evolution

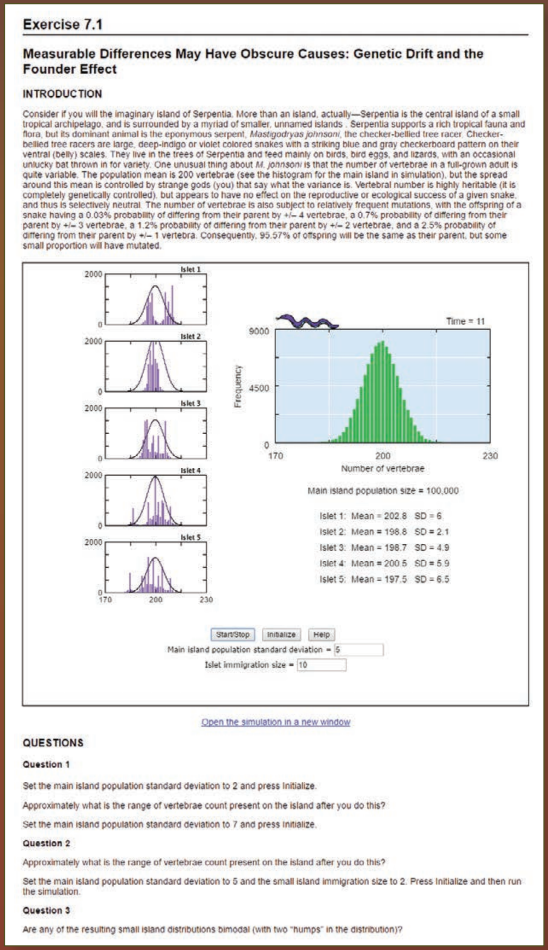
FOURTH EDITION

DOUGLAS J. FUTUYMA
MARK KIRKPATRICK

evolution FOURTH EDITION

Companion Website

The **Evolution** Companion Website provides you with a range of valuable study and review tools to help you master the material presented in the textbook. Available free of charge, the site is designed to help you understand the concepts and learn the terminology introduced in each chapter, analyze real-world research, and work with simulations of evolutionary systems.


Exercise 7.1

Measurable Differences May Have Obscure Causes: Genetic Drift and the Founder Effect

INTRODUCTION

Consider if you will the imaginary island of Serpentia. More than an island, actually—Serpentia is the central island of a small tropical archipelago, and is surrounded by a myriad of smaller, unnamed islands . Serpentia supports a rich tropical fauna and flora, but its dominant animal is the eponymous serpent, *Mastigodryas johnsoni*, the checker-bellied tree racer. Checker-bellied tree racers are large, deep-indigo or violet colored snakes with a striking blue and gray checkerboard pattern on their ventral (belly) scales. They live in the trees of Serpentia and feed mainly on birds, bird eggs, and lizards, with an occasional unlucky bat thrown in for variety. One unusual thing about *M. johnsoni* is that the number of vertebrae in a full-grown adult is quite variable. The population mean is 200 vertebrae (see the histogram for the main island in simulation), but the spread around this mean is controlled by strange gods (you) that say what the variance is. Vertebral number is highly heritable (it is completely genetically controlled), but appears to have no effect on the reproductive or ecological success of a given snake, and thus is selectively neutral. The number of vertebrae is also subject to relatively frequent mutations, with the offspring of a snake having a 0.03% probability of differing from their parent by +/– 4 vertebrae, a 0.7% probability of differing from their parent by +/– 3 vertebrae, a 1.2% probability of differing from their parent by +/– 2 vertebrae, and a 2.5% probability of differing from their parent by +/– 1 vertebra. Consequently, 95.57% of offspring will be the same as their parent, but some small proportion will have mutated.

Open the simulation in a new window

QUESTIONS

Question 1

Set the main island population standard deviation to 2 and press Initialize.

Approximately what is the range of vertebrae count present on the island after you do this?

Set the main island population standard deviation to 7 and press Initialize.

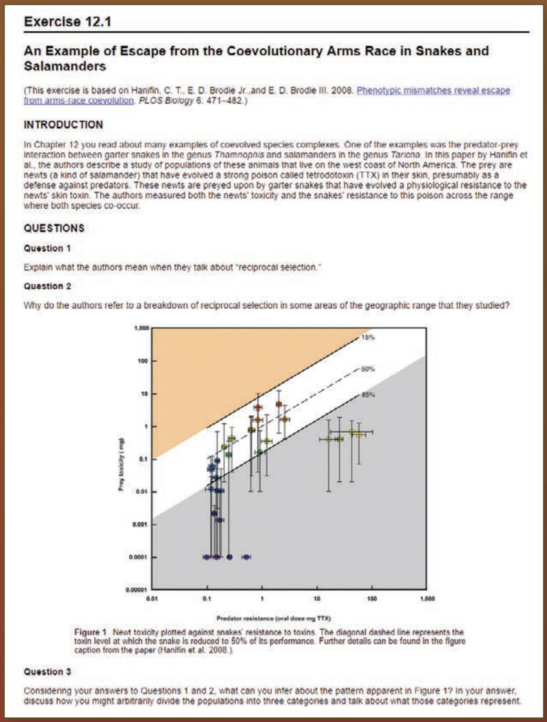
Question 2

Approximately what is the range of vertebrae count present on the island after you do this?

Set the main island population standard deviation to 5 and the small island immigration size to 2. Press Initialize and then run the simulation.

Question 3

Are any of the resulting small island distributions bimodal (with two "humps" in the distribution)?


Exercise 12.1

An Example of Escape from the Coevolutionary Arms Race in Snakes and Salamanders

(This exercise is based on Hanifin, C. T., E. D. Brodie Jr.,and E. D. Brodie III. 2008. Phenotypic mismatches reveal escape from arms-race coevolution. *PLOS Biology* 6: 471–482.)

INTRODUCTION

In Chapter 12 you read about many examples of coevolved species complexes. One of the examples was the predator-prey interaction between garter snakes in the genus *Thamnophis* and salamanders in the genus *Taricha*. In this paper by Hanifin et al., the authors describe a study of populations of these animals that live on the west coast of North America. The prey are newts (a kind of salamander) that have evolved a strong poison called tetrodotoxin (TTX) in their skin, presumably as a defense against predators. These newts are preyed upon by garter snakes that have evolved a physiological resistance to the newts' skin toxin. The authors measured both the newts' toxicity and the snakes' resistance to this poison across the range where both species co-occur.

QUESTIONS

Question 1

Explain what the authors mean when they talk about "reciprocal selection."

Question 2

Why do the authors refer to a breakdown of reciprocal selection in some areas of the geographic range that they studied?

Figure 1 Newt toxicity plotted against snakes' resistance to toxins. The diagonal dashed line represents the toxin level at which the snake is reduced to 50% of its performance. Further details can be found in the figure caption from the paper (Hanifin et al. 2008.).

Question 3

Considering your answers to Questions 1 and 2, what can you infer about the pattern apparent in Figure 1? In your answer, discuss how you might arbitrarily divide the populations into three categories and talk about what those categories represent.

Features of the Companion Website

Data Analysis Exercises: These inquiry-based exercises challenge you to think as a scientist and to analyze and interpret experimental data. Based on real papers and experiments, these exercises involve answering questions by analyzing the data from the experiments.

Simulation Exercises: These exercises include interactive modules that allow you to explore some of the dynamic processes of evolution. Each exercise poses questions that you answer by running a simulation and observing and analyzing the outcomes.

Online Quizzes: For each chapter of the textbook, the site includes a multiple-choice quiz that covers all the main topics presented in the chapter. Your instructor may assign these quizzes, or they may be made available to you as self-study tools. (Instructor registration is required for student access to the quizzes.)

Flashcards: Flashcards help you learn and review the many new terms introduced in the textbook. Each chapter's set of flashcards includes all of the key terms introduced in the chapter.

Chapter Summaries: Concise overviews of the important concepts and topics covered in each chapter.

Chapter Outlines: A convenient outline of each chapter's sections and sub-sections.

Glossary: A complete online version of the glossary, for quick access to definitions of important terms.

evolution4e.sinauer.com

evolution

FOURTH EDITION

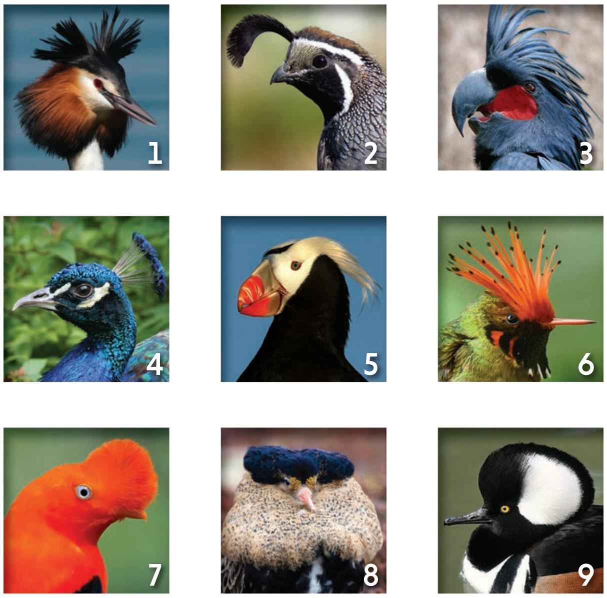
evolution

FOURTH EDITION

DOUGLAS J. FUTUYMA
Stony Brook University

MARK KIRKPATRICK
University of Texas at Austin

Sinauer Associates, Inc. • Publishers
Sunderland, Massachusetts U.S.A.



Key to the Back Cover

Natural selection acting on reproductive success has produced dramatic head ornaments in many species of birds.

1: great crested grebe (*Podiceps cristatus*); **2:** California quail (*Callipepla californica*); **3:** palm cockatoo (*Probosciger aterrimus*); **4:** Indian peafowl (*Pavo cristatus*); **5:** tufted puffin (*Fratercula cirrhata*); **6:** rufous-crested coquette (*Lophornis delattrei*); **7:** Andean cock-of-the-rock (*Rupicola peruvianus*); **8:** ruff (*Philomachus pugnax*); **9:** hooded merganser (*Lophodytes cucullatus*).

evolution, FOURTH EDITION

Sinauer Associates, Inc., 23 Plumtree Road, Sunderland, MA 01375 U.S.A.
Phone: 413-549-4300
Fax: 413-549-1118
Email: publish@sinauer.com, orders@sinauer.com
Website: www.sinauer.com

Library of Congress Cataloging-in-Publication Data

Names: Futuyma, Douglas J., 1942- author. | Kirkpatrick, Mark, 1956- author.
Title: Evolution / Douglas J. Futuyma, Stony Brook University, Mark Kirkpatrick, University of Texas, Austin.
Description: Fourth edition. | Sunderland, Massachusetts : Sinauer Associates, Inc., Publishers, 2017.
Identifiers: LCCN 2017000562 | ISBN 9781605356051 (casebound)
Subjects: LCSH: Evolution (Biology)
Classification: LCC QH366.2 .F87 2017 | DDC 576.8--dc23
LC record available at https://lccn.loc.gov/2017000562

Printed in the U.S.A
8 7 6 5 4 3 2 1

To the members of the Department of Ecology and Evolution at Stony Brook, past and present,
in gratitude for many years of support and intellectual sustenance.
DJF

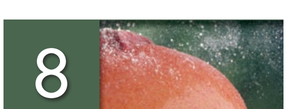
To Sharon, who kept the ship afloat, and to Don, who first pointed
the prow in this direction.
MK

Brief Contents

Contents

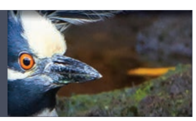
CHAPTER 6
Phenotypic Evolution 135

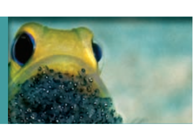
CHAPTER 7
Genetic Drift: Evolution at Random 165

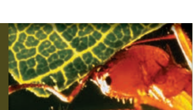


CHAPTER 8
Evolution in Space 191

9 

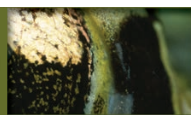
10 

11 

12 

19 

CHAPTER 19
The Evolution of Biological Diversity 491

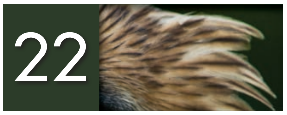
20 

CHAPTER 20
Macroevolution: Evolution above the Species Level 515

UNIT V Evolution and *Homo sapiens* 545

21 

CHAPTER 21
The Evolutionary Story of *Homo sapiens* 547



CHAPTER 22
Evolution and Society 573

Preface

It is thoroughly established that all known organisms descended from a single ancient common ancestor. This means that all characteristics of organisms, in all their glorious diversity, have evolved. Anatomical and cellular traits, biochemical, molecular, neural and developmental processes, life histories and ecological relationships—all can be viewed from the dual perspectives of current mechanism (how they work) and of history (how and why they came to be). The disciplines of organismal biology, including paleobiology, ecology, animal behavior, physiology, and systematics, continue to be central to evolutionary science, but are now being enriched by the genomic revolution, new analytical methods, and new evolutionary theory.

The fourth edition of *Evolution* keeps pace with this explosively developing field. There are now two authors with broadly overlapping but complementary areas of expertise. The organization, content, and style of the book are reworked to such an extent that it is largely a new book. Key changes include:

- Many human examples are used throughout, and there is an all-new chapter on human evolution.
- A new primer in statistics gives a concise and accessible introduction to the field.
- Theoretical concepts are developed in a more informal and inviting style.
- The book has been entirely re-illustrated.

The book is organized into these units:

I. An Idea that Changed the World

Chapter 1 opens with an overview of evolutionary biology and its history. The next two chapters introduce two of the most fundamental ideas in evolution: evolutionary trees (Chapter 2) and the concepts of natural selection and adaptation (Chapter 3).

II. How Evolution Works

The first four chapters of this unit develop genetics and inheritance (Chapter 4), one-locus population genetics (Chapter 5), quantitative genetics (Chapter 6), and genetic drift (Chapter 7). Chapter 8, which is entirely new, discusses spatial patterns and the evolution of dispersal. Chapter 9 then tackles species and speciation in a coherent treatment that has been streamlined relative to the third edition. Every chapter in this unit has been completely rewritten.

III. Products of Evolution: What Natural Selection Has Wrought

This unit treats key aspects of the evolution of phenotypes and genotypes: the all-new Chapter 10 on sexual selection and sexual reproduction, Chapter 11 with a rewritten exposition of the evolution of life histories and ecological niches, Chapter 12 on cooperation and conflict with new topics that include the evolution of virulence in pathogens, Chapter 13 on interactions among species, Chapter 14 on the evolution of genes and genomes, and Chapter 15 on evolution and development. These last two chapters have been rewritten in their entirety.

IV. Macroevolution and the History of Life

Chapter 16 develops the topic of phylogeny in detail. Chapter 17 provides a grand tour through the history of life. We turn to analysis of these historical data in Chapter 18, on biogeography, and Chapter 19, on patterns and causes of changes in biological diversity through time. Concepts drawn from throughout the book culminate in Chapter 20, which treats macroevolution.

V. Evolution and Homo sapiens

Perhaps no topic in biology has captured the imagination of scientists and the public alike than the tremendous recent advances in understanding human evolution. Chapter 21 conveys this excitement with a synthesis of sources that include paleontology, genomics, and cultural anthropology. Our final chapter (22) looks at how evolutionary biology impacts society, including belief systems and our understanding of human behavior.

More than any other science, evolutionary biology has had to prove its validity: in the United States, about half the population does not accept evolution by natural selection, and many of them are college students. *To teach evolution, then, is to teach the nature of science, the habit of reasoning between hypothesis and evidence, and the habit of critical evaluation*. At a time when science and evidence are increasingly misunderstood or even dismissed, we feel it is important to teach students what science is, how it works, and why it is the most reliable way of knowing that has yet been developed. Evolutionary biology is an ideal vehicle for this important function.

ACKNOWLEDGMENTS

Countless colleagues and students have contributed indirectly to this book, through their lectures, publications, conversations, and questions. We are indebted to the reviewers of chapter drafts for abundant, invaluable advice and corrections: Anurag Agrawal, Richard Bambach, Brian Barringer, David Begun, Andrew Brower, Brian Charlesworth, Jerry Coyne, Christopher Dick, Diego Figueroa, John Fleagle, Jacob Gardner, Kenneth Hayes, David Hillis, Gene Hunt, David Innes, David Jablonski, Elizabeth Jockusch, Joel Kingsolver, David Lohman, Greg Mayer, Duane McKenna, Mark McPeek, Monica Medina, Christopher Organ, Sally Otto, David Queller, Kaustuv Roy, Michael Ryan, Ellen Simms, Montgomery Slatkin, David Spiller, Stephen Stearns, Joseph Travis, Mark Welch, Noah Whiteman, Michael Whitlock, David Sloan Wilson, Greg Wray, Stephen Wright, Yaowu Yuan, and Roman Yukilevich. We are very grateful to David Hall, J. Matthew Hoch, and David Houle for writing the Problems and Discussion Topics at the chapter ends.

For advice, references, answers to questions, corrections, and many other favors, Douglas Futuyma is grateful to Richard Bambach, Michael Bell, Jackie Collier, Stefan Cover, Jerry Coyne, Joel Cracraft, Liliana Dávalos-Álvarez, Charles Davis, Christopher Dick, Daniel Dykhuizen, Walter Eanes, John Fleagle, Brenna Henn, Andreas Koenig, Spencer Koury, Harilaos Lessios, Jeffrey Levinton, James Mallet, Ross Nehm, Sally Otto, Joshua Rest, Martin Schoenhals, David Stern, Ian Tattersall, Robert Thacker, and Krishna Veeramah. Douglas Futuyma thanks Rob DeSalle and the American Museum of Natural History for generously providing work space in that marvelous institution, and the Department of Ecology and Evolution at Stony Brook for unending support and intellectual sustenance.

Mark Kirkpatrick is most grateful to the following people for their generous help with countless aspects of this project: Diego Ayala, Claudia Bank, Daniel Bolnick, Andrius Dagilis, Larry Gilbert, Shyamalika Gopalan, Matthew Hahn, David Hall, David Hillis, Robin Hopkins, David Houle, Matheiu Joron, Tom Juenger, Peter Keightley, Marcus Kronfrost, Curtis Lively, James Mallet, Richard Merrill, Michael Miyagi, Nancy Moran, Rasmus Nielsen, Mohamed Noor, Howard Ochman, Kenneth Olson, Sally Otto, Daven Presgraves, Trevor Price, David Queller, Fernando Racimo, Michael Ryan, Sara Sawyer, Dolph Schluter, Michael Shapiro, Stephen Shuster, Montgomery Slatkin, Ammon Thompson, Michael Wade, Stuart West, and Harold Zakon. Mark Kirkpatrick also thanks his colleagues and members of his laboratories at the University of Texas and the University of Montpellier for countless enlightening discussions.

This book was only made possible by the tireless work of many people at Sinauer Associates, consistently done with professionalism and a sense of humor. We are particularly in debt to Joanne Delphia, Laura Green, David McIntyre, Andy Sinauer, and Chris Small.

How to Learn Evolutionary Biology

The great geneticist François Jacob, who won the Nobel Prize in Physiology and Medicine for discovering mechanisms by which gene activity is regulated, wrote that "there are many generalizations in biology, but precious few theories. Among these, the theory of evolution is by far the most important." Why? Because, he said, evolution explains a vast range of biological information and unites all of the biological sciences, from molecular biology to ecology. "In short," he wrote, "it provides a causal explanation of the living world and its heterogeneity."

Jacob did not himself do research on evolution, but like most thoughtful biologists, he recognized its pivotal importance in the biological sciences. Evolution provides an indispensable framework for understanding phenomena that range from the structure and size of genomes to the ecological interactions among different species. And it has many philosophical implications and practical applications, ranging from understanding human diversity and behavior to health and medicine, food production, and environmental science.

Your course on evolution is likely to differ from almost any other course in biology you may have had, and it may present an unfamiliar challenge. Because all organisms, and all their characteristics, are products of a history of evolutionary change, the scope of evolutionary biology is far greater than any other field of biological science. In a course in cell biology, you are expected to learn many factual aspects of cell structure and function, which apply very broadly to various types of cells in almost all organisms. But courses in evolution generally do not emphasize the factual details of the evolution of particular groups of organisms—the amount of information would be impossibly overwhelming. There certainly are some important facts—for example, you should learn about major events in the history of life. But for the most part, your course is likely to emphasize the *general principles* of evolution, especially the *processes of evolutionary change* that apply to most or all organisms, *how we can learn what has happened in the evolutionary past*, and the *most common patterns of change*, those that have characterized many different groups of organisms.

For example, you will learn that natural selection is a consistent, statistical difference between groups of reproducing entities (such as large versus small individuals of a species) in the number of descendants they have. By understanding how a characteristic can affect survival or reproduction, we can arrive at generalizations about how certain characteristics are likely to evolve. For instance, it is easy for us to understand why a feature would be likely to evolve if it made males more attractive to females so that they have more offspring. But evolution by natural selection equally well explains why about half of the human genome consists of repeated DNA sequences that do nothing of value to the human organism! (The reason is that DNA sequences are also reproducing entities, and any sequence that can make more copies of itself will automatically increase more than a sequence that makes fewer copies. This is the essence of natural selection.) So the abstract concept of natural selection has a great range of applications and implications that will make up much of what you will want to learn about evolution.

It is important to learn *how evolutionary hypotheses have been tested*, in other words, what the evidence is for (or against) postulated histories and causes of evolutionary change. Evolutionary biology largely concerns events that happened in the past, so it differs from most other biological disciplines, which analyze the properties and functions of organisms' characteristics without reference to their history. We often must make inferences about past events and about ongoing processes that are difficult to see in action (e.g., differences in the replication rate of different DNA sequences). We make inferences by (1) posing informed hypotheses, then (2) generating predictions (making deductions) from these hypotheses about data that we can actually obtain, and finally (3) judging the validity of each hypothesis by the match between our observations and what we expect to see if the hypothesis were true.

For example, if you imagine that the long tail feathers of males in a species of bird evolved because such males attract more females and therefore have more offspring, you might predict that if you lengthened males' tail feathers, they will mate with more females. (The experiment has been done, with exactly this outcome.) You will find that throughout this book, we develop an idea, or hypothesis, theoretically, and then present one or two examples of empirical (i.e., real-world) studies that biologists have done, which provide evidence supporting the idea. *Understanding the theoretical ideas, and how and why the empirical study provides evidence for them, is the key to learning evolutionary biology.*

It is also the key to understanding how science works. Science isn't merely accumulating facts. In every field, scientists try to develop general principles that explain how natural phenomena work. Often, there are several conceivable explanations. The community of scientists in a field develops fuller understanding by devising alternative hypotheses and thinking of what kind of data would support one while refuting another. There is a competition of ideas (and competition among scientists) that results in a closer approach to reality. We cannot prove that a scientific hypothesis is absolutely true, but we can hope for very high confidence—and no other method of knowing can be shown to come as close. You can have very high confidence that DNA is the basis of inheritance, that human consumption of fossil fuels causes global climate change, and that humans have evolved from the same ancestor as all other animals, and from a much older ancestor of all the living things we know of.

In every field of science, the unknown greatly exceeds the known. Thousands of research papers on evolutionary topics are published each year, and many of them raise new questions even as they attempt to answer old ones. No one, least of all a scientist, should be afraid to say "I don't know" or "I'm not sure." To recognize where our knowledge and understanding are uncertain or lacking is to see where research may be warranted, or where exciting new research trails might be blazed. We hope that some readers will find evolution so rich a subject, so intellectually challenging, so fertile in insights, and so deep in its implications that they will adopt our subject as a career. But all readers, we hope, will find in evolutionary biology the thrill of understanding and the excitement of finding both answers and intriguing new questions about the living world, including ourselves. *Felix, qui potuit rerum cognoscere causas*, wrote Virgil: happy is the person who could learn the nature of things.

Media and Supplements

to accompany *Evolution*, Fourth Edition

FOR STUDENTS

Companion Website (evolution4e.sinauer.com)

Evolution's Companion Website features review and study tools to help students master the material presented in the textbook. Access to the site is free of charge, and requires no passcode. The site includes:

- *Chapter Outlines and Summaries*: Concise overviews of the important topics covered in each chapter.
- *Data Analysis Exercises*: These inquiry-based problems are designed to sharpen the student's ability to reason as a scientist, drawing on data from real experiments and published papers.
- *Simulation Exercises*: Interactive modules that allow students to explore many of the dynamic processes of evolution and answer questions based on the results they observe.
- *Online Quizzes*: Quizzes that cover all the major concepts introduced in each chapter. These quizzes are assignable by the instructor. (Instructor registration is required.)
- *Flashcards*: Easy-to-use flashcard activities that help students learn and review all the key terminology introduced in each chapter.
- The complete *Glossary*

FOR INSTRUCTORS

(Available to qualified adopters)

Instructor's Resource Library

The *Evolution* Instructor's Resource Library includes a variety of resources to help instructors in developing their courses and delivering their lectures. The IRL includes the following:

- *Textbook Figures and Tables*: All of the figures (including photographs) and tables from the textbook are provided as JPEGs, reformatted and relabeled for optimal readability when projected.
- *PowerPoint Presentations*: For each chapter, all of the figures and tables are provided in a ready-to-use PowerPoint presentation that includes titles and full captions.
- *Answers* to the textbook end-of-chapter Problems and Discussion Topics.
- *Quiz Questions*: All of the questions from the Companion Website's online quizzes are provided in Microsoft Word format.
- *Data Analysis and Simulation Exercises*: All of the exercises from the Companion Website are provided as Word documents, with answers, for use in class or as assignments.

Online Quizzing

The Companion Website includes an online quiz for each chapter of the textbook. Via the instructor's area of the companion website, these quizzes can be assigned or opened for use by students as self-quizzes. Custom quizzes can be created using any combination of publisher-provided questions and instructor-created questions. Quiz results are stored in an online gradebook and can be exported. (*Note*: Instructors must register with Sinauer Associates in order for their students to access the quizzes.)

Value Options

eBook

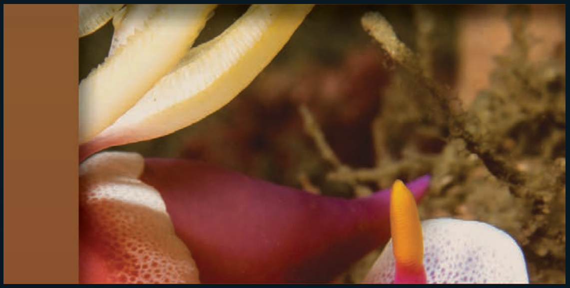
Evolution, Fourth Edition is available as an eBook, in several different formats, including VitalSource, RedShelf, Yuzu, and BryteWave. All major mobile devices are supported. For details on the eBook platforms offered, please visit www.sinauer.com/ebooks.

Looseleaf Textbook

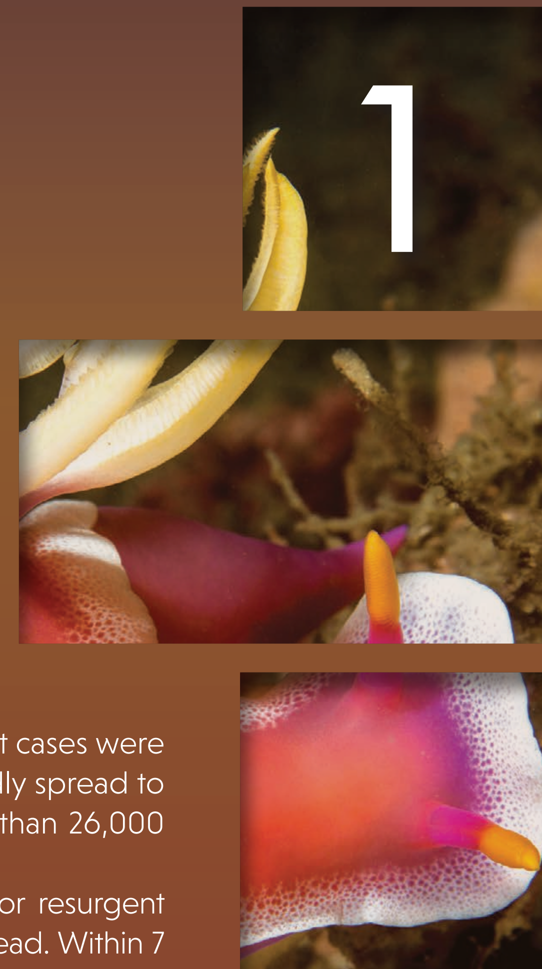
(ISBN 978-1-60535-696-9)

Evolution is also available in a three-hole punched, looseleaf format. Students can take just the sections they need to class and can easily integrate instructor material with the text.

UNIT I
An Idea that Changed the World



1



Evolutionary Biology

In February 2014, in the West Africa country Sierra Leone, the first cases were reported of the horrifying disease caused by Ebola virus. It rapidly spread to Liberia and Guinea, and within 15 months it had stricken more than 26,000 people and killed more than 11,000.

Among the first questions epidemiologists ask about a new or resurgent infectious disease are where it originated and by what paths it spread. Within 7 months after the start of the Ebola outbreak, a team of health scientists, molecular biologists, and evolutionary biologists had an answer [7]. Based on an evolutionary analysis of the viral genomes from several patients, the researchers concluded that the West Africa virus had almost certainly spread from central Africa about a decade earlier, and that the 2014 outbreak originated from a single person who contracted the virus from another host species, probably a bat. This was an important point, because it indicated that although the virus is readily transmitted from one person to another, it is only rarely contracted by humans from other species.

This was by no means the first time evolutionary methods had been used to trace the origin of an infectious disease. This approach has been routine ever since the origin of the human immunodeficiency virus (HIV), which causes AIDS, was determined in 1989. Two distinct HIVs (HIV-1 and HIV-2) infect humans; the pandemic is caused by HIV-1. Both HIVs are lentiviruses, a group of retroviruses that infect diverse mammals. In monkeys and other primates, the viruses are called simian immunodeficiency viruses, or SIVs (**FIGURE 1.1**). An evolutionary analysis showed that HIV-2 recently evolved from an SIV carried by sooty

This pink nudibranch (*Hypselodoris bullocki*) is a spectacular example of a group of marine mollusks renowned for their unusual shapes and bright coloration. Many nudibranchs contain toxins as a defense against predation and their unusual colors may be an adaptation that warns potential predators not to eat them. The only scientific explanation of such adaptations is the theory of evolution by natural selection.

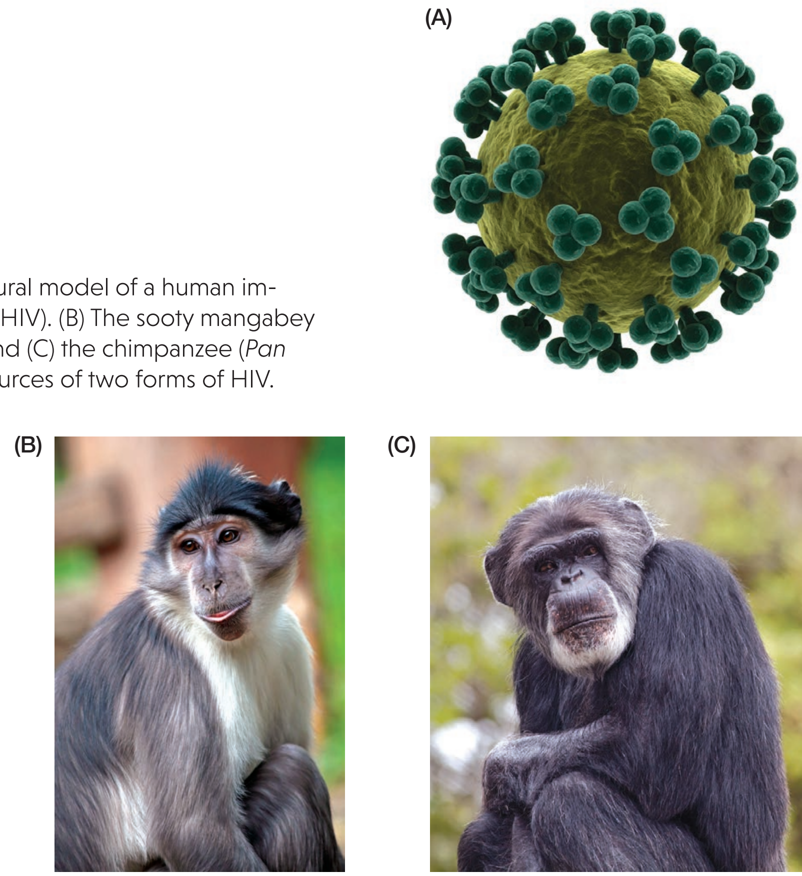


FIGURE 1.1 (A) Structural model of a human immunodeficiency virus (HIV). (B) The sooty mangabey (*Cercopithecus atys*) and (C) the chimpanzee (*Pan troglodytes*) are the sources of two forms of HIV.

mangabey monkeys, and that HIV-1 evolved from SIV_{cpz}, the virus that infects wild chimpanzees (**FIGURE 1.2**) [9, 25]. The evolutionary analysis showed, moreover, that HIV-1 entered the human population near the beginning of the twentieth century, decades before it spread beyond Africa. It is thought that humans became infected with SIVs by contact with the blood of chimpanzees and mangabeys that they killed for food.

These viruses do not have a fossil record, so how could biologists infer their evolution and spread? They used methods that have been developed to reconstruct evolutionary history, and that are based on understanding the processes of evolutionary change.

Understanding the processes of evolution is highly relevant to human health. For example, the first drug approved to treat HIV-infected people was AZT, in 1987. Within a few years, however, AZT failed to prevent many infected patients from developing AIDS, and it has been necessary to develop other drugs. What happened? Populations of HIV had *adapted* to AZT by *evolving* resistance. Ever since the first antibiotic—penicillin—came into use, bacteria and other pathogenic microbes have rapidly evolved resistance to every antibiotic that has been widely used (**FIGURE 1.3**) [20, 22]. *Staphylococcus aureus*, a bacterium that causes many infections in surgical patients, has evolved resistance to a vast array of antibiotics, starting with penicillin and working its way through many others. Drug-resistant strains of *Neisseria gonorrheae*, the bacterium that causes gonorrhea, have steadily increased in abundance, and many strains of the tuberculosis, pneumonia, and cholera bacteria are highly resistant to antibiotics. Throughout the tropics, the microorganism that causes malaria is now resistant to chloroquine and is becoming resistant to other drugs as well. Worldwide, more than a half million people die yearly from drug-resistant infections. The evolution of antibiotic resistance is a major crisis in public health [3, 22].

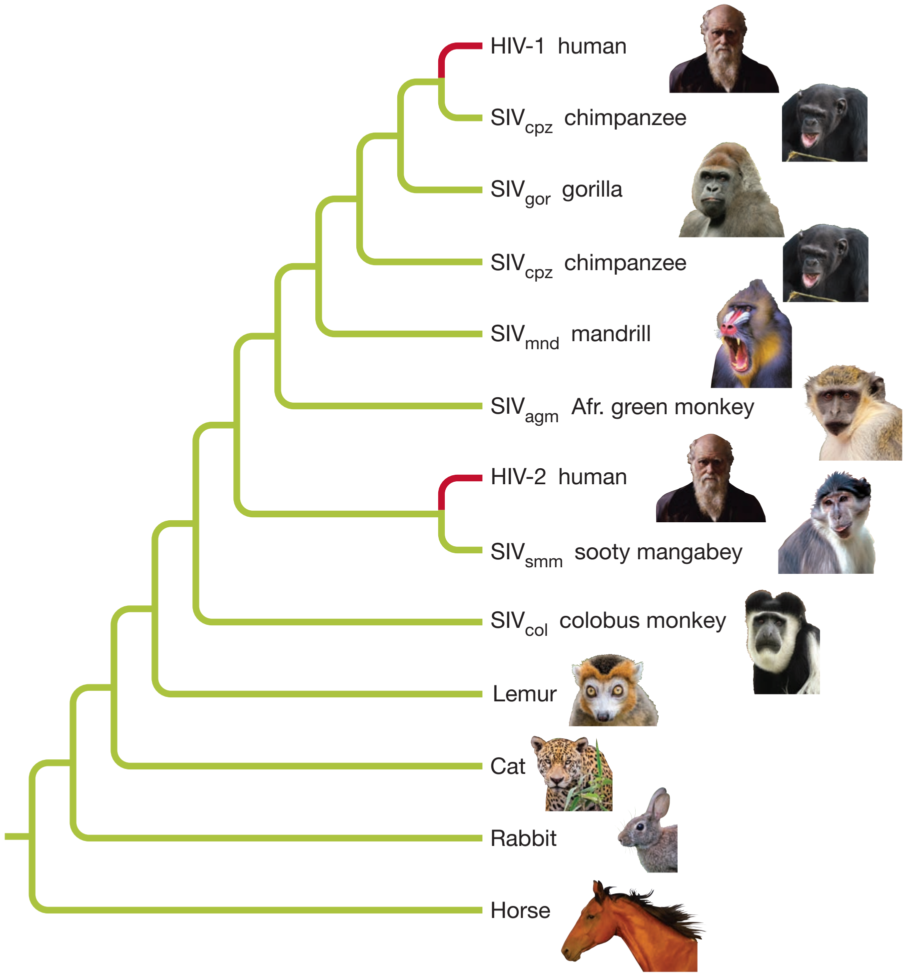


FIGURE 1.2 A phylogenetic tree showing the history by which various immunodeficiency viruses have evolved. Time runs from left to right, and the common ancestor of all the viruses is at the left (the "root" of the tree). One lineage gave rise to the viruses that infect primates: lemurs, monkeys, and apes. These simian immunodeficiency viruses (SIVs) are labeled with abbreviations of the names of the infected species (e.g., SIV_{cpz} in chimpanzee). The human immunodeficiency viruses HIV-2 and HIV-1 arose from SIVs that infected monkeys and chimpanzees, respectively. (After [25].)

Almost every hospital in the world treats casualties in this battle against changing opponents, but as the use of antibiotics increases, so does the incidence of bacteria that are resistant to those antibiotics; thus any gains made are almost as quickly lost (see Figure 1.3). Why is this happening? Do the drugs cause drug-resistant mutations in the bacteria's genes? Do the mutations occur even without

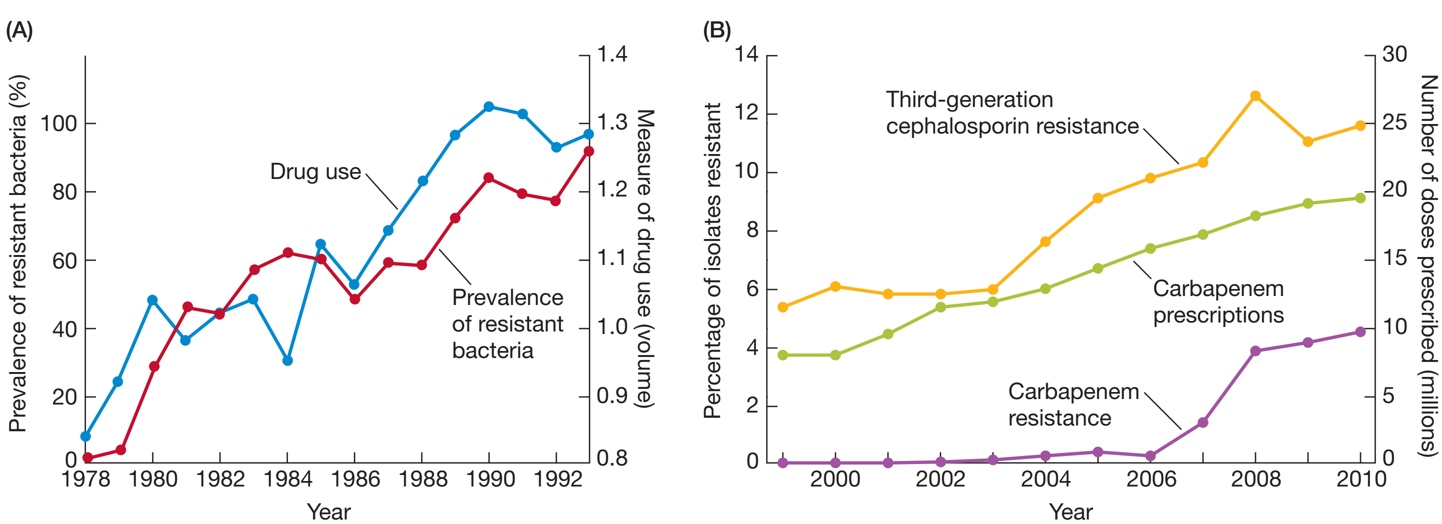


FIGURE 1.3 Evolution of drug resistance. (A) An increase in the use of a penicillin-like antibiotic in a community in Finland between 1978 and 1993 was matched by a dramatic increase in the percentage of antibiotic-resistant isolates of the bacterium *Moraxella catarrhalisis* from middle-ear infections in young children. (B) Resistance of the pneumonia-causing bacterium *Klebsiella pneumoniae* to cephalosporin and carbapenem antibiotics has recently begun to increase in the United States. The use of carbapenems approximately doubled during the period shown. (A after [15]; B after [23].)

exposure to drugs—that is, are they present in unexposed bacterial populations? Do the mutations spread among different species of bacteria? Can the evolution of resistance be prevented by using lower doses of drugs? Higher doses? Combinations of different drugs?

Microbial adaptation to drugs is the same, in principle, as the countless adaptations of every species to its environment, so it is very familiar to evolutionary biologists. The principles and methods of evolutionary biology have provided some answers to these questions about antibiotic resistance, and have shed light on many other problems that affect society. Evolutionary biologists have studied the evolution of insecticide resistance in disease-carrying and crop-destroying insects. They have helped devise methods of nonchemical pest control and have laid the foundations for transferring genetic resistance to diseases and insects from wild plants to crop plants. Evolutionary principles and knowledge are being used in biotechnology to design new drugs and other useful products, and in medical genetics to identify and analyze inherited diseases as well as variation in susceptibility to infectious diseases. In the fields of computer science and artificial intelligence, "evolutionary computation" uses principles taken directly from evolutionary theory to solve mathematically difficult practical problems, such as constructing complex timetables and processing radar data.

The importance of evolutionary biology goes far beyond its practical uses. An evolutionary framework provides answers to many questions about ourselves. How do we account for human variation—the fact that almost everyone is genetically and phenotypically unique? What accounts for behavioral differences between men and women? How did exquisitely complex, useful features such as our hands and our eyes come to exist? What about apparently useless or even potentially harmful characteristics such as our wisdom teeth and appendix? Why do we age, senesce, and eventually die? Evolution raises still larger questions. As soon as Darwin published *On the Origin of Species* in 1859, the evolutionary perspective was perceived to bear on long-standing questions in philosophy. If humans, with all their mental and emotional complexity, originated by natural processes, where do ethics and moral precepts find a foundation and origin? What, if anything, does evolution imply about the meaning and purpose of life? Must one choose between evolution and religious belief?

"Nothing in Biology Makes Sense except in the Light of Evolution"

If you suppose that scientists study evolution by analyzing fossils, you are right—but as the analyses of infectious diseases show, students of evolution also employ many other approaches and address a wide range of questions. Evolutionary biology is concerned with explaining and understanding the diversity of living things and their characteristics: what has been the *history* that produced this diversity, and what have been the *causes* of this history? Some evolutionary scientists try to elucidate the history of viruses, how they became capable of infecting diverse species of animals, and how antibiotic resistance evolves. Others ask similar questions about the origin of humans and human characteristics—or of mammals, plants, beetles, or dinosaurs. And because all features of all organisms have evolved, evolutionary biologists study the evolution of DNA sequences, proteins, biochemical pathways, embryological development, anatomical features, behaviors, life histories, interactions among different species: all of biology. Facing such an overwhelming profusion of subjects, evolutionary scientists aim to develop broad principles and to document common *patterns of evolution*—to arrive at *general principles* that apply to diverse organisms

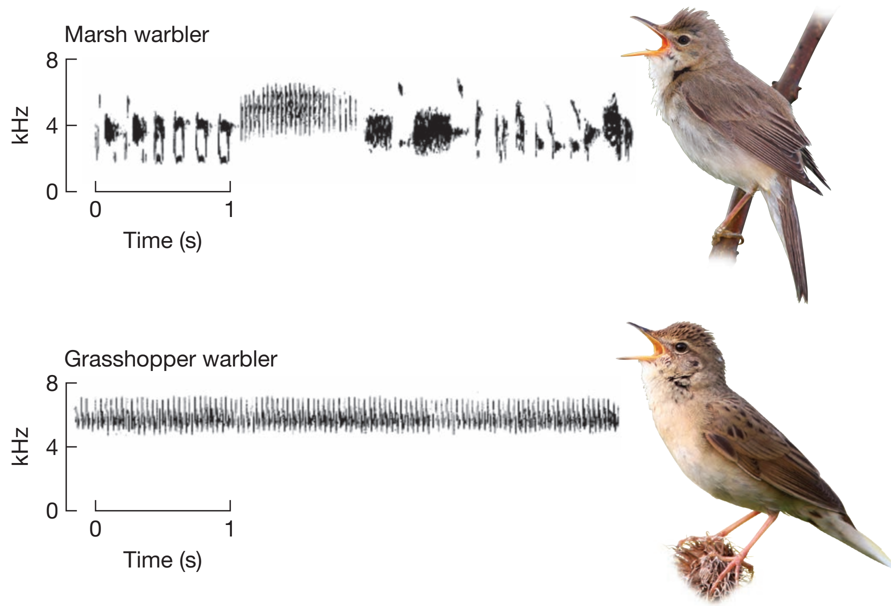


FIGURE 1.4 The song of a male marsh warbler (*Acrocephalus palustris*) is much more complex than the song of a male grasshopper warbler (*Locustella naevia*), which is a simple buzz. The sonograms (diagrams of the song) show frequency in relation to time. The song nucleus in the brain is larger in the marsh warbler than in the grasshopper warbler. Female marsh warblers prefer males with more complex songs. The proximate causes of the song difference include the brain structure; the ultimate causes include natural selection owing to the reproductive success of males whose songs attract more females. (Sonograms from [30].)

and diverse kinds of characteristics. Most of this book attempts to convey these general principles, although we illustrate the principles with studies of particular organisms and characteristics.

Evolutionary biology extends and amplifies the explanation of biological phenomena. It complements studies of the **proximate causes** (immediate, mechanical causes) of biological phenomena—the subject of cell biology, neurobiology, and many other biological disciplines—with analysis of the **ultimate causes** of those phenomena: their historical causes, especially the action of natural selection. If we ask what causes a male bird to sing, the proximate causes include the action of testosterone or other hormones, the structure and action of the singing apparatus (syrinx), and the operation of certain centers in the brain (**FIGURE 1.4**). The ultimate causes lie in the history of events that led to the evolution of singing in the bird's remote ancestors. For example, past individuals whose genes inclined them to sing may have been more successful in attracting females or in driving away competing males, and thus may have transmitted their genes to more descendants than did their less vocal competitors. Proximate and ultimate explanations may interact [14], and together provide more complete understanding than either does alone. As the great evolutionary biologist Theodosius Dobzhansky [5] wrote, "Nothing in biology makes sense except in the light of evolution."

What Is Evolution? Is It Fact or Theory?

The word "evolution" comes from the Latin *evolvere*, "to unfold or unroll"—to reveal or manifest hidden potentialities. Today "evolution" has come to mean, simply, "change." But changes in individual organisms, such as those that transpire in development (ontogeny) are not considered evolution. **Biological** (or **organic**) **evolution** is *inherited change in the properties of groups of organisms over the course of generations*. As Darwin elegantly phrased it, evolution is *descent with modification*.

As the HIV and SIV viruses illustrate, a single group, or **population**, of organisms may be modified over the course of time (e.g., becoming drug-resistant). A population may become subdivided, so that several populations are descended from a *common ancestral population*. If different changes transpire in the several populations, the populations **diverge** —that is, they become different from each other (e.g., as the various HIVs and SIVs have done).

Is evolution a fact, a theory, or a hypothesis? Biologists often speak of the "theory of evolution," but they usually mean by that something quite different from what most nonscientists understand by that phrase. Biologists talk about the "theory of evolution" in the same way that physicists talk about the "theory of gravitation." Scientists are as confident about the reality of evolution as they are of the reality of gravity.

In science, a **hypothesis** is an informed conjecture or statement of what might be true. Most philosophers (and scientists) hold that we do not know anything with absolute certainty. What we call "facts" are in some cases simple, confirmed observations; in other cases, a "fact" is a hypothesis that has acquired so much supporting evidence that we act as if it is true. A hypothesis may be poorly supported at first, but it can gain support to the point that it is effectively a fact. For Copernicus, the revolution of Earth around the Sun was a hypothesis with modest support; for us, this hypothesis has such strong support that we consider it a fact. Occasionally, an accepted "fact" may need to be revised in the face of new evidence; for example, humans have 46 chromosomes, not 48 as once thought.

In everyday use, "theory" refers to an unsupported speculation. Like many words, however, this term has a different meaning in science. Strictly speaking, a **scientific theory** is a comprehensive, coherent body of interconnected statements, based on reasoning and evidence, that explain some aspect of nature—usually many aspects. Thus atomic theory, quantum theory, and the theory of plate tectonics are elaborate schemes of interconnected ideas, strongly supported by evidence, that account for a great variety of phenomena. "Theory" is a term of honor in science; the greatest accomplishment a scientist can aspire to is to develop a valid, successful new theory.

In *The Origin of Species*, Darwin propounded *two major hypotheses*: that organisms have descended, with modification, from common ancestors; and that the chief cause of modification is natural selection acting on hereditary variation. Darwin provided abundant evidence for descent with modification; since then, hundreds of thousands of observations from paleontology, geographic distributions of species, comparative anatomy, embryology, genetics, biochemistry, and molecular biology have confirmed that all known species are related to one another through a history of common ancestry. Thus the hypothesis of descent with modification from common ancestors has long had the status of a scientific fact. (We will describe some of the evidence in Chapters 2 and 22.)

The explanation of how modification occurs and how ancestors give rise to diverse descendants constitutes the scientific theory of evolution. We now know that Darwin's hypothesis that evolution occurs by natural selection acting on hereditary variation was correct. We also know that there are more causes of evolution than Darwin realized and that natural selection and hereditary variation are more complex than he imagined. A body of ideas about the causes of evolution, including mutation, recombination, gene flow, isolation, random genetic drift, the several forms of natural selection, and other factors constitutes our current theory of evolution, or "evolutionary theory." Like all theories in science, it is a work in progress, for we do not entirely know the causes of all of evolution, or of all the biological phenomena that evolutionary biology will have to explain. In evolutionary biology, as in every other scientific discipline, there are "core" principles that have withstood skeptical challenges and are highly unlikely to require revision, and there are "frontier" areas in which research actively continues. Some widely held ideas about frontier subjects may prove to be wrong, but the uncertainty at the frontier does not undermine the core. The main tenets of evolutionary theory—descent with modification from a common ancestor, in part caused by natural selection—are so well supported that almost all biologists confidently accept evolutionary theory as the foundation of the science of life.

The Evolution of Evolutionary Biology

That the past is often the key to the present may be a cliché, but it happens to be true. Just as evolutionary history has shaped today's organisms, and just as social and political history is the key to understanding today's nations and conflicts, so the content of any science or other intellectual discipline cannot be fully understood without reference to its history.

Before Darwin

Darwin's theory of biological evolution is one of the most revolutionary ideas in Western thought, perhaps rivaled only by Newton's and Einstein's theories of physics. It profoundly challenged the prevailing worldview, which had originated largely with Plato and Aristotle, who developed the notion that species have fixed properties. Later, Christians interpreted the biblical account of Genesis literally and concluded that each species had been created individually by God in the same form it has today. (This belief is known as "special creation.") Christian theologians and philosophers argued that since existence is good and God's benevolence is complete, He must have bestowed existence on every creature of which He could conceive. Because order is superior to disorder, God's creation must follow a plan: specifically, a gradation from inanimate objects and barely animate forms of life through plants and invertebrates and up through ever "higher" forms of life. Humankind, being both physical and spiritual in nature, formed the link between animals and angels. This "Great Chain of Being," or *scala naturae* (the scale, or ladder, of nature), must be permanent and unchanging, since change would imply that there had been imperfection in the original creation [16].

As late as the nineteenth century, natural history was justified partly as a way to reveal the plan of creation so that we might appreciate God's wisdom. **Carolus Linnaeus** (1707–1778), who established the framework of modern taxonomy in his *Systema Naturae* (1735), won worldwide fame for his exhaustive classification of plants and animals, undertaken in the hope of discovering the pattern of the creation. Linnaeus classified "related" species into genera, "related" genera into orders, and so on. To him, "relatedness" meant propinquity in the Creator's design.

Carolus Linnaeus

Belief in the literal truth of the biblical story of creation started to give way in the eighteenth century, when a philosophical movement called the Enlightenment, largely inspired by Newton's explanations of physical phenomena, adopted reason as the major basis of authority and marked the emergence of science. The foundations for evolutionary thought were laid by astronomers, who developed theories of the origin of stars and planets, and by geologists, who amassed evidence that Earth had undergone profound changes, that it had been populated by many creatures now extinct, and that it was very old. The geologists James Hutton and Charles Lyell expounded the principle of **uniformitarianism**, holding that the same processes operated in the past as in the present and that the data of geology should therefore be explained by causes that we can now observe. Darwin was greatly influenced by Lyell's teachings, and he adopted uniformitarianism in his thinking about evolution.