PREFACE

We envy the student taking a class in evolutionary biology today. It is an exciting time to study science, and the science of evolutionary biology is more vibrant now than ever. In part, this is due to the new tools now available to scientists—tools that just a generation ago were the stuff of dreams. But there is more to it than that. Evolutionary biology is increasingly important in integrating the biological sciences. Evolutionary biologists are now collaborating in new, dynamic ways with researchers in many disciplines, and in so doing, they are bringing together a diverse set of perspectives—from areas like phylogenetics, population genetics, the study of adaptation, molecular genetics, and developmental biology, to name just a few. The result is a much deeper understanding of the history and diversity of life on Earth over the last 4 billion years or so. Our job as the authors of this book is to capture the exciting work that has gone into this effort, and to present it in a rigorous and engaging fashion.

To achieve this goal, we draw on our dual roles as researchers in and teachers of evolutionary biology. We each run active labs abuzz with the excitement that surrounds the science of evolution; we both lecture about evolution to students at our own universities and to audiences around the world. And we are each enthusiasts about the history of science in general and the history of evolutionary biology in particular. The successful strategies we've developed for communicating with these diverse audiences have informed the tone, emphases, and features in this textbook in a way that we hope will excite the scientific imaginations of students and instructors alike.

First and foremost, we relish the fact that *all science* is about testing hypotheses. Hypothesis-driven science has proven to be the most powerful approach ever devised for understanding the nature of the physical world we live in. We convey this through the abundant use of examples in which evolutionary biologists generate and test hypotheses. In this way, students can gain an intimate understanding of how theoretical ideas translate into testable predictions, and how this process of hypothesis testing leads to refinements of theory.

More generally, we understand that learning is an interactive process, and that such a process is greatly facilitated by the use of *stories*. And so, in each chapter, we make use of the natural human inclination to acquire and process information in the form of stories. Within the field of evolutionary biology are fascinating stories on many levels: stories of individual scientists and how they came to their discoveries, stories of how human thought has changed over the centuries, stories of how major evolutionary innovations arose in the history of life, stories of how individual species have changed over millennia through biological evolution or, as in the case of many microbes, how a population can change dramatically in a matter of weeks.

To tell these stories, we reference the primary literature as would any working scientist, acknowledging that the ideas in this book come from the endeavors of individual

researchers—many of whom are active today—rather than from some accepted body of traditional wisdom that lies beyond challenge. But rather than re-using the same stable of illustrative examples that appear in text after text, a large majority of the examples used to illustrate principles in this book appear here for the first time in a biology textbook, and a great fraction of these are drawn from papers published within the past decade. Through the lens of current research, students can see how the scientific understanding of evolutionary biology is ever-changing, and that built into science is a system that allows each assumption to be challenged and refined or even rejected based on a preponderance of evidence.

Because models play a fundamental role in much of the current research in evolutionary biology today, we will devote considerable attention to simple conceptual models of evolutionary processes. Often such models can be profitably expressed through the language of mathematics, and one of our principal aims in the text is to help students become comfortable with this approach. We have found that one of the most important things that students learn in college-level physics or economics classes is how to formulate questions about the real world in the language of mathematical models, and how to answer these questions appropriately using mathematical analysis. We believe that this should be a critical component of a college education in the biological sciences as well. But we also recognize that students enter this course with varying degrees of mathematical preparedness. Thus, we have placed the more advanced concepts in boxes in an effort to offer instructors maximum flexibility in integrating mathematical models into their course.

So that students will gain a firm understanding of the essential foundations of evolutionary reasoning, we introduce several fundamental components of evolutionary thought in Chapter 1, and emphasize them throughout this textbook. These include:

- **Phylogenetics**. All living things on the planet today—and indeed all life that has ever existed—are linked by a shared evolutionary history that evolutionary biologists represent using phylogenetic trees. Thus, in order to understand evolutionary relationships, whether between two HIV strains or among the three major domains of life, students must learn to think in terms of phylogenetic relationships. We consider it critical that any textbook on evolution seamlessly integrates phylogenetic thinking throughout, and we have done so here. If students walk away remembering just one thing about this book—though of course we hope they walk away remembering much, much more—it will be the importance of phylogenetic thinking.
- **Population thinking**. Evolutionary change occurs in populations, but in our experience students are often more comfortable thinking at the level of the individual, as one would in a physiology course, for example. In this book, we demonstrate how to think at the population level as well, paying careful attention to the properties of populations: population composition, variation among individuals within and between populations, change in the properties of a population over time, and so forth. This population-level perspective, particularly as it relates to the process of natural selection, permeates our book. Because we know that some students initially struggle to master this type of population-level thinking, we devote considerable space to teaching this skill.
- **Natural selection**. Evolution is often defined as "descent with modification." As a population geneticist (CTB) and a behavioral evolutionary biologist (LAD), we both study the processes responsible for such "modification." We convey the importance of this topic to students by teaching them how the process of natural selection has shaped the diversity of life on this planet, and how other processes—most notably genetic drift—have also contributed to the myriad forms of life around us.

Features

This textbook integrates the big themes in evolutionary biology—phylogenetics and population thinking—in a way that is both current and accessible. Extensive, in-depth, current research examples, an emphasis on problem solving, and a stunning art program engage students, helping them understand fundamental concepts and processes. Major features:

- Extensive coverage of **phylogenetics**, which is introduced in Chapter 1 through the examination of a few engaging examples that demonstrate the power of phylogenetic thinking. Soon after, in Chapter 4, Phylogeny and Evolutionary History, and Chapter 5, Inferring Phylogeny, students are taught how to interpret and then build trees that generate testable hypotheses about evolutionary history and compare the relatedness of living organisms. This strong foundation in phylogenetic reasoning is then integrated into the text and art in virtually every chapter that follows.
- Examination of fundamental concepts through the lens of phylogenetics and population thinking are reinforced by **current research examples**, many of which are drawn from research done in the last decade. From Chapter 4's in-depth examination of Bryan Fry's study of venomousness in snakes to find the evolutionary origins of snake venom, to Chapter 11's coverage of Natasha Paul and Gerald Joyce's research on self-replicating RNA to find clues to the RNA world, to Chapter 19's discussion of Toby Kier's work on the mutualism between a soybean legume and a rhizobial bacterium to examine coevolution and the response to cheaters, the excitement of current research is captured throughout.
- Significant coverage of **contemporary topics** such as genomics, evo–devo, and molecular evolution, including full chapters on the following subjects: Genome Evolution (Chapter 10), Evolution and Development (Chapter 13), Coevolution (Chapter 19), and Evolution and Medicine (Chapter 20).
- An in-depth focus on **a few research studies** in each chapter promote a more complete understanding of how evolutionary biologists come to understand specific concepts. The examples were carefully chosen to offer a **balance of classic and contemporary studies** that most fully illustrate the concept being discussed.
- A beautiful and information-rich **art program** was carefully developed to promote understanding of key concepts described in the text by both engaging students visually and providing them with just the right amount of detail. The art includes distinctive figures that help students in the following ways:
  1. **Phylogenetic relationships** are made clear through the many phylogenetic trees that appear in virtually every chapter. Many of these trees also include in-figure captions, photographs, and line art that enrich students' understanding of the concept or example.

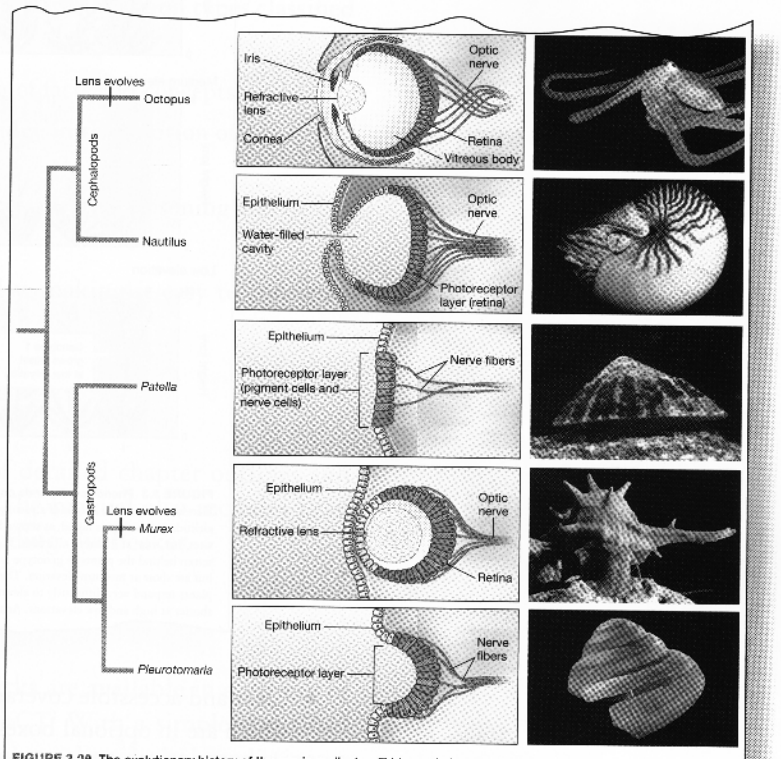

FIGURE 3.29 The evolutionary history of the eye in mollusks. Taking a phylogenetic perspective on eye morphology in the mollusks, we see that complex eyes with a lens evolved independently in the cephalopods and in the gastropods (Oakley and Pankey 2008). From top to bottom: The octopus eye uses a lens to focus light on the retina, much as does the vertebrate eye. The nautilus eye functions like a pinhole camera, casting a sharp image on the retina at the expense of a loss in brightness due to its small aperture. The limpet *Patella* has only a light-sensitive patch that can distinguish between light and dark. The predatory snail *Murex* uses a simple lens to focus incoming light. The snail *Pleurotomaria* has an indented eye cup that can detect the direction of a light source. Phylogeny is inspired by Oakley and Pankey (2008) and informed by Ponder and Lindberg (1997).

2. **Research-style data graphics** are presented much like they appear in the primary literature, but with carefully developed labels and in-figure captions that teach students to interpret and analyze the image or graph visually.

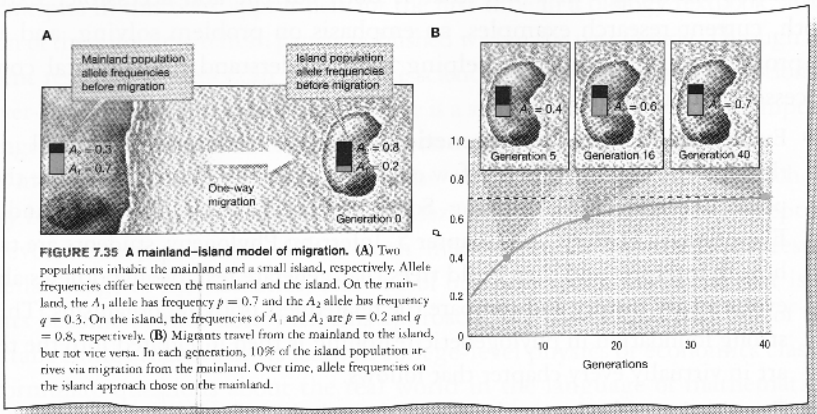

FIGURE 7.35 A mainland–island model of migration. **(A)** Two populations inhabit the mainland and a small island, respectively. Allele frequencies differ between the mainland and the island. On the mainland, the A_1 allele has frequency $p = 0.7$ and the A_2 allele has frequency $q = 0.3$. On the island, the frequencies of A_1 and A_2 are $p = 0.2$ and $q = 0.8$, respectively. **(B)** Migrants travel from the mainland to the island, but not vice versa. In each generation, 10% of the island population arrives via migration from the mainland. Over time, allele frequencies on the island approach those on the mainland.

3. Diagrams of **experimental processes** encourage students to visualize not just the outcome of a research study, but the specifics of how the experiment was constructed so that they can better understand the meaning behind the data.

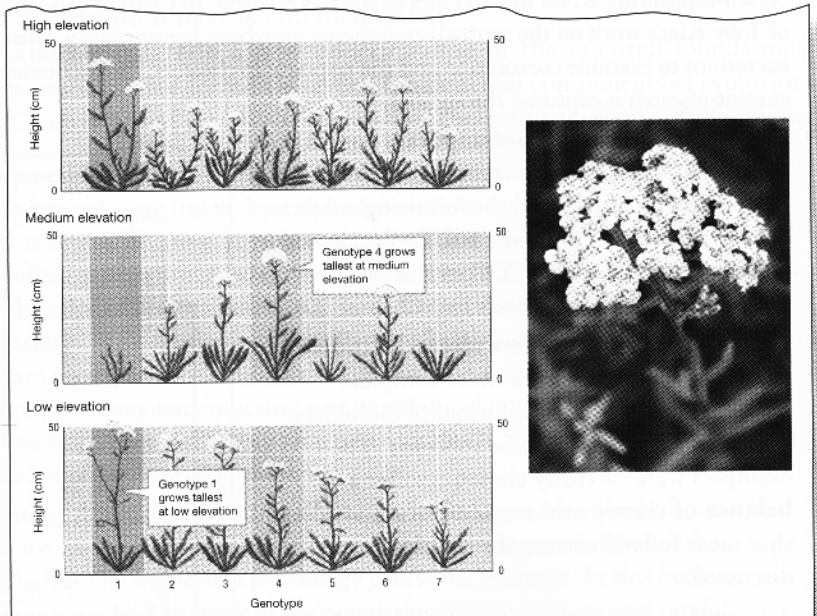

FIGURE 3.3 Phenotype depends on the effects of both genotype and environment. Here we see how the height of a yarrow plant (*Achillea millefolium*) depends on its genotype and the altitude at which it is raised, as shown by populations of yarrow plants grown in gardens at three sites that were at different altitudes: high, medium, and low elevation. For example, the green screen behind the plants in genotype 1 shows that these plants grow tall at high and low elevations, but are short at medium elevation. The blue screen behind the plants in genotype 4 shows that the plants respond very differently to elevation. This genotype grows tallest at medium elevation and shorter at high and low elevations. Adapted from Clausen, Keck, and Hiesey (1940, 1948).

- Clear and accessible coverage of **quantitative methods**, the most difficult of which are in optional boxes. This teaches students how to formulate questions about evolutionary processes and relationships the ways researchers do—in the language of quantitative models.
- High-quality **problem sets** in the end-of-chapter material and online provide students with extensive practice in formulating and solving problems.

Resources for Instructors

Instructor's Resource Disc

This disc includes the following presentation features that can be used in your lectures:

- Labeled and unlabeled versions of every figure and photograph in the textbook, offered in JPEG and PowerPoint formats.
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The Test Bank has been developed using the Norton Assessment Guidelines and provides a quality bank of 1000 items consisting of multiple-choice and short answer/essay questions. Each chapter of the Test Bank consists of three question types classified according to Norton's taxonomy of knowledge types:

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- Applied questions require students to apply knowledge in the solution of a problem.
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Questions are further classified by section and difficulty, making it easy to construct tests and quizzes that are meaningful and diagnostic.

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This helpful online resource for instructors consists of detailed chapter outlines and guides to key readings in the text for every chapter. The manual also includes brief guides to accessing and using online simulations, including EvoBeaker.

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At no cost to instructors or students, Norton coursepacks are available in a variety of formats, including all versions of Blackboard and WebCT. With a simple download from our instructor's website, an adopter can bring high-quality digital media into a new or existing online course (with no additional student passwords or logins required). Content includes chapter-based assignments, test banks, quizzes, and animations from the StudySpace student website.

Resources for Students

StudySpace

Students rely on effective and well-designed online resources to help them succeed in their courses. StudySpace is a free and open website that shows students what they need to know, what they still need to review, and provides them with an organized study plan for mastering the material. Resources for students on StudySpace:

- Process animations based on topics nominated by more than 100 reviewers and based directly on powerful and information-rich art in the textbook. These animations bring to life fundamental concepts such as genetic drift, phylogenetics, the Hardy–Weinberg equilibrium, and mutation. In addition to being available online to students, offline access is available on the Instructor's Resource Disc.
- Quiz+ Diagnostic Quizzes provide a customized study plan based on students' right and wrong quiz answers by offering specific page references and links to the ebook and other online learning tools, including the animations.
- Detailed Study Plans guide students through the core concepts for each chapter and help them utilize all the online resources for the chapter.
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- A news feed links to current articles on the web relating to evolutionary biology.

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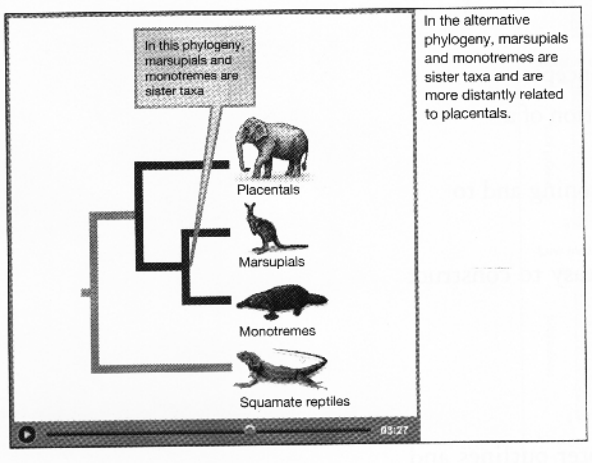

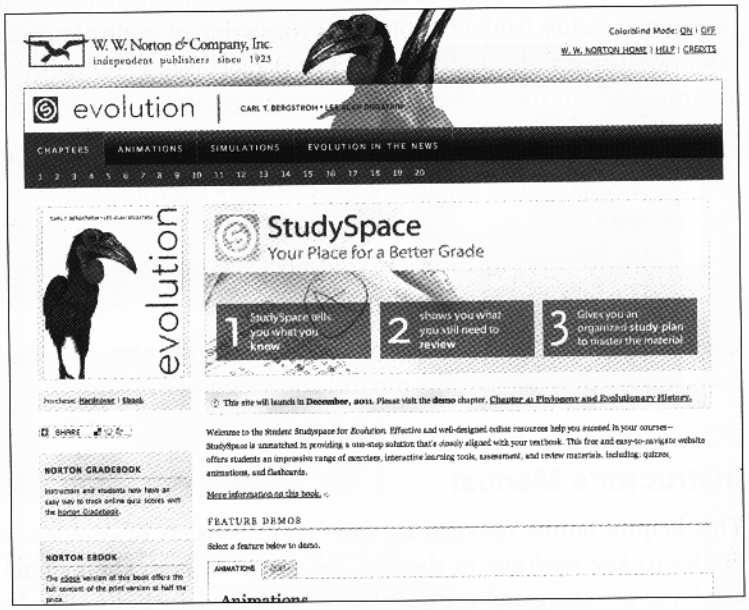

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