BIOLOGY

NINTH EDITION

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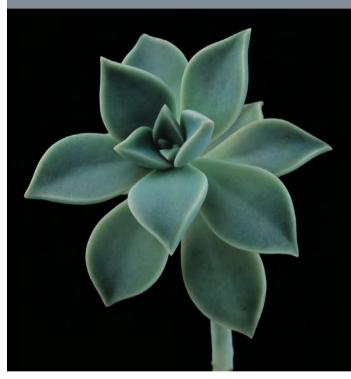


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CAMPBELL BIOLOGY

NINTH EDITION



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About the Authors



The Ninth Edition author team's contributions reflect their biological expertise as researchers and teaching sensibilities gained from years of experience as instructors at diverse institutions. The team's highly collaborative style continues to be evident in the cohesiveness and consistency of the Ninth Edition.

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Lisa Urry (Chapter 1 and Units 1–3) is a professor and developmental biologist and recent Chair of the Biology Department at Mills College. After graduating from Tufts University with a double major in Biology and French, Lisa completed her Ph.D. in molecular and developmental biology at Massachusetts Institute

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Jane B. Reece



The head of the Ninth Edition author team, Jane Reece was Neil Campbell's longtime collaborator. She has participated in every edition of *BIOLOGY*. Earlier, Jane taught biology at Middlesex County College and Queensborough Community College. She holds an A.B. in Biology from Harvard University, an M.S. in Micro-

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Steve Wasserman (Unit 7) is a professor at the University of California, San Diego (UCSD). He earned his A.B. in Biology from Harvard University and his Ph.D. in Biological Sciences from MIT. Through his research on regulatory pathway mechanisms in the fruit fly *Drosophila*, Steve has contributed to the fields of developmen-

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years and just finished a term as the Vice President of Science for the Ecological Society of America. Rob has received numerous awards, including a Presidential Early Career Award in Science and Engineering from the National Science Foundation. He also enjoys popular writing, having published a trade book about the environment, *The Earth Remains Forever*, and two books of poetry for children, *Animal Mischief* and *Weekend Mischief*.

Neil A. Campbell



Neil Campbell combined the investigative nature of a research scientist with the soul of an experienced and caring teacher. He earned his M.A. in Zoology from UCLA and his Ph.D. in Plant Biology from the University of California, Riverside, where he received the Distinguished Alumnus Award in 2001. Neil published numer-

ous research articles on desert and coastal plants and how the sensitive plant (*Mimosa*) and other legumes move their leaves. His 30 years of teaching in diverse environments included general biology courses at Cornell University, Pomona College, and San Bernardino Valley College, where he received the college's first Outstanding Professor Award in 1986. Neil was a visiting scholar in the Department of Botany and Plant Sciences at the University of California, Riverside. In addition to his authorship of this book, he coauthored *Biology: Concepts & Connections* and *Essential Biology* with Jane Reece. For the Ninth Edition of this book, we honor Neil's contributions to biology education by adopting the title *CAMPBELL BIOLOGY*.

Preface

Biology is an enormous subject, one that can seem overwhelming to students and scientists alike. Moreover, discoveries are being made at an unprecedented pace—from new kinds of small RNA molecules to the Neanderthal genome, from new biofuels to communities of organisms thriving beneath vast glaciers, from emerging infectious diseases to cancer vaccines. As a result, a general biology course faces a daunting challenge: to keep students from suffocating under an avalanche of information. *CAMPBELL BIOLOGY* addresses this challenge by providing a strong foundation for understanding both current knowledge and new developments in the context of underlying biological concepts.

Key Concepts and Unifying Themes

In each chapter of this textbook, a framework of three to six carefully chosen **Key Concepts** provide context for supporting details, helping students distinguish the "forest" from the "trees." The numbered Key Concepts are presented at the beginning of the chapter and then serve as headings for each chapter section. *Concept Check Questions* at the end of each section provide a hierarchical framework for self-assessment that builds students' confidence and then challenges them to push the limits of their understanding with several types of critical thinking questions. The *Summary of Key Concepts* at the end of the chapter refocuses students on the main points. *CAMPBELL BIOLOGY* also helps students organize and make sense of what they learn on a grander scale by emphasizing **evolution and other uni-fying themes** that pervade biology. These themes are introduced in Chapter 1 and integrated throughout the book.

New to This Edition: An Emphasis on Making Connections

In addition to Key Concepts and themes, we've created new features for the Ninth Edition that help students see the big picture by *making connections*. These include the following:

New Make Connections Questions: Making connections across chapters

New **Make Connections Questions** help students see how different areas of biology tie together, helping them overcome the tendency to compartmentalize information. Each question challenges students to move beyond memorization and gain a deeper understanding of biological principles by asking them to relate chapter content to material they learned earlier in the course. For example, we ask students to connect

- DNA replication (Chapter 16, see p. 319) to the cell cycle (Chapter 12);
- Soil formation (Chapter 37, see p. 789) to the properties of water (Chapter 3); and
- Aquatic biomes (Chapter 52, see p. 1163) to osmoregulation (Chapter 44).

At least three Make Connections Questions appear in each chapter. In addition, online *Make Connections Tutorials* in MasteringBiology[®] (see p. xi) connect content from two different chapters using figures from the book.

Expanded Evolution Coverage: Making connections to evolution in every chapter

Evolution is the core theme of biology, and in this edition it is more evident than ever. At least one **Evolution section in every chapter** focuses on evolutionary aspects of the chapter material, highlighted by a new Evolution banner. See, for example, the new discussions of enzyme evolution (p. 157), coevolution of flowers and pollinators (p. 806), and evolution of hormone function in animals (pp. 988–989).

New Impact Figures: Making connections between scientific advances and the real world

Our new **Impact Figures** motivate students by highlighting the dramatic impact of recent discoveries in biology. These figures feature high-interest topics such as induced pluripotent stem cells and regenerative medicine (Chapter 20, p. 417), the discovery of *Tiktaalik* (Chapter 34, p. 710), and the use of forensic ecology to track elephant poaching (Chapter 56, p. 1243). The *Why It Matters* section of each figure explains the relevance of the research to students' lives, global problems, or the field of biology itself. Each Impact Figure ends with a suggestion for *Further Reading* and a *What If?* or *Make Connections Question* to develop critical thinking skills.

New Visual Organizers and 3-D Art: Making connections visually

The new **Visual Organizer** format highlights the main parts of a figure, helping students see the key categories at a glance. See, for instance, Figure 17.24 on types of small-scale mutations (p. 345) or Figure 27.3, Gram staining (p. 557). Throughout the book, selected figures have been rendered in a more **3-D art style** while keeping an appropriate balance between realism and teaching effectiveness. Figure 52.3, Exploring Global Climate Patterns (p. 1146), is one example.

Restructured Chapter Reviews: Making connections at a higher level

In the chapter summaries, each concept section now concludes with a new Summary of Key Concepts Question that is tied to a major learning goal. Also, this edition increases student awareness of different levels of thinking by organizing the endof-chapter questions into three levels based on Bloom's taxonomy, which classifies types of thinking that are important in learning. Our levels are (1) Knowledge/Comprehension, (2) Application/Analysis, and (3) Synthesis/Evaluation. (These same levels are used in the Campbell Test Bank.) The range of question types helps students develop critical thinking skills and prepare for the kinds of questions they'll encounter on exams. New Write About a Theme Questions give students practice writing short, coherent essays that connect the chapter's content to one of the book's themes. (A suggested grading rubric can be found on p. xv, and sample answers are provided for instructors in the MasteringBiology Instructor Resources area.) A new MasteringBiology preview section at the end of each chapter lists Assignments-tutorials, activities, and questions that instructors can assign. This section also directs students to the eText and Study Area for online self study.

New Content: Making connections to advances in science

As in each new edition, the Ninth Edition incorporates **new** scientific content and organizational improvements. These are summarized on pp. viii–ix, following this Preface.

MasteringBiology[®]: Making connections outside of class

MasteringBiology, the most widely used online assessment and tutorial program for biology, provides an extensive library of homework assignments that are graded automatically. In addition to BioFlix® Tutorials, other Tutorials, Activities, Reading Quiz Questions in every chapter, and 4,500 Test Bank Questions, MasteringBiology for the Ninth Edition features an **improved user interface** and the following **new Tutorials and Questions**: Make Connections Tutorials, Student Misconceptions Questions for every chapter, Data Analysis Tutorials, Experimental Inquiry Tutorials, Video Tutor Sessions, and MasteringBiology: Virtual Biology Labs. For more information, see pp. xvi–xix and www.masteringbiology.com.

Our Hallmark Features

Besides our Key Concepts and unifying themes, several other features have contributed to the success of *CAMPBELL BIOLOGY*. Because text and illustrations are equally important for learning biology, **integration of figures and text** has been a hallmark of this book since its inception. Our popular *Exploring Figures* on selected topics epitomize this approach:

Each is a learning unit of core content that brings together related illustrations and text. Another example is our *Guided Tour Figures*, which use descriptions in blue type to walk students through complex figures like an instructor would, pointing out key structures, functions, and steps of processes.

To encourage **active learning**, recent editions have incorporated new types of questions: *What If? Questions, Figure Legend Questions*, and *Draw It Questions* that ask students to sketch a structure, annotate a figure, or graph data. In the Ninth Edition, these questions are augmented by the new *Make Connections Questions*. Online, the highly interactive *MasteringBiology tutorials* are sophisticated active-learning tools.

Finally, CAMPBELL BIOLOGY features scientific inquiry, an essential component of any biology course. Complementing stories of scientific discovery in the text narrative and the unitopening interviews, Inquiry Figures help students understand "how we know what we know" and provide a model of how to think like a scientist. Each one begins with a research question and then describes how researchers designed an experiment, interpreted their results, and drew conclusions. The source article is referenced, and a What If? Question asks students to consider an alternative scenario. Selected Inquiry Figures invite students to read and analyze the original research article in the supplement Inquiry in Action: Interpreting Scientific Papers (see p. xxi). At the end of each chapter, Scientific Inquiry Questions give students additional opportunities to practice critical thinking by developing hypotheses, designing experiments, and analyzing real research data. Beyond the book, activities involving scientific inquiry are featured in MasteringBiology and other supplements, both print and electronic (see pp. xviii-xxi).

Our Partnership with Instructors

A core value underlying all our work as authors is our belief in the importance of our partnership with instructors. Our primary way of serving instructors, of course, is providing a textbook, supplements, and media resources that serve their students well. In addition, Benjamin Cummings makes available a rich variety of instructor resources, in both print and electronic form (see p. xx). In our continuing efforts to improve the book and its supplements, we benefit tremendously from instructor feedback, not only in formal reviews from hundreds of scientists, but also via informal communication, often by e-mail.

The real test of any textbook is how well it helps instructors teach and students learn. We welcome comments from the students and instructors who use *CAMPBELL BIOLOGY*. Please address your suggestions to any of us:

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New Content

This section provides just a few highlights of new content and organizational improvements in *CAMPBELL BIOLOGY*, Ninth Edition.

CHAPTER 1 Introduction: Themes in the Study of Life

We have added a separate new theme on energy flow while retaining a theme on environmental interactions. Concept 1.3, on the scientific method, has been reframed to more accurately reflect the scientific process, with a focus on observations and hypotheses. A new Concept 1.4 discusses the value of technology to society while emphasizing the cooperative nature of science and the value of diversity among scientists.

UNIT ONE The Chemistry of Life

For this edition, the basic chemistry is enlivened by new content connecting it to evolution, ecology, and other areas of biology. Examples of new material include omega-3 fatty acids, the isomeric forms of methamphetamine, arsenic contamination of groundwater, and the basis of mad cow disease. The burgeoning importance of nucleic acids throughout biology has prompted us to expand our coverage of DNA and RNA structures in this first unit. In fact, a general aim for the first two units is to infuse the chapters with more detail about nucleic acids, genes, and related topics. Another enhancement, in this and the next two units, is the inclusion of more computer models of important proteins in contexts where they support students' understanding of molecular function.

UNIT TWO The Cell

For Chapter 6, we developed an Exploring Figure on microscopy, which includes new types of microscopy, and we added micrographs of various cell types to the Exploring Figure on eukaryotic cells. We also expanded our description of chromosome composition, with the goal of preempting some common student misconceptions about chromosomes and DNA. New connections to evolution include an introduction to the endosymbiont theory in Chapter 6 and some interesting evolutionary adaptations of cell membranes in Chapter 7. We've added a new section to Chapter 8 on the evolution of enzymes with new functions, which not only strengthens enzyme coverage but also provides an early introduction to the concept that mutations contribute to molecular evolution. In Chapter 9, we simplified the glycolysis figure and emphasized pyruvate oxidation as a separate step to help students focus on the main ideas. In keeping with our increased focus on global issues in the Ninth Edition, Chapter 10 has an Impact Figure on biofuels and a discussion of the possible effect of climate change on the distribution of C_3 and C_4 plants. In Chapter 11, we have added an Impact Figure to highlight the importance and medical relevance of G protein-coupled receptors.

UNIT THREE Genetics

In Chapters 13–17, we have added material to stimulate student interest—for example, a new Impact Figure on genetic testing for disease-associated mutations. As done throughout the Ninth Edition, we ask students to make connections between chapters so that they avoid the trap of compartmentalizing the information in each chapter. For instance, Chapter 15 discusses the Philadelphia chromosome associated with chronic myelogenous leukemia and asks students to connect this information to what they learned about signaling in the cell cycle in Chapter 12. Also, we encourage students to connect what they learn about DNA replication and chromosome structure in Chapter 16 to the material on chromosome behavior during the cell cycle in Chapter 12. Chapter 16 has a new figure showing a current 3-D model of the DNA replication complex, with the lagging strand looping back through it.

Chapters 18-21 are extensively updated, with the changes dominated by new genomic sequence data and discoveries about the regulation of gene expression. (The introduction to genes, genomes, and gene expression in Units One and Two should help prepare students for these revisions.) Chapter 18 includes a new section on nuclear architecture, which describes the organization of chromatin in the nucleus in relation to gene expression. The roles of various types of RNA molecules in regulation also receive special attention. In the section on cancer, we describe how technical advances can contribute to personalized cancer treatments based on the molecular characteristics of an individual's tumor. Chapter 19 discusses the 2009 H1N1 flu pandemic. Chapter 20 includes advances in techniques for DNA sequencing and for obtaining induced pluripotent stem (iPS) cells. Finally, the heavily revised Chapter 21 describes what has been learned from the sequencing of many genomes, including those of a number of human individuals.

UNIT FOUR Mechanisms of Evolution

For this edition, we have continued to bolster our presentation of the vast evidence for evolution by adding new examples and figures that illustrate key conceptual points throughout the unit. For example, Chapter 22 now presents research data on adaptive evolution in soapberry bugs, fossil findings that shed light on the origins of cetaceans, and an Impact Figure on the rise of methicillin-resistant *Staphylococcus aureus*. Chapter 23 examines gene flow and adaptation in songbird populations. Chapter 24 incorporates several new examples of speciation research, including reproductive isolation in mosquitofish, speciation in shrimp, and hybridization of bear species. Other changes strengthen the storyline of the unit, ensuring that the chapters flow smoothly and build to a clear overall picture of what evolution is and how it works. For instance, new connections between Chapters 24 and 25 illustrate how differences in speciation and extinction rates shape the broad patterns in the history of life. We've also added earlier and more discussion of "tree thinking," the interpretation and application of phylogenetic trees, beginning in Chapter 22.

UNIT FIVE The Evolutionary History of Biological Diversity

One of our goals for the diversity unit was to expand the coverage of the scientific evidence underlying the evolutionary story told in the chapters. So, for example, Chapter 27 now presents new findings on the evolutionary origin of bacterial flagella. In keeping with our increased emphasis on big-picture "tree thinking," we've added an "evogram" on tetrapod evolution in Chapter 34. (An evogram is a diagram illustrating the multiple lines of evidence that support the hypothesis shown in an evolutionary tree.) In addition, to help engage students, we've included new applications and woven more ecological information into our discussions of groups of organisms. Examples include new material on global growth of photosynthetic protists (Chapter 28), endangered molluscs (Chapter 33), and the impact of a pathogenic chytrid fungus on amphibian population declines (Chapters 31 and 34).

UNIT SIX Plant Form and Function

Plant biology is in a transitional phase; some professors prefer strong coverage of classical botany while others seek more in-depth coverage of the molecular biology of plants. In developing the Ninth Edition, we have continued to balance the old and the new to provide students with a basic understanding of plant anatomy and function while highlighting dynamic areas of plant research and the many important connections between plants and other organisms. One major revision goal was to provide more explicit discussion of the evolutionary aspects of plant biology, such as the coevolution of flowering plants and pollinators (Chapter 38). Updates include new findings in plant development in Concept 35.5 and new material on the dynamism of plant architecture as it relates to resource acquisition in Chapter 36.

UNIT SEVEN Animal Form and Function

In revising this unit, we strove to introduce physiological systems through a comparative approach that underscores how adaptations are linked to shared physiological challenges. In particular, we have highlighted the interrelationship of the endocrine and nervous systems at multiple points in the unit, helping students appreciate how these two forms of communication link tissues, organs, and individuals. Other revisions aim to keep students focused on fundamental concepts amid the details of complex systems. For example, many figures have been reconceived to emphasize key information, including new figures comparing single and double circulation (Chapter 42) and examining the function of antigen receptors (Chapter 43), as well as new Exploring Figures on the vertebrate kidney (Chapter 44) and the structure and function of the human eye (Chapter 50). Chapter 43 has been significantly revised to support students' conceptual understanding of basic immunological responses and the key cellular players. Throughout the unit, new state-of-the-art images and material on current and compelling topics-such as circadian rhythms (Chapter 40), novel strains of influenza (Chapter 43), the effects of climate change on animal reproductive cycles (Chapter 46), and advances in understanding brain plasticity and function (Chapter 49)-will help engage students and encourage them to make connections beyond the text.

UNIT EIGHT Ecology

Our revision was informed by the fact that biologists are increasingly asked to apply their knowledge to help solve global problems, such as climate change, that already are profoundly affecting life on Earth. As part of our increased emphasis on global ecology in this edition, we have made significant changes to Unit Eight's organization and content. The organizational changes begin with the introductory chapter of the unit (Chapter 52), which includes a new Key Concept 52.1: "Earth's climate varies by latitude and season and is changing rapidly." Introducing the global nature of climate and its effects on life at the beginning of the chapter provides a logical foundation for the rest of the material. New content in Chapters 53 and 54 highlights factors that limit population growth, the ecological importance of disease, positive interactions among organisms, and biodiversity. Chapter 55 now explores restoration ecology together with ecosystem ecology because successful restoration efforts depend on understanding ecosystem structure and function. Finally, the new title of the unit's capstone, Chapter 56, reflects its emphasis on the combined importance of conservation and our changing Earth: "Conservation Biology and Global Change." Several new Impact Figures in the unit show students how ecologists apply biological knowledge and ecological theory at all scales to understand and solve problems in the world around them.

To the Student: How to Use This Book

Focus on the Key Concepts.

Each chapter is organized around a framework of 3 to 6 **Key Concepts** that will help you stay focused on the big picture and give you a context for the supporting details. 52

An Introduction to Ecology and the Biosphere



Before you begin reading the chapter, get oriented by reading the **list of Key Concepts**, which introduces the big ideas covered in the chapter.

> Each **Key Concept** serves as the heading for a major section of the chapter.

▲ Figure 52.1 What threatens this amphibian's survival?

KEY CONCEPTS

- 52.1 Earth's climate varies by latitude and season and is changing rapidly
- 52.2 The structure and distribution of terrestrial biomes are controlled by climate and disturbance
- 52.3 Aquatic biomes are diverse and dynamic systems that cover most of Earth 52.4 Interactions between organisms and the
- and the environment limit the distribution of species

OVERVIEW

Discovering Ecology

When University of Delaware undergraduate Justin Yeager spent his summer abroad in Costa Rica, all he wanted was to see the tropical rain forest and to practice his Spanish. Instead, he rediscovered the variable harlequin toad (*Atelopus varius*), a species thought to be extinct in the mountain slopes of Costa

After reading a concept section, check your ► understanding using the **Concept Check Questions** at the end of the section. Work through these questions on your own or in a study group—they're good practice for the kinds of questions you might be asked on an exam.

What If? Questions ask you to apply what you've learned. New Make Connections Questions ask you to relate content in the chapter to a concept you learned earlier in the course.

If you can answer these questions (see Appendix A to check your work), you're ready to move on.

Rica and Panama where it once lived (Figure 52.1). During the 1980s and 1990s, roughly two-thirds of the 82 known species of harlequin toads vanished. Scientists think that a diseasecausing chytrid fungus, *Batrachochytrium dendrobatidis* (see Figure 31.26), contributed to many of these extinctions. Why was the fungus suddenly thriving in the rain forest? Cloudier days and warmer nights associated with global warming appear to have created an environment ideal for its success. As of 2009, the species that Yeager found was surviving as a single known population of fewer than 100 individuals.

What environmental factors limit the geographic distribution of harlequin toads? How do variations in their food supply or interactions with other species, such as pathogens, affect the size of their population? Questions like these are the subject of **ecology** (from the Greek *oikos*, home, and *lagos*, study), the scientific study of the interactions between organisms and the environment. Ecological interactions occur at a hierarchy of scales that ecologists study, from single organisms to the globe (Figure 52.2).

Ecology's roots are in our basic human interest in observing other organisms. Naturalists, including Aristotle and Darwin, have long studied the living world and systematically recorded their observations. However, modern ecology involves more than observation. It is a rigorous experimental science that requires a breadth of biological knowledge. Ecologists generate hypotheses, manipulate environmental variables, and observe the outcome. In this unit, you will encounter many examples of ecological experiments, whose complex challenges have made ecologists innovators in experimental design and statistical inference.

In addition to providing a conceptual framework for understanding the field of ecology, Figure 5.2. provides the organizational framework for our final unit. In this chapter, we first describe Earth's climate and the importance of climate and other physical factors in determining the location of major life zones on land and in the oceans. We then examine how ecologists determine what controls the distribution and abundance of individual species. The next three chapters investigate population, community, and ecosystem ecology in detail, including approaches for restoring degraded ecosystems. The final chapter explores conservation biology and global ecology as we consider how ecologists apply biological knowledge to predict the global consequences of human activities and to conserve Earth's biodiversity.

CONCEPT 52.1

Earth's climate varies by latitude and season and is changing rapidly

The most significant influence on the distribution of organisms on land and in the oceans is **climate**, the long-term, prevailing weather conditions in a given area. Four physical

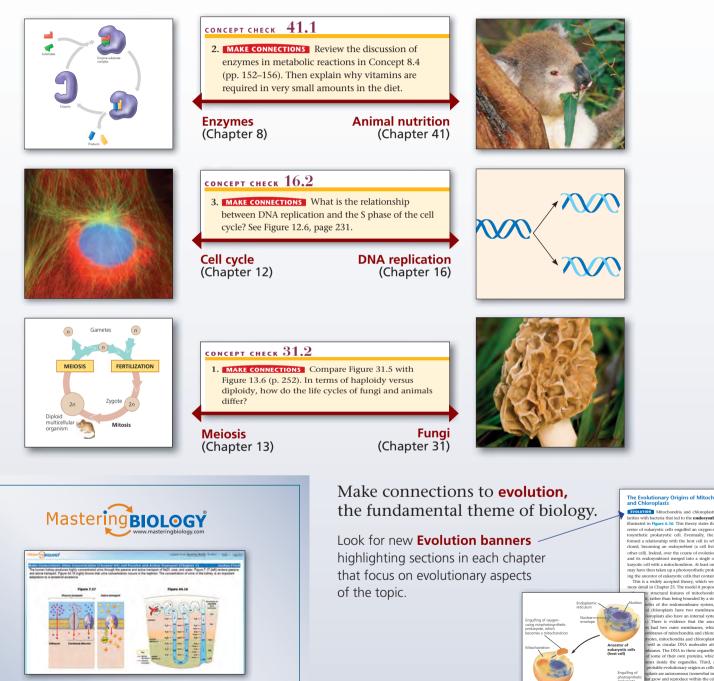
CONCEPT CHECK 52.1

- Explain how the sun's unequal heating of Earth's surface leads to the development of deserts around 30° north and south of the equator.
- 2. What are some of the differences in microclimate between an unplanted agricultural field and a nearby stream corridor with trees?
- 3. WHAT IF? Changes in Earth's climate at the end of the last ice age happened gradually, taking centuries to thousands of years. If the current global warming happens very quickly, as predicted, how may this rapid climate change affect the ability of long-lived trees to evolve, compared with annual plants, which have much shorter generation times?
- 4. MAKE CONNECTIONS In Concept 10.4 (pp. 199–201), you learned about the important differences between C₃ and C₄ plants. Focusing just on the effects of temperature, would you expect the global distribution of C₄ plants to expand or contract as Earth becomes warmer? Why?

For suggested answers, see Appendix A

Make connections across biology.

By relating the content of a chapter to material you learned earlier in the course, new **Make Connections Questions** help you develop a deeper understanding of biological principles.



New **Make Connections Tutorials** help you connect biological concepts across chapters in an interactive way.

To the Student: How to Use This Book **xi**

Practice thinking like a scientist.

New Impact Figures demonstrate the

dramatic impact of recent discoveries in biology and show that biology is constantly changing as new discoveries add to our understanding.

Inquiry Figures reveal "how we know what we know" by highlighting how researchers designed an experiment, interpreted their results, and drew conclusions.

INQUIRY

▼ Figure 37.14

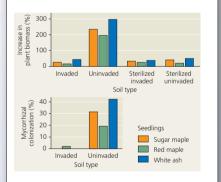
Does the invasive weed garlic mustard disrupt mutualistic associations between native tree seedlings and arbuscular mycorrhizal fungi?

EXPERIMENT Kristina Stinson, of Harvard University, and colleagues investigated the ef-fect of invasive garlic mustard on the growth of native tree seedlings and associated mycorrhizal fungi. In one experiment, they grew seedlings of three North American trees-sugar maple, red maple, and white ash—in four different soils. Two of the soil samples were collected from a location where garlic mustard was growing, and one of these samples was sterilized. The other two soil samples were collected from a location devoid of gar-lic mustard, and one was then sterilized. After four months of growth, the researchers harvested the shoots and



roots and determined the dried biomass. The roots were also analyzed for percent colonization by arbuscular mycorrhizal fungi

RESULTS Native tree seedlings grew more slowly and were less able to form mycorrhizal associations when grown either in sterilized soil or in unsterilized soil collected from a location that had been invaded by garlic mustard



suppresses growth of native trees by affecting the soil in a way that dis-rupts mutualistic associations between the trees and arbuscular mycor-rhizal fungi. CONCLUSION The data support the hypothesis that garlic mustard

SOURCE K. A. Stinson et al., Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mu (Public Library of Science: Biology) 4(5): e140 (2006) ind mutualisms, PLoS Biol

INQUIRY IN ACTION Read and analyze the original paper in Inquiry in Action: Interpreting Scientific Papers

WHAT IF? What effect would applying inorganic phosphate to soil invaded by garlic mustard have on the plant's ability to outcompete native species?

After exploring the featured experiment, test your analytical skills by answering the What If? Question. Suggested answers are provided in Appendix A to help you gauge your understanding.

- Why It Matters explains the > relevance of the research.
- Further Reading directs you > to articles to explore.

A Make Connections or What If? Question encourages critical thinking.

▼ Figure 56.9 IMPACT

Forensic Ecology and Elephant Poaching



his array of severed tusks is part of an illegal shipment of 6,000 kg of ivory intercepted on its way from Africa to Singapore in 2002. Investigators wondered whether the elephants slaughtered for the ivory-perhaps as many as 6,500-were killed in the area where the shipment originated, primarily Zambia, or instead were killed across Africa, indicating a broader smuggling ring. Samuel Wasser, of the University of Washington, and colleagues amplified specific segments of DNA from the tusks using the polymerase chain reaction (PCR). These segments included stretches of DNA containing short tandem repeats (STRs; see Concept 20.4, pp. 420-421), the number of which varies among different elephant populations. The researchers then compared alleles at seven or more loci with a reference DNA database they had generated for elephants of known geographic origin. Their results showed conclusively that the elephants came from a narroy east-west band centered on Zambia rather than from across Africa

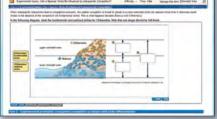
WHY IT MATTERS The DNA analyses suggested that poaching rates were 30 times higher in Zambia than previously estimated. This news led to improved antipoaching efforts by the Zambian government. Techniques like those used in this study are being employed by conservation biologists to track the harvesting of many endangered species, including whales, sharks, and orchids

- FURTHER READING S. K. Wasser et al., Forensic tools battle ivorv poachers, Scientific American 399:68-76 (2009); S. K. Wasser et al., Using DNA to track the origin of the largest ivory seizure since the 1989 trade ban, Proceedings of the National Academy of Sciences USA 104:4228-4233 (2007)
- MAKE CONNECTIONS Figure 26.6 (p. 539) describes another example in which conservation biologists used DNA analyses to compare harvested samples with a reference DNA database. How are these examples similar, and how are they different? What limitations might there be to using such forensic methods in other suspected cases of poaching?

Some Inquiry Figures invite you to read and analyze the original research paper in its complete form. You can find the journal article, along with a worksheet guiding you through it, in the separate book Inquiry

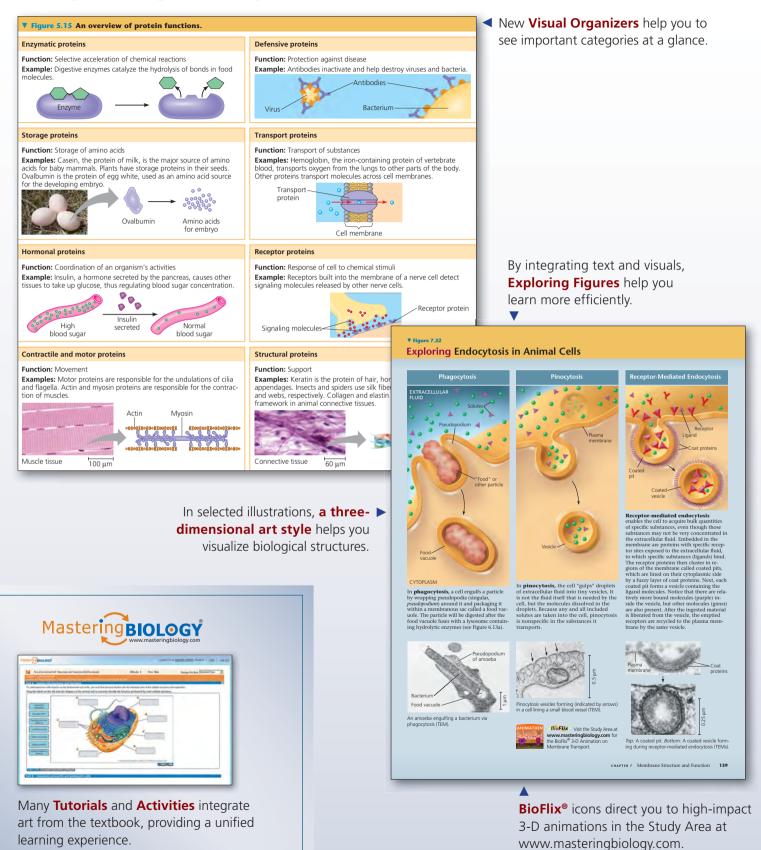
in Action: Interpreting Scientific Papers.





New Experimental Inquiry Tutorials give you practice analyzing experimental design and data and drawing conclusions.

Study the figures as you read the text.



Review what you've learned.

Chapter Reviews help you efficiently master the chapter content by focusing on the main points of the chapter and offering opportunities to practice for exams.

The Evolution of Populations 23.1 Is this finch ev EVOLUTION KEY CONCEPTS 23.1 Genetic variation makes evolution possible 23.2 The Hardy-Weinberg equation can be used to test whether a population is evolving 23.3 Natural selection, genetic drift, and gene flow can alter allele frequencies in a population 23.4 Natural selection is the only mechanism that consistently causes adaptive evolution OVERVIEW The Smallest Unit of Evolution One common misconception about evolution is that individual organisms evolve. It is true that natural selection acts on individuals: Each organism's traits affect its survival and reproductive success compared with other individuals. But the evolutionary impact of natural selection is only appar ent in the changes in a population of organisms over tim

Key Concepts, which were

introduced in the beginning of the chapter and developed in the text, are summarized in the Chapter Review.

New Summary of Key Concepts

Questions appear at the end of each concept summary. Check your answers using Appendix A.

23 chapter review

SUMMARY OF KEY CONCEPTS

CONCEPT 23.1

- Genetic variation makes evolution possible (pp. 469-473) Genetic variation refers to genetic differences among indi-
- viduals within a population. The nucleotide differences that provide the basis of genetic variation arise by mutation and other processes that produce
- new alleles and new genes. New genetic variants are produced rapidly in organisms with short generation times. In sexually reproducing organisms, most of the genetic differences among individuals result from crossing over, the independent assortment of chromosomes, and fertilization.
- ? Why do biologists estimate gene variability and nucleotide vari-ability, and what do these estimates represent?

CONCEPT 23.2

The Hardy-Weinberg equation can be used to test whether a population is evolving (pp. 473–476)

- A population, a localized group of organisms belonging to one species, is united by its **gene pool**, the aggregate of all the alleles in the population.
- The **Hardy-Weinberg principle** states that the allele and genotype frequencies of a population will remain constant if the population is large, mating is random, mutation is negligible, there is no gene flow, and there is no natural selection. For such a population, if p and q represent the frequencies of the only two possible alleles at a particular locus, then p^2 is the frequency of one kind of homozygote, q^2 is the frequency of the other kind of homozygote, and 2pq is the frequency of the heterozygous genotype.
- Is it circular reasoning to calculate p and q from observed geno-type frequencies and then use those values of p and q to test if the population is in Hardy-Weinberg equilibrium? Explain your answer. (Hint: Consider a specific case, such as a population with 195 individuals of genotype AA, 10 of genotype Aa, and 195 of genotype aa.)

CONCEPT 23.3

Natural selection, genetic drift, and gene flow can alter allele frequencies in a population (pp. 476–480)

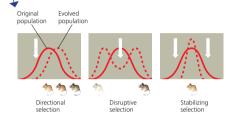
- In natural selection, individuals that have certain inherited traits tend to survive and reproduce at higher rates than other individuals *because of* those traits.
 In genetic drift, chance fluctuations in allele frequencies over
- generations tend to reduce genetic variation. • Gene flow, the transfer of alleles between populations, tends
- to reduce genetic differences between populations over time
- ? Would two small, geographically isolated populations in very dif-ferent environments be likely to evolve in similar ways? Explain.

CONCEPT 23.4

- Natural selection is the only mechanism that consistently causes adaptive evolution (pp. 480–485)
- · One organism has greater relative fitness than a second organism if it leaves more fertile descendants than the second
- UNIT FOUR Mechanisms of Evolution

organism. The modes of natural selection differ in how selection acts on phenotype (the white arrows in the summary diagram below represent selective pressure on a population).

Summary Figures present key information in a visual way.



- · Unlike genetic drift and gene flow, natural selection consistently increases the frequencies of alleles that enhance survival and reproduction, thus improving the match between organisms and their environment.
- Sexual selection influences evolutionary change in secondary sex characteristics that can give individuals advantages in
- mating.Despite the winnowing effects of selection, populations have considerable genetic variation. Some of this variation represents **neutral variation**; additional variation can be maintained by diploidy and balancing selection.
- There are constraints to evolution: Natural selection can act only on available variation; structures result from modified ancestral anatomy; adaptations are often compromises; and chance, natural selection, and the environment interact.
- **?** How might secondary sex characteristics differ between males and females in a species in which females compete for mates?

TEST YOUR UNDERSTANDING

LEVEL 1: KNOWLEDGE/COMPREHENSION

- 1. Natural selection changes allele frequencies because some _______ survive and reproduce more successfully than others. a. alleles c. gene pools e. individuals b. loci d. species
- 2. No two people are genetically identical, except for identical twins. The main source of genetic variation among human individuals is
 - new mutations that occurred in the preceding generation. b. genetic drift due to the small size of the population
 c. the reshuffling of alleles in sexual reproduction.
- d. geographic variation within the population.
 e. environmental effects.
- 3. Sparrows with average-sized wings survive severe storms better than those with longer or shorter wings, illustrating a. the bottleneck effect.
- b. disruptive selection
- c. frequency-dependent selection.
- d. neutral variation
- e. stabilizing selection

To help you prepare for the various kinds of questions that may appear on a test, the end-of-chapter questions are now organized into three levels based on Bloom's Taxonomy:

Level 1: Knowledge/Comprehension Level 2: Application/Analysis Level 3: Synthesis/Evaluation

Evolution Connection

Ouestions in the Chapter Review ask you to think critically about how an aspect of the chapter relates to evolution. ►

Scientific Inquiry

Questions at the end of each chapter give you opportunities to practice scientific thinking by developing hypotheses, designing experiments, and analyzing real research data.

Draw It Exercises in

each chapter ask you to put pencil to paper and draw a structure, annotate a figure, or graph experimental data.

4

3

2

1

0

Essay shows no

understanding of theme

FVEL 2: APPLICATION/ANALYSIS

- LEVEL 2: APPLICATION, ANALYSIS
 4. If the nucleotide variability of a locus equals 0%, what is the gene variability and number of alleles at that locus?
 a. gene variability = 0%; number of alleles = 0
 b. gene variability = 0%; number of alleles = 1
 c. gene variability = 0%; number of alleles = 1
 c. gene variability = 0%; number of alleles = 2
 d. gene variability = 0%; number of alleles = 2
 d. gene variability = 0%; number of alleles = 2
 e. Without more information, gene variability and number of alleles = 1

- ancies cannot be determined. There are 40 individuals in population 1, all with genotype A1A1, and there are 25 individuals in population 2, all with genotype A2A2. Assume that these populations are located far from each other and that their environmental conditions are very similar. Based on the information given here, the ob-
- served genetic variation is most likely an example of a. genetic drift. d. discrete variatio d. discrete variation e. directional selection.
- b. gene flow.
 c. disruptive selection.
- A fruit fly population has a gene with two alleles, *AI* and *A2*. Tests show that 70% of the gametes produced in the population contain the *AI* allele. If the population is in Hardy-Weinberg equilibrium, what proportion of the flies carry both *AI* and *A2*?
 a. 0.7 b. 0.49 c. 0.21 d. 0.42 e. 0.09

LEVEL 3: SYNTHESIS/EVALUATION

7 EVOLUTION CONNECTION How is the process of evolution revealed by the imperfections of living organisms?

8. SCIENTIFIC INQUIRY DRAW IT Richard Koehn, of the State University of New York, Stony Brook, and Thomas Hilbish, of the University of outh Carolina, studied genetic variation in the marine mus sel Mytilus edulis around Long Island, New York. They mea sured the frequency of a particular allele (lap^{94}) for an enzyme involved in regulating the mussel's internal saltwater balance. The researchers presented their data as a series of pie charts linked to sampling sites within Long Island Sound, where salinity is highly variable, and along the coast of the open where the cean where salinity is constant

(1-8 represent pairs of sites) Sampling sites (1–8 represent Allele frequencies lap⁹⁴ alleles Other *lap* alleles Data from R. K. Koehn and T. J. Hilbish, The adaptive Salinity increases toward the open ocea Atlantic

(Question & continued)

uestion 8, continued) Create a data table for the 11 sampling sites by estimating the frequency of lap⁰⁴ from the pic charts. (*Hint*: Think of each pic chart as a clock face to help you estimate the proportion of the shaded area.) Then graph the frequencies for sites 1–8 to show how the frequency of this allele changes with increas-ing salinity in Iong Island Sound (from southwest to north-east). How do the data from sites 9–11 compare with the data from the sites within the Sound? Construct a hypothesis that explains the patterns you ob-serve in the data and that accounts for the following observa-tions: (1) the lap⁸⁴ allele helps mussels maintain osmotic balance in water with a high salt concentration but is costly to use in less salty water; and C2 mussels produce larvae that can disperse long distances before they settle on rocks and grow into adults.

grow into adults

WRITE ABOUT A THEME

Emergent Properties: Heterozygotes at the sickle-cell locus produce both normal and abnormal (sickle-cell) hemoglo-bin (see Concept 14.4). When hemoglobin molecules are packed into a heterozygote's red blood cells, some cells repacket into a netrozygore's red mode tens, some cens re-ceive relatively large quantities of abnormal hemoglobin, making these cells prone to sickling. In a short essay (ap-proximately 100–1500 words), explain how these molecular and cellular events lead to emergent properties at the indi-vidual and population levels of biological organization.

For selected answers, see Appendix A

MasteringBIOLOGY www.masteringbiology.com 1. MasteringBiology® Assignments 1. Wastering boody Assignments Make Connections Tutorial Hardy-Weinberg Principle (Chapter 23) and Inheritance of Alleles (Chapter 14) Experimental Inquiry Tutorial Did Natural Selection of Ground Finches Occur When the Environment Changed?

Finches Occur When the Environment Changed? BioFlips' Tutorial Mechanisms of Evolution Tutorial Hardy-Weinberg Principle Activities Cenetic Variation from Sexual Recombination • The Hardy-Weinberg Principle • Causes of Evolutionary Change • Three Modes of Natural Selection Questions Student Misconceptions • Reading Quiz • Multiple Choice • End-of-Chapter

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CHAPTER 23 The Evolution of Populations

errors detract from essay

Essay is very poorly

written

487

New Write About a **Theme Questions**

give you practice writing a short essay that connects the chapter's content to one of the bookwide themes introduced in Chapter 1.

 Each chapter now ends with a preview of the **MasteringBiology®** resources that can help you succeed in the course.

Use of Supporting Understanding of Theme Appropriate Use and Relationship to Topic Examples or Details of Terminology Quality of Writing Evidence of full and Examples well chosen, Excellent organization, Accurate scientific complete understanding terminology enhances sentence structure, details accurate and applied to theme the essav and grammar Examples or details are Terminology is Evidence of good Good sentence flow. understanding generally well applied correctly used sentence structure, to theme and grammar Evidence of a basic Supporting examples Terminology used is Some organizational and understanding and details are adequate not totally accurate grammatical problems or appropriate Evidence of limited Examples and details Poorly organized. Appropriate understanding are minimal terminology is Grammatical and spelling

Examples lacking

or incorrect

not present

or incorrect

Terminology lacking

Suggested Grading Rubric for "Write About a Theme" Short-Answer Essays

This Writing Rubric explains criteria on which your writing may be graded. The rubric and tips for writing good short-answer essays can be found in the Study Area at

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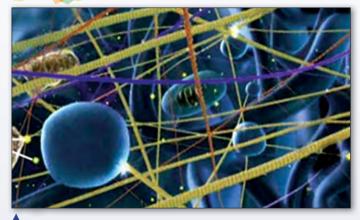
To the Student: How to Effectively



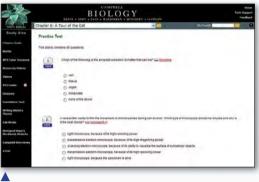
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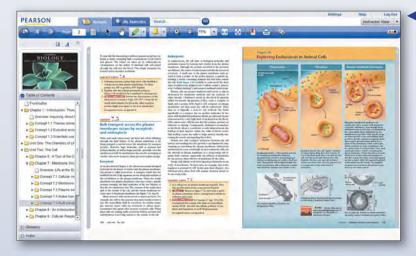


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Chapter 6 Chapter 6 Chapter 9 Chapter 10	Chapter 18 Chapter 18 Chapter 19 Chapter 20	Chapter 28 Chapter 29 Chapter 30	Chapter 38 Chapter 38 Chapter 39 Chapter 40	Chapter 48 Chapter 49 Chapter 50	
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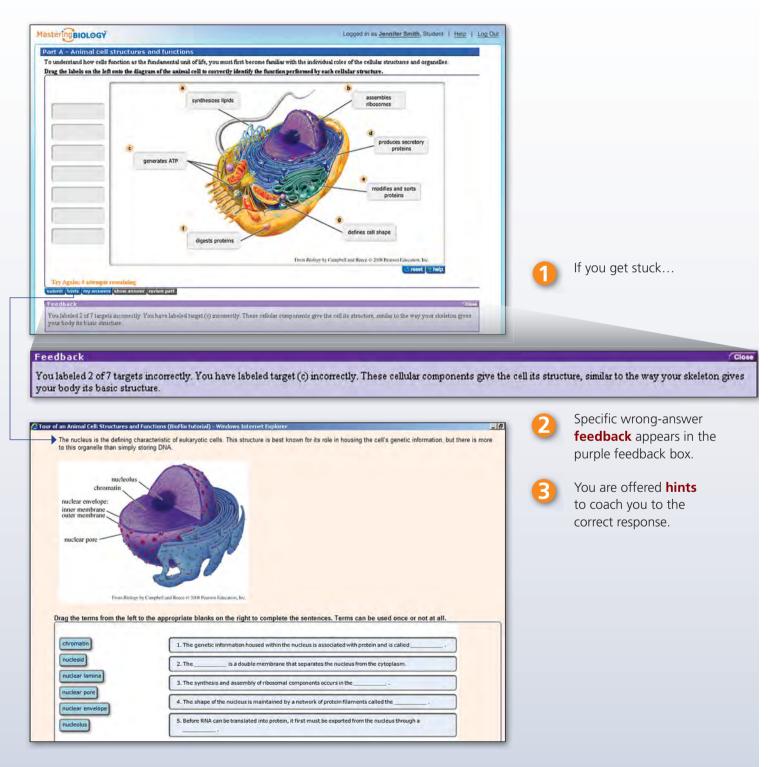
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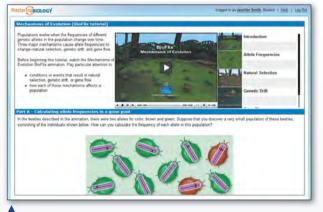


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Patel Index	1	101	104	14.14	10.5	37.7	100	96.2	100	19.2	100	19.0	72.0	17.2	843		16.3
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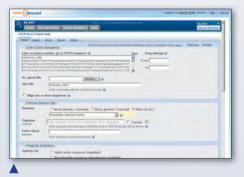




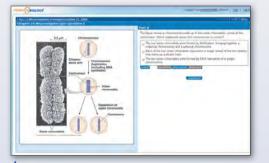
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- Homeostasis: Regulating Blood Sugar
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- Population Ecology
- The Carbon Cycle

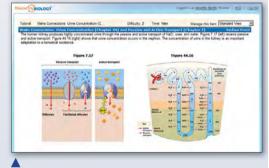


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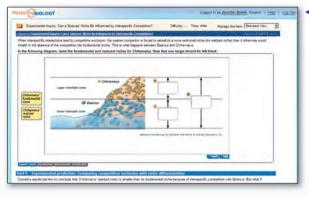
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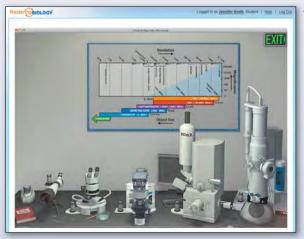


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- Does DNA Replication Follow the Conservative, Semiconservative, or Dispersive Model?
- Did Natural Selection of Ground Finches Occur When the Environment Changed?
- What Effect Does Auxin Have on Coleoptile Growth?
- What Role Do Genes Play in Appetite Regulation?
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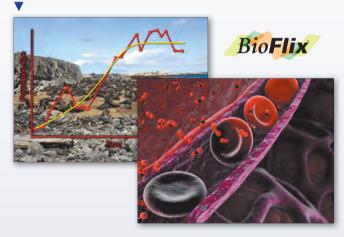
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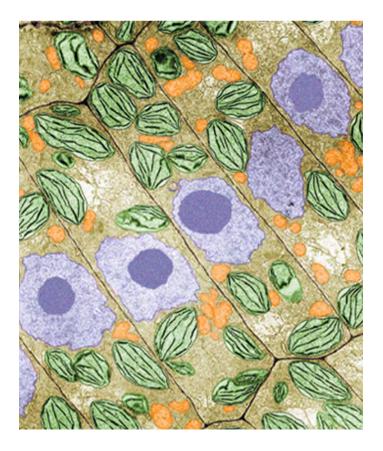
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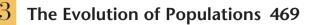
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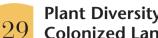
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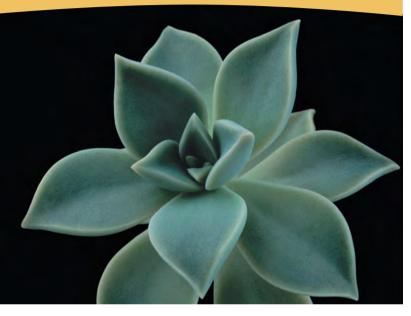
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Introduction: Themes in the Study of Life



▲ Figure 1.1 How is the mother-of-pearl plant adapted to its environment?

KEY CONCEPTS

- **1.1** The themes of this book make connections across different areas of biology
- **1.2** The Core Theme: Evolution accounts for the unity and diversity of life
- **1.3** In studying nature, scientists make observations and then form and test hypotheses
- **1.4** Science benefits from a cooperative approach and diverse viewpoints

OVERVIEW

Inquiring About Life

he mother-of-pearl plant, or ghost plant (**Figure 1.1** and cover), is native to a single mountain in northeastern Mexico. Its fleshy, succulent leaves and other features allow this plant to store and conserve water. Even when rain falls, the plant's access to water is limited because it grows in crevices of vertical rock walls, where little soil is present to hold rainwater (Figure 1.2). The plant's water-conserving characteristics help it survive and thrive in these nooks and crannies. Similar features are found in many plants that live in dry environments, allowing them to eke out a living where rain is unpredictable.

An organism's adaptations to its environment, such as adaptations for conserving water, are the result of **evolution**, the process of change that has transformed life on Earth from its earliest beginnings to the diversity of organisms living today. Evolution is the fundamental organizing principle of biology and the core theme of this book.

Although biologists know a great deal about life on Earth, many mysteries remain. For instance, what exactly led to the origin of flowering among plants such as the one pictured here? Posing questions about the living world and seeking science-based answers—scientific inquiry—are the central activities of **biology**, the scientific study of life. Biologists' questions can be ambitious. They may ask how a single tiny cell becomes a tree or a dog, how the human mind works, or how the different forms of life in a forest interact. Most people wonder about the organisms living around them, and many interesting questions probably occur to you when you are out-of-doors, surrounded by the natural world. When they do, you are already thinking like a biologist. More than anything else, biology is a quest, an ongoing inquiry about the nature of life.

What is life? Even a small child realizes that a dog or a plant is alive, while a rock or a lawn mower is not. Yet the phenomenon we call life defies a simple, one-sentence definition. We recognize life by what living things do. **Figure 1.3**, on the next page, highlights some of the properties and processes we associate with life.

While limited to a handful of images, Figure 1.3 reminds us that the living world is wondrously varied. How do biologists



▲ Figure 1.2 The mother-of-pearl plant (*Graptopetalum paraguayense*). This plant's thick leaves hold water, enabling it to live where soil is scarce. The leaves vary in color, as seen here.

 Order. This close-up of a sunflower illustrates the highly ordered structure that characterizes life.





Evolutionary adaptation. The appearance of this pygmy sea horse camouflages the animal in its environment. Such adaptations evolve over many generations by the reproductive success of those individuals with heritable traits that are best suited to their environments.

Response to the environment. This Venus flytrap closed its trap rapidly in response to the environmental stimulus of a damselfly landing on the open trap.





▲ **Regulation.** The regulation of blood flow through the blood vessels of this jackrabbit's ears helps maintain a constant body temperature by adjusting heat exchange with the surrounding air.

▲ Figure 1.3 Some properties of life.



Energy processing. This

hummingbird obtains fuel

in the form of nectar from

flowers. The hummingbird

stored in its food to power

will use chemical energy

flight and other work.

Reproduction. Organisms (living things) reproduce their own kind. Here, a baby giraffe stands close to its mother.



Growth and development. Inherited information carried by genes controls the pattern of growth and development of organisms, such as this Nile crocodile.

make sense of this diversity and complexity? This opening chapter sets up a framework for answering this question. The first part of the chapter provides a panoramic view of the biological "landscape," organized around some unifying themes. We then focus on biology's core theme, evolution, with an introduction to the reasoning that led Charles Darwin to his explanatory theory. Next, we look at scientific inquiry—how scientists raise and attempt to answer questions about the natural world. Finally, we address the culture of science and its effects on society.

CONCEPT 1.1

The themes of this book make connections across different areas of biology

Biology is a subject of enormous scope, and news reports reveal exciting new biological discoveries being made every day. Simply memorizing the factual details of this huge subject is most likely not the best way to develop a coherent view of