reduced, the tail was lengthened for swimming, and the jaws were modified for feeding on plankton.

clearly that different characters evolve independently, rather than appearing together all at once or accumulating as a linear, progressive sequence. For example, we will see in **Chapter 25** that hominid fossils show this pattern of mosaic evolution—increased brain size, sexual dimorphism, changes in dentition, and adaptations for walking upright all change more or less independently.

### Objections to Natural Selection as the Cause of Adaptation

Until Darwin discovered the process of natural selection, the existence of complex and functional structures was taken to imply creation by an intelligent designer. As we saw in **Chapter 1** this long-standing philosophical **argument from design** was especially influential in the **natural theology** of the early 19th century (**Chapter 1.x**). Natural selection provides an alternative explanation for the appearance of design, which relies solely on natural causes. In this section, we refute some of the objections to the adequacy of this process.



**FIGURE 3.19.** R.A. Fisher. “Natural selection is a mechanism for generating an exceedingly high degree of improbability.”

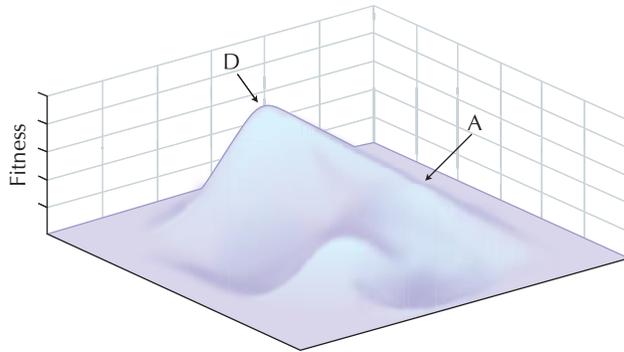
*Argument: Chance cannot generate complexity.*

*Rebuttal:* The influential 19th century astronomer John Herschel objected to the random element in natural selection, calling it the “law of the higgledy-piggledy.” Subsequently, it has often been objected that random mutations cannot lead to ordered complexity. The structures assembled by natural selection are indeed highly improbable: The number of possible sequences of 100 nucleotides is  $4^{100}$ , or more than  $10^{60}$ . However, as explained in detail in **Chapters 17** and **24**, the cumulative effect of selection is precisely to build highly improbable structures (Fig. 3.19). Although the reproduction of each individual and the generation of new mutations are each highly random, the outcome of large numbers of such events can be essentially deterministic—just as the random movements of individual molecules average out to give the precise laws of thermodynamics.

This objection does have some force when applied to the origin of the first reproducing system—before natural selection had started to act. We know very little about how the very first living organisms originated, but as we will see in **Chapter 4**, there are several plausible hypotheses. In particular, the first replicating molecule need not have required a *precise* sequence of 100 bases: A large number of different and perhaps shorter sequences might have sufficed. Indeed, the very first **replicators** may well have been much simpler than present-day nucleic acids.

*Argument: The first step toward complex adaptation could not have been favored.*

*Rebuttal:* Darwin felt this was one of the strongest objections to evolution by natural selection and devoted a section of *On the Origin of Species* to refuting it; as an example, he used the vertebrate eye. More recently, the term **irreducibly complex** has been used to describe systems that cannot function if any one of their components is missing: The bacterial flagellum has been proposed as one example. We discuss such arguments in detail in **Chapter 24** but can make two general points here. First, the initial steps need only give some slight selective advantage. As the eminent and extremely nearsighted evolutionist John Maynard Smith put it, his imperfect vision was far better than complete blindness. Second, the initial stages may have evolved for a quite different purpose than that of the final complex structure (see **Chapter 24.x**). Finally, although the present function may be entirely destroyed by changes to most of its components, there only needs to be one path of increasing fitness that connects the ancestor with the present structure (Fig. 3.20). This point is discussed in more detail in **Chapters 22.x** and **24.x**.



**FIGURE 3.20.** A complex structure can evolve even if every change to it reduces fitness: All that is required is that there was at least one path from ancestor (*A*) to descendant (*D*), along which fitness was high and increasing. The diagram shows an **adaptive landscape** (see **Chapter 17.x**), which plots average fitness against the state of the population (morphology, allele frequencies, etc.). In reality, the landscape fluctuates, giving further pathways for evolutionary change. Moreover, evolution can proceed in many directions, not just the two shown here.

*Argument: Natural selection creates nothing new.*

*Rebuttal:* A single round of selection does indeed just pick from existing variation. However, successive rounds of selection increase the frequency of each favorable variant, so that very soon new combinations are seen that were vanishingly rare in the original population (**Fig. 1.x**). As we explain in **Chapter 17.x**, this criticism is no more valid than saying that an author merely rearranges existing letters, but creates nothing new.

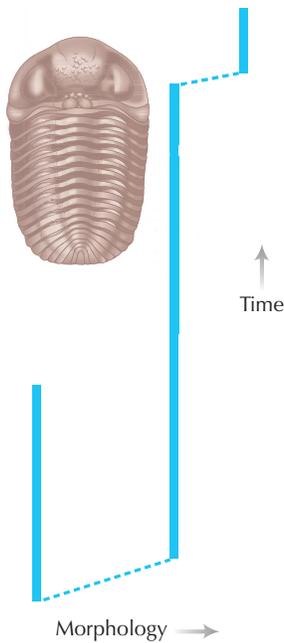
*Argument: Natural selection violates the second law of thermodynamics.*

*Rebuttal:* In a *closed* system, disorder must necessarily increase. More precisely, the **entropy** of any closed system—a quantitative measure of its disorder—will almost certainly increase. However, living systems are *open*: They take in nutrients and free energy (ultimately from sunlight or from some source of chemical energy) and export waste products and heat. Overall, entropy increases in open systems. Organisms grow and reproduce in an orderly way, but this is more than offset by the heat and chemical waste that they produce.

*Argument: Human intellect could not have evolved by natural selection.*

*Rebuttal:* We have already considered arguments that selection can create complex adaptations such as human language, which have obvious selective value. (In **Chapter 25**, we consider the detailed steps that could have led to complex language.) A distinct objection is that many human abilities—musical and mathematical talent, religious feelings, and so on—could have no survival value and so could not have been selected. (Wallace, who discovered natural selection independently of Darwin [**Chapter 1.x**], held to this argument and so never accepted a fully natural explanation of human nature.) There are two responses to this argument. First, we know that apparently quite useless traits can increase fitness—for example, by influencing social status or mate choice (**Chapter 20.x**). Second, traits that have no direct effect on fitness readily evolve as side effects of direct selection on other traits (**Chapter 17.x**). Thus, mathematical abilities might be a side effect of a general reasoning ability and intellectual curiosity.

Abstract reasoning, facilitated by symbolic language, is clearly of enormous value to individual humans, both directly (allowing better hunting, toolmaking, and much more) and indirectly (by enhancing social skills and attractiveness to mates). As was



**FIGURE 3.21.** An example of punctuated equilibrium. Shown schematically is the evolution of the Devonian trilobite *Phacops rana* (one of the organisms used to develop this theory). Time is on the vertical axis (*solid lines*) and morphology is on the horizontal axis (*dotted lines*). Time ranges of three species are illustrated (the three *vertical lines*). Punctuated equilibrium is evidenced by the abrupt changes in morphology that occur during the relatively short periods of time indicated by the *dotted lines*.

just noted and is covered in more detail in **Chapter 17**, a curiosity about the world and an interest in explaining subtle patterns could lead to intellectual abilities that have no direct effect on fitness.

*Argument:* Punctuated equilibrium implies that natural selection within species is ineffective.

*Rebuttal:* In 1972, the paleontologists Niles Eldredge and Stephen Jay Gould proposed a theory known as **punctuated equilibrium**. They emphasized that species often persist unchanged for millions of years, but then shift abruptly to a new form (Fig. 3.21). If these sudden shifts correspond to formation of a new species, then extinction and speciation—in effect, selection among species—would be more effective than selection within species in shaping **macroevolution**.

Eldredge and Gould accepted that natural selection within species shapes adaptation. They were instead concerned with large-scale macroevolutionary trends—increases in body size, for example. However, their theory has been misinterpreted by others as a criticism of evolution by natural selection. In fact, the pattern of punctuated equilibrium is entirely consistent with change through natural selection. It simply implies that selection maintains the same phenotype for long periods, but that when change does occur, it can be rapid. Although “punctuations” are fast on an evolutionary timescale, they span thousands of years and can easily be accounted for by natural selection (see **Fig. 17.30**). Conversely, as we show in **Chapter 21**, selection among species is very slow, simply because species originate and go extinct so much less often than individuals are born or die. Thus, while species selection may lead to macroevolutionary trends, it cannot build complex adaptations.

*Argument:* The human genome is too simple to account for such a complex organism.

*Rebuttal:* When the draft sequence of the human genome was published in 2001, many scientists were surprised that only about 30,000 genes were identified—only twice the number in a fly and fewer than in maize (see **Chapter 8.x**). Previously, it had been estimated that our genome contains 80,000 or more genes, although there was no reliable data on which to base such an estimate. The unexpectedly low number of genes caused surprise that such a complex organism could be encoded by so little genetic information. It is indeed remarkable that less than 20 Mb of information can instruct human development and, especially, can determine the structure of our brain with so many intricate connections between its 100 billion neurons. However, this puzzle was apparent even before sequence data gave such a surprisingly low estimate of gene number. As we discuss in **Chapters 21** and **24**, gene number is a poor guide to complexity; for one thing, alternative splicing of RNA transcripts gives many more proteins than genes (**Box 13.1**). In any case, many biological differences involve changes in gene regulation, determined by sequences that do not code for protein.

As we will see in **Chapter 14**, there is no simple relationship between genotypes and phenotypes; each gene affects many traits, and each trait is influenced by many genes. The DNA sequence does not *code* for the phenotype. Rather, a large number of genes interact with each other and with the cellular machinery to allow the organism to develop. The arrangement of neurons in our brains is not specified exactly, but rather develops through interactions among neurons and with our environment (**Chapter 24.x**). The DNA sequence itself is meaningless—it must be expressed in the context of the cell. Most of the information required to build an organism is contained in the cellular machinery, rather than in the genome itself.

A clearer comparison is to ask whether the *differences* between (say) human and chimpanzee can be accounted for by the differences in their genomes. There are approximately 40,000 amino acid differences, perhaps one-third established by selec-

tion, plus a similar number of differences in noncoding regions that are maintained by selection and so are likely to be functional (see **Chapter 19.14**). As we will see later, this many differences can readily be established by selection over 6 million years of divergence (**Chapter 19.x**). It does not seem implausible that our differences from our closest relatives are due to these many thousands of differences.

## SCIENCE AND SOCIETY

### The Fact of Evolution Is Explained by Evolutionary Theory

Popular debate over evolution and its mechanism is marked by confusion over the scientific use of the terms “fact” and “theory.” Sometimes, it is said that evolution is “only a theory,” suggesting that it is a mere speculation, with little support. In science, however, a **theory** means a web of interconnected hypotheses, which makes predictions that are consistent with what we see and makes new predictions that stimulate further research. A theory that has survived many different tests may be so well supported that we take it as a *fact*. This applies to the theories of gravitation, of plate tectonics, of quantum mechanics, and of evolution—all are treated as thoroughly established facts.

The fact of evolution is explained by a sophisticated body of theory that shows how it has come about. Much is firmly established. We understand how all the evolutionary processes work, and we have very many examples where we understand how they have generated adaptation and divergence. We also know a great deal about the history of life, through paleontology and phylogenetics. As we emphasize throughout this book, many questions remain open. Just what fraction of variation is selected, and how? What is the genetic basis of complex phenotypes? What role does the exchange of genes among different evolutionary lineages play in the diversification of bacteria and archaea? Why do most eukaryotes reproduce sexually? How do originally free-living organisms come together to cooperate in the eukaryotic cell, in multicellular organisms, and in social colonies? Evolutionary biologists are making rapid progress in answering such questions, but no doubt new puzzles will arise. The strength of evolutionary theory and the reason why it was so rapidly accepted is that it explains a wide range of phenomena in terms of a few simple principles. It continues to be a fertile source of ideas that can be tested in nature or in the laboratory.

Of course, everything we see could be consistent with special creation—species might be created with features *as if* they had evolved, and fossils might have been placed into geological strata in the same order *as if* they had evolved. However, such a perverse alternative explains nothing. Each species would be just the way it is, and we would have no explanation for any of the patterns described above. Special creation only explains the facts of biology by making arbitrary assumptions that can fit any observations. The hypothesis of special creation cannot be tested and so is not considered to be scientific.

Many accept evolution, and many admit that natural selection accounts for evolution within species or perhaps larger taxonomic groupings. However, they suppose that occasional interventions by a supernatural being (often referred to as an “intelligent designer”) have created some particularly complex adaptations. Again, if such interventions are arbitrary, then this hypothesis cannot be tested—anything might happen. On the other hand, if the designer is supposed to have certain properties (always giving optimal designs or designs favorable to humans, say) then the hypothesis *can* be refuted. As we saw in the previous section, adaptations in the natural world show just the kinds of imperfections that we would expect from natural selection, but not from an omnipotent designer. In any case, invoking a “God of the Gaps” is unsatisfactory from a theological point of view, because as science advances, it explains more, which causes the gaps to become more and more restricted in scope.

## Understanding Nature and Humanity

Objections to evolution by natural selection have come from those who see a clash with their religious beliefs or, more broadly, from those who object to a materialist worldview. Objections also come from those who worry that evolution could be used to justify moral positions that they object to or that belief in evolution might undermine morality. (As one woman said at hearings on the teaching of evolution in the Louisiana Senate in 1981, “I think that if you teach children that they are evolved from apes, then they will start acting like apes.”)

Plainly, evolution does contradict *literal* readings of the Bible and other sacred books. However, a literal interpretation contradicts science as a whole—not just evolution—and in any case, Genesis includes two different accounts of creation. Most major religions see no inconsistency between their beliefs and the scientific account of evolution. For example, the Catholic view now accepts evolution by natural selection, including the physical evolution of our own species. A common position is that God works through natural law, including natural selection and other evolutionary processes. At an individual level, many evolutionary biologists have no difficulty in reconciling their various religions with their scientific beliefs. Many hold the view eloquently expounded by Gould that science and religion are separate domains—one concerned with explaining the natural world, the other with interpreting the meaning of human life.

The ideas of evolution and natural selection have sometimes been used to justify bad policies. Racial segregation has been justified by supposed innate differences; **positive eugenics** (e.g., compulsory sterilization of the mentally ill) has been justified as aiding natural selection; and **Social Darwinism** extolled the “survival of the fittest” in economic and social policy. However, the scientific justification for such policies is now seen as baseless. Indeed, our knowledge of evolution has quite properly supported many policies that most would agree with. Hermann Muller campaigned to ban atmospheric tests of nuclear weapons on the grounds that radiation-induced mutations place a severe load on future generations; the close genetic similarity between human populations and the absence of distinct “races” supports equal treatment of all humans (**Chapters 25.x** and **26.x**); and the importance of cooperation in evolution (**Chapter 21**) has been emphasized as a contrast to the naive view that emphasizes conflict (in Tennyson’s words, “nature red in tooth and claw”).

More fundamentally, neither evolution nor its mechanism in themselves justify any particular moral position. Philosophers term this the **naturalistic fallacy**, an argument that claims that *what is* justifies *what should be*. The same point applies, of course, to religious beliefs about how the world is—beliefs about how the world began or the existence of God do not in themselves tell us how we should behave. Nevertheless, both scientific and religious beliefs do change our perspective on our place in the world and so may indirectly influence the values that we choose. For example, an awareness of our continuity with the living world may make us value the existence of other species, rather than seeing them purely as useful to ourselves. Similarly, an awareness of the importance of variation for evolution may make us set more value on diversity, both of different species and within our own species. We share with Darwin the sentiment with which he closed his private *Sketch* of his theory, written in 1842:

There is a simple grandeur in the view of life with its powers of growth, assimilation and reproduction, being originally breathed into matter under one or a few forms, and that whilst our planet has gone circling on according to fixed laws, and land and water, in a cycle of change, have gone on replacing each other, that from so simple an origin, through the process of gradual selection of infinitesimal changes, endless forms most beautiful and most wonderful have been evolved.

## SUMMARY

Evolution is accepted among biologists as explaining the diversification of life, and natural selection is accepted as the sole cause of adaptation. Yet, many outside biology still do not accept this scientific consensus.

Evidence for evolution comes from the nested classification of group within group, consistent across varied molecular and morphological traits, from direct observation in the laboratory or on the farm, and from the fossil record. Evidence for natural selection comes from analogy with artificial selection, from the characteristic imperfections of natural adaptations (e.g., vestigial organs), and from the recruitment of ancestral structures for new purposes. We briefly summarize arguments against various misunderstandings and objections here and discuss

these further later in the book (especially in **Chapters 17 and 24**).

The fact of evolution is explained by evolutionary theory—which is as well established as other scientific theories, such as quantum mechanics, plate tectonics, or molecular genetics. This theory is consistent with the major theologies and with the varied religious beliefs held by evolutionary biologists. Although it does not justify any particular morality (and cannot be held responsible for any lack of morality), the theory of evolution does give us a radically new perspective on the place of humanity in nature. As Darwin wrote at the end of *On the Origin of Species*, “There is grandeur in this view of life... .”

## FURTHER READING

Eldredge N. 2005. *Darwin: Discovering the tree of life*. W.W. Norton, New York.

Written as an accompaniment to the 2005–2006 Darwin exhibition at the American Museum of Natural History ([www.amnh.org](http://www.amnh.org)), it combines an account of the development of Darwin’s ideas with their present place in biology and in society.

Futuyma D.J. 1995. *Science on trial: The case for evolution*. Sinauer Associates, Sunderland, Massachusetts.

A counter to creationism, but written before arguments for “intelligent design” emerged. For a more recent concise summary of the arguments, see Futuyma D.J. 2005. *Evolution*. Sinauer Associates, Sunderland, Massachusetts.

Pennock R. 1999. *The tower of Babel: Evidence against the new creationism*. MIT Press, Cambridge, Massachusetts; Young M. and Edis T. (eds.). 2004. *Why intelligent design fails*. Rutgers University Press, Piscataway, New Jersey.

Two out of several recent books refuting arguments for “intelligent design.”

Pope John Paul II. 1996. *Message to the Pontifical Academy of Sciences*. Reprinted in *Q. Rev. Biol.* **72**: 381–406, together with four com-

mentaries, which discuss the relation between science and religion more generally.

## Web Resources

[www.NationalAcademies.org/evolution/](http://www.NationalAcademies.org/evolution/)

Resources and statements from the National Academy of Sciences.

[www.amnh.org/exhibitions/darwin/](http://www.amnh.org/exhibitions/darwin/)

A guide to the exhibition celebrating the bicentenary of Darwin’s birth (see Eldredge, 2005).

[www.pbs.org/wgbh/evolution/](http://www.pbs.org/wgbh/evolution/)

A wide range of material accompanying the PBS television series, *Evolution*.

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

A newsgroup devoted to the discussion and debate of biological and physical origins.

[www.pamd.uscourts.gov/kitzmiller/kitzmiller\\_342.pdf](http://www.pamd.uscourts.gov/kitzmiller/kitzmiller_342.pdf)

The decision in a 2005 case against the Dover district school board in Pennsylvania; summarizes the nature of science and the scientific arguments against “intelligent design.”