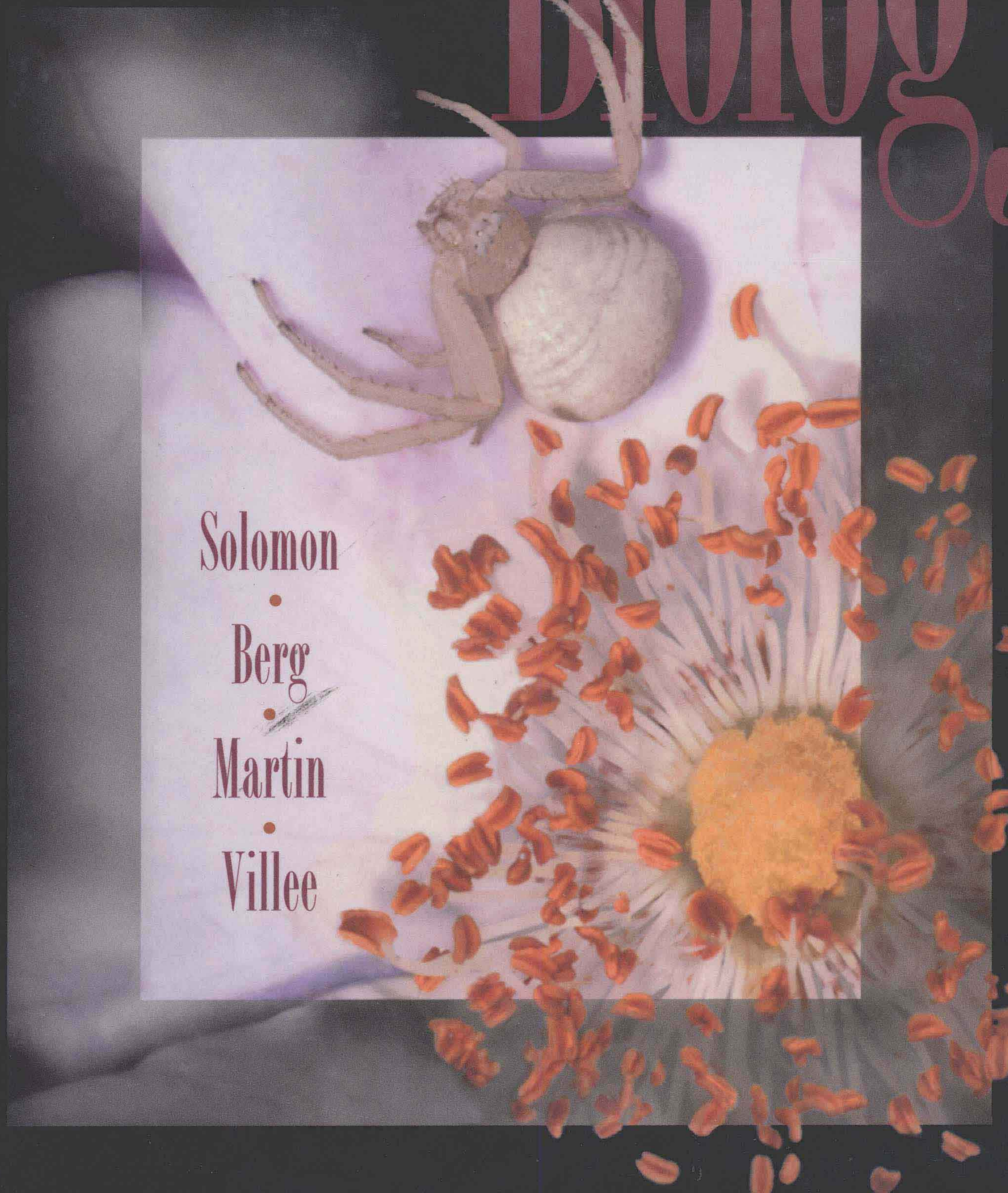
# Biology

FOURTH EDITION



Solomon • Berg • Martin • Villee

# Biology

FOURTH EDITION

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To our families, friends, and colleagues
who gave freely of their love, support, knowledge, and time
as we labored over this revision of BIOLOGY . . .

Especially, to . . .

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## ABOUT THE COVER

A flower spider (*Misumena vatia*) blends into the white petals of a rose (*Rosa rugosa*) as it waits to ambush unwary insects that visit the flower. The camouflage of the flower spider, which is white or yellow depending on the color of the flower on which it hides, enables it to catch insect prey more effectively. The requirement that certain animals consume other animals in order to survive has resulted in the evolution of very efficient ways to catch prey.

# Preface

As we enter the 21st century, we reflect on the important contributions of the biological sciences to modern society. As biologists have studied life, we have gained greater understanding of human life processes and have become more aware of our interdependence with the vast diversity of organisms with which we share our planet. With new advances in biological research, our lives have become healthier, safer, more comfortable, and also more challenging.

One of our principal goals in developing *Biology,* fourth edition, has been to share with beginning biology students our sense of excitement about the biological sciences. We want students to understand and appreciate the diverse organisms on Earth, their remarkable adaptations to the environment, and their evolutionary and ecological relationships. Special emphasis is placed on the basic unity of life and the fundamental similarities of the challenges that have been faced and solved by all living organisms. We are very aware of our responsibility to impress upon our readers our interdependence with the many life forms with which we share planet Earth.

## Important Features of the Fourth Edition

The evolution of *Biology* through its editions reflects the advances in the biological sciences and in biological education. Every effort has been made to update its content and pedagogy so that this book accurately presents modern biology.

### Student Focus Groups

A significant effort was made in the preparation of this edition to speak directly to students and determine how they use the text and what might be done to enhance its efficacy in teaching biology. To that end, student focus groups were conducted at a number of colleges and universities to gauge how students felt we could improve the utility of the text, artwork, and pedagogy. Students at Delaware County Community College, Montgomery County Community College, Ohio University, Orange Coast Community College, and the University of Delaware met with our editors and told them how they study, which pedagogical elements are most helpful, and which pieces of art are effective in helping them learn the subject matter.

Our student focus group participants told us that illustrations paired with electron micrographs are a very effective visual teaching aid, so we've added more to this edition. They told us that the energy chapters represent some of the most challenging topics for them to comprehend. In response, we made revision of the energy chapters a priority, and applied a step by step approach to build the key concepts of energy transfer through living systems. Students suggested that a key terminology list would help them focus on the important terms they must know. A **Selected Key Terms** list is now featured in every chapter.

Additionally, focus group participants told us that analogies linking the biology presented in the text to real-life examples help them synthesize difficult material. Thus an effort was made to increase such analogies throughout the text. Finally, students were concerned about the depth and quality of the glossary. The glossary has been completely revised and expanded in this edition. Overall, our student focus groups were a key factor in determining how we revised the fourth edition, and we thank the students who participated for their thoughtful suggestions.

### Themes

Throughout the book, we emphasize three basic themes of biology — transmission of information, evolution of life, and flow of energy through living systems. As we introduce the concepts of modern biology, we explain how these three themes are connected and how life depends upon them. In this new edition, we also emphasize the process of science and the role of the many scientists who have contributed to our current understanding of biology.

### The Author Team

Rapid advances in the biological sciences require a multi-author team who specialize in particular areas of biology. The author team of the fourth edition includes Dr. Eldra Solomon, zoologist and physiologist; botanist Dr. Linda Berg; and cell biologist/geneticist, Dr. Diana Martin. We also acknowledge the legacy of Dr. Claude A. Villee, Professor Emeritus, Harvard University, who contributed to previous editions. All of the authors are experienced college biology teachers.

### Tools for Learning

Learning the principles of biology is a challenging endeavor. A variety of learning aids are included within the textbook to help the student achieve mastery of the concepts presented.

1. **Learning Objectives** at the beginning of each chapter indicate what the student must be able to do in order to demonstrate mastery of the material in the chapter.
2. **Concept-statement heads** introduce each section, previewing and summarizing the key idea that will be discussed in that section.
3. **Making the Connection boxes** and **Focus boxes** facilitate integration of concepts and spark interest. For example, in Chapter 12, Making the Connection: "Split Genes and Evolution" relates the discussion of interrupted coding sequences in DNA to the evolution of eukaryotes. This box emphasizes the scientific process.
4. **On the Cutting Edge boxes** present exciting research areas that are currently being explored.
5. **Career Visions** present a variety of professional possibilities in the biological sciences for students to explore. An interview with a professional who majored in biology is presented in each part of the book. Those interviewed discuss how they decided on and prepared for their career, and what they do professionally. Careers new to the fourth edition include science journalism and bioremediation specialist.
6. Numerous **tables,** many of them illustrated, summarize and organize material presented in the text.
7. Carefully rendered **illustrations,** many of them new in this edition, support concepts covered in the text. Many of the illustrations are sequential, with close-ups "exploded" to reveal greater detail. Composite pieces of line art and photographs help students interpret electron micrographs. **Scale bars** accompany micrographs to provide information regarding magnification.
8. **Sequence Summaries** review sequential material discussed in the text.
9. **Boldface terms** facilitate identification of key terms and their definitions and also provide emphasis.
10. A **Chapter Summary** in outline form at the end of each chapter provides a review of the material presented.
11. **Selected Key Terms** at the end of each chapter provides the student with an alphabetical list of many of the important terms defined in the chapter.
12. A **Post Test,** which tests knowledge of the Key Terms, provides the opportunity to evaluate mastery of the material within the chapter; answers are provided in an Appendix.
13. **Review questions** test knowledge of important concepts and applications. They are designed to help students test their mastery of the chapter learning objectives.
14. Many **You Make the Connection** questions challenge the student to relevant principles in other chapters. Others require the student to apply concepts to new situations. These questions can be used for class discussions or essay assignments.
15. A list of **Recommended Readings** at the end of each chapter provides references for further learning.
16. A separate **Glossary,** completely revised and expanded for the fourth edition, facilitates rapid definition of terms.
17. **Appendices** provide help in understanding biological terms, measurement, career information, and biological classification.

## THE ORGANIZATION OF *BIOLOGY,* FOURTH EDITION

Educators present the major topics of an introductory biology course in a variety of orders. A lack of consensus regarding sequence of topics is understandable, because reasonable arguments can be advanced for each of the many possible combinations and permutations. All aspects of biology are intimately related, and each could be grasped much more readily if all other topics had been mastered previously. Because this feat cannot be accomplished, each instructor must select the topic sequence that seems most reasonable. For this reason, we have carefully designed each of the eight parts so that they do not depend heavily on preceding chapters and parts. The eight parts and their chapters can be presented in any number of sequences with pedagogic success.

## PART 1: THE ORGANIZATION OF LIFE

Chapter 1, *A View of Life: Basic Concepts of Biology* introduces several major concepts of biology, including the fundamental similarities of all living things; the organization of life on individual and ecological levels; the transfer of information; the evolution of life on our planet; the diversity of life and how biologists classify organisms; energy transfer among organisms; and how science works. Chapters 2 and 3 focus on the molecular level of organization and lay the foundations in chemistry needed for an understanding of biological processes. Chapters 4 and 5 focus on the cellular level of organization, with emphasis on recent advances in cell biology.

## PART 2: THE ENERGY OF LIFE

Part 2, which focuses on the metabolism and energy transactions involved in life processes, has been thoroughly revised for the fourth edition. Chapter 6 introduces energy in cells and organisms. Chapters 7 and 8 discuss the metabolic adaptations by which organisms obtain and use energy through photosynthesis and cellular respiration. Chapters 7 and 8 have been rewritten so that they can be taught in either order.

## PART 3: THE CONTINUITY OF LIFE: GENETICS

This unit begins with a discussion of mitosis and meiosis in Chapter 9. Chapter 10 describes Mendelian genetics and related patterns of inheritance. Chapter 11 discusses the structure and replication of DNA and Chapter 12 presents RNA and protein synthesis. Gene regulation is discussed in Chapter 13. In Chapter 14, we focus on genetic engineering and in Chapter 15 we focus on human genetics. In Chapter 16, we introduce the role of genes in development, including the latest findings in this exciting and rapidly changing area of biology.

## PART 4: THE CONTINUITY OF LIFE: EVOLUTION

The unit on evolution has been revised for this edition. Chapter 17 introduces Darwinian evolution and presents scientific evidence for evolution. In Chapter 18, we examine evolution at the population level. Chapter 19 describes the evolution of new species and discusses aspects of macroevolution. Chapter 20 summarizes the evolutionary history of life on Earth. In Chapter 21 we recount the evolution of the primates, including humans.

## PART 5: THE DIVERSITY OF LIFE

An evolutionary framework is used in our survey of the kingdoms of organisms. In Chapter 22 we discuss why and how organisms are classified. Chapter 23, devoted to the viruses and to Kingdom Prokaryotae, has been revised for this edition. Chapter 25 describes the fungi. Chapters 26 and 27 present the members of the plant kingdom. Chapters 28 through 30 focus on the diversity of animals. The discussion of each group of organisms focuses on their evolutionary relationships and on their structural and functional adaptations. Several new, illustrated tables summarize groups of organisms, such as the bacteria in Chapter 23 and the orders of insects in Chapter 29.

## PART 6: STRUCTURE AND LIFE PROCESSES IN PLANTS

This part integrates plant structure and function, beginning in Chapter 31 with a discussion of plant structure, growth, and differentiation. New tables, complete with labeled micrographs, have been added in this edition. Chapters 32 through 34 discuss the structural and physiological adaptations of leaves, stems, and roots. Chapter 35 describes reproduction in flowering plants, including asexual reproduction, flowers, fruits, and seeds. Chapter 36 focuses on growth responses and regulation of growth. New topics include thigmomorphogenesis, genetic regulation of auxin, circadian clock mutants, and new chemical regulators.

## PART 7: STRUCTURE AND LIFE PROCESSES IN ANIMALS

This part emphasizes the structural, functional, and behavioral adaptations that animals have evolved to meet environmental challenges. As each system of the animal body is discussed, a comparative approach is used to examine how various animal groups have solved similar and diverse problems. Chapter 37 is devoted to the architecture of the animal body, emphasizing the various tissues and organ systems. Then Chapters 38 through 49 present animal life processes. After a comparison of how different animal groups carry on a particular process—digestion, gas exchange, internal transport, etc.—each chapter considers the human adaptations for that process. The unit ends with a discussion of behavioral adaptations in Chapter 50.

## PART 8: THE INTERACTIONS OF LIFE: ECOLOGY

The ecology unit has been updated for this edition. Chapters 51 through 54 provide the foundations of ecology with the final chapter (55) focusing on environmental problems caused by humans. New topics include coral reef ecology, chaos theory, scramble and contest competition, new human population data, ENSO, keystone species and conservation, and expanded coverage of predation.

## SUPPLEMENTS

To further facilitate learning and teaching, a supplement package has been carefully designed for the student and instructor. It includes a **Study Guide, Instructor's Resource Manual, Test Bank, Computerized Test Bank** (available for the IBM PC and Apple Macintosh series), and **BIOXL** (available for both IBM and Macintosh formats). Other important components of *Biology's* supplement package are a set of 250 **Overhead Transparencies** based on diagrams in the book; a set of 150 **Electron Micrograph Overhead Transparencies; BioArt,** which is composed of 100 black-and-white unlabeled line drawings from the text; and 50 **General Sequence Overhead Transparencies,** which contain topics displayed in a series of stages or layers.

A **Laboratory Manual** written by Russell V. Skavaril, Mary M. Finnen, and Steven M. Lawton, all of Ohio State University, and an accompanying **Laboratory Instructor's Manual** are available. Also available is a **Laboratory Manual** written by Carolyn Eberhard of Cornell University. Additionally, a **Custom Publication** service is available from which a wide variety of individual laboratory exercises may be selected and combined in a single volume. Two supplementary texts are available by Randy Moore of the University of Akron. *Writing to Learn Science* and *Classic and Modern Readings in Biology* provide interesting articles and numerous exercises that will enhance understanding of science and biological concepts.

### Multi Media Offerings

The **Saunders General Biology Videodisc** has been prepared to enhance lecture or laboratory presentation of material that is difficult to visualize. The 60-minute videodisc contains more than 1500 still images and a collection of video clips from *Encyclopedia Britannica* and other sources, in addition to animated figures from the text. The videodisc is accompanied by the **Saunders General Biology Videodisc Directory,** which contains complete descriptions, barcode labels, reference numbers, and instructions for using the videodisc, and by LectureActive™, a software interface that enables instructors to customize the videodisc for lectures as well as enabling students to use the videodisc for self-directed study.

## Acknowledgments

The development and production of this new edition of *Biology* required extensive interaction and cooperation among the authors and many individuals in our home and professional environments. We appreciate the valuable input and support from editors, colleagues, students, family, and friends.

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We appreciate the help of our Project Editor Nancy Lubars who expertly guided the project through the complexities of production. We thank Art Director Joan Wendt and Illustrations Supervisor Sue Kinney for coordinating the art program and design. We appreciate the efforts of Sue Westmoreland, Product Manager, in marketing our book. All of these dedicated professionals and many others at Saunders provided the skill and attention needed to produce *Biology*, fourth edition. We thank them for their help and support throughout this project.

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Our colleagues and students who have used our book have provided valuable input by sharing their responses to the third edition of *Biology* with us. We thank them and ask again for their comments and suggestions as they use this new edition. We can be reached through our editors at Saunders College Publishing. We express our thanks to the many biologists who have read the manuscript during various stages of its preparation and provided us with valuable suggestions for improving it. Their input has contributed greatly to our final product. Fourth edition reviewers include:

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# To The Student

Biology is one of the most varied subjects one can study. It is therefore not surprising that biologists are a diverse group, with different interests, talents, and personalities. Almost anyone who has a desire to understand living things can find a suitable niche in the field of biology.

The thousands of students we have taught have differed in their life goals and learning styles. Some have had excellent backgrounds in science, others poor ones. Regardless of their backgrounds, it is common for students taking their first college biology course to find they must work harder than they expected. You can make the task easier by using approaches to learning that are usually successful for a broad range of students.

Many students "study" passively. An active learner always has questions in mind and is constantly making connections. For example, in biology there are many processes that must be understood. Do not try to blindly memorize these; instead think about causes and effects, so that every process becomes a story. Eventually you will see that many processes are connected by common elements.

Active learning is facilitated if you do some of your studying in a small group. In a study group the roles of teacher and learner should become interchangeable, for the best way to make sure you understand is to teach. A study group allows you to be challenged in a nonthreatening environment and can provide some emotional support.

One stumbling block for many students is the necessity to learn a great deal of terminology. In fact, it would be much more difficult to learn and communicate if we did not have this terminology, for words are really "tools for thinking." Learning terminology generally becomes easier because most biological terms are modular. They are composed of mostly Latin and Greek roots, and once you learn many of these you will find you may have a good idea of the meaning of a new word even before it is defined. For this reason we have included Appendix A, Understanding Biological Terms. Of course, to make sure you understand the precise definition, you will want to use the Index and Glossary. The more you use biological terms, in both speech and writing, the more comfortable you will be.

Although biology is a demanding subject, the time and effort you spend studying will be well spent, because this is a very exciting time to be a biologist. Today we have the tools to study living things in ways that were only a dream in the not too distant past. As we gain new information, our concepts are constantly evolving. We find this to be one of the most exhilarating aspects of biology, and we hope you will too!

# INTRODUCING *BIOLOGY*, FOURTH EDITION

Many features of ***Biology,* fourth edition** have been designed, or increased in number from the third edition, to address specific needs of students, as revealed in student focus groups.

*Making the Connection* boxes—now in every chapter—encourage students to integrate concepts from various chapters.

180 *Part 2 Energy Transfer Through Living Systems*

## *Making the Connection*

### Electron Transport and Heat

What is the source of our body heat? Essentially, it is a byproduct of various exergonic reactions, especially those involving the electron transport chains in our mitochondria. Some organisms are able to produce unusually large amounts of heat by uncoupling electron transport from ATP production. As a consequence, most of the energy of glucose is converted to heat rather than to ATP energy. Even some plants (which we don't generally consider to be "warm" organisms) have this capability. For example, skunk cabbage, which lives in North American swamps and wet woodlands, generally flowers when the ground is still covered with snow. Its uncoupled mitochondria generate large amounts of heat, enabling the plant to melt the snow and attract pollinators. ▲

**Skunk cabbage** *(Symplocarpus foetidus).* (Earth Scenes © 1996 Leonard Lee Rue III)

ing energy as they go. Finally, the last cytochrome in the chain, cytochrome $a_3$, passes two electrons to oxygen. The electrons simultaneously unite with protons from the surrounding medium to form hydrogen; the chemical reaction between hydrogen and oxygen produces water.

Because oxygen is the final electron acceptor in the electron transport system, organisms that respire aerobically require oxygen. What happens when cells that are strict aerobes are deprived of oxygen? When no oxygen is available to accept them, the last cytochrome in the chain is stuck with its electrons. When that occurs, each acceptor molecule in the chain remains stuck with electrons (i.e., is reduced), and the entire system is blocked all the way back to NADH. Because phosphorylation is coupled to electron transport, no further ATPs are produced by way of the electron transport system. Most cells of complex organisms cannot live long without oxygen because the amount of energy they produce in its absence is insufficient to sustain life processes.

Lack of oxygen is not the only factor that interferes with the electron transport system. Some poisons, including cyanide, inhibit the normal activity of the cytochrome system. Cyanide binds tightly to the iron in cytochrome $a_3$, making it unable to transport electrons on to oxygen. This blocks the further passage of electrons through the chain, halting ATP production.

***The chemiosmotic model explains the coupling of ATP synthesis to electron transport***

The flow of electrons in electron transport is usually tightly coupled to the production of ATP and does not occur unless the phosphorylation of ADP can also proceed. This prevents a waste of energy, because high-energy electrons do not flow unless ATP can be produced. If electron flow were uncoupled from the phosphorylation of ADP, there would be no production of ATP, and the energy of the electrons would be converted to heat (see *Making the Connection: Electron Transport and Heat*).

For decades scientists were aware that oxidative phosphorylation occurs in mitochondria, and many experiments had shown that the transfer of two electrons from each NADH to oxygen (via the electron transport chain) usually results in the production of up to three ATP molecules. However, for a long time, just *how* ATP synthesis is related to electron transport remained a mystery. Then, in 1961 Peter Mitchell proposed the **chemiosmotic model,** based on his experiments with bacteria. His model was

High-interest *Focus On* boxes draw attention to interesting biological phenomena and current research.

*Chapter 18 Population Genetics* 425

## *Focus On*

### Evolution of the Africanized Honeybee

Periodically newspapers report on the migration of "killer bees," or Africanized honeybees, into North America (see figure). The movement of these bees is of concern for several reasons. First, the Africanized honeybee, which looks just like any other honeybee, is considered dangerous because it is unpredictable and aggressive. Groups of them have been reported to attack at the slightest provocation. Also, the Africanized honeybee interbreeds or competes with the European honeybee, the type of bee raised commercially in this country. It is feared that interbreeding will adversely affect the European honeybees' important roles in pollination and honey production.

Africanized honeybees are descended from a small number of African honeybees introduced into Brazil in 1956. (The European honeybee does not fare well in the tropical climate of Brazil.) The number of introduced African honeybees was small, and as a result, they contained only a fraction of the genes present in the gene pool of African honeybees. Because of the founder effect, the few alleles present in the introduced population formed the gene pool on which natural selection acted in the new South American environment. Natural selection of this limited gene pool resulted in the Africanized honeybee.

Africanized honeybees, which are better adapted than European honeybees to tropical areas, have spread beyond their original point of origin in Brazil to occupy large areas of Latin America. Wherever they have migrated, decreases in honey production have initially occurred. Beekeeping in countries occupied by the Africanized bees has also changed, because the beekeepers must now wear more protective equipment. However, as beekeepers develop new methods to handle the Africanized bees, honey production often increases. For example, Brazil was 47th in world honey production before the African bees were introduced; today it ranks 7th.

**A swarm of Africanized honeybees covers a tree trunk in Mexico.** (Scott Camazine/Photo Researchers, Inc.)

Africanized honeybees currently range from Argentina to the southern United States. How far will they migrate? Will they stop in the southern United States because of a climate barrier? Or is it possible that they can expand into the northerly areas of North America? Because Africanized honeybees survive on snow-clad mountains in Latin America, biologists predict that climate will pose no barrier.

Some biologists advocate using artificial selection (see Chapter 17) to improve Africanized honeybees. The bees have a number of desirable traits, including resistance to disease and mites, a particularly serious problem for commercial beekeepers in the United States. Artificial selection might even give rise to a honeybee variety that is as important commercially as the European honeybee. ■

The evolution of ***Biology,* fourth edition** is particularly apparent in the incorporation of superb artwork—much of it revised or new. Students and instructors will respond enthusiastically to this visual enhancement, which includes

- **Sequential art** that incorporates the use of close-ups "exploded" to reveal greater detail
- **Composite pieces of line art and photographs** to help students interpret electron micrographs
- **Scale bars** accompanying the electron micrographs, providing a guide that clarifies size
- **Sequence summaries** show biological processes at a glance and help students review for exams



particle binds to receptor proteins on plasma membrane → coated pit forms → coated vesicle forms by endocytosis → "uncoating" of vesicle → vesicles fuse to form endosome → division of endosome:

→ some vesicles return receptors to plasma membrane
→ other vesicles fuse with lysosomes and contents are digested and processed

Cholesterol in the blood is taken up by animal cells by receptor-mediated endocytosis. Much of the receptor-mediated endocytosis pathway was detailed through studies of the receptor for low-density lipoprotein (LDL—a primary cholesterol carrier in blood) by M. Brown and J. Goldstein. In 1986 these investigators were awarded the Nobel Prize for their pioneering work. Their findings have important medical implications, for cholesterol that remains in the blood instead of entering the cells can become deposited on the artery walls and increase the risk of heart attack.

The recycling of the LDL receptor to the plasma membrane through vesicles illustrates a problem common to all cells that employ endocytotic and exocytotic mechanisms. In cells that are constantly involved in secretion, an equivalent amount of membrane must be returned to the interior of the cell for each vesicle that fuses with the plasma membrane; if it is not, the cell surface will keep expanding even though the growth of the cell itself may be arrested. A similar situation exists for cells that use endocytosis. A macrophage, for example, ingests the equivalent of its entire surface membrane in about 30 minutes, requiring an equivalent amount of recycling or new membrane synthesis for the cell to maintain its surface area.

## JUNCTIONS ARE SPECIALIZED CONTACTS BETWEEN CELLS

Cells in close contact with each other may develop specialized intercellular junctions that involve their plasma membranes as well as other components. These structures may allow neighboring cells to form strong connections with each other, prevent passage of materials, or establish rapid communications between adjacent cells. In animals there are three common types of intercellular contacts: desmosomes, tight junctions, and gap junctions. Plant cells are connected by plasmodesmata.

### Desmosomes are points of attachment between some animal cells

Adjacent epithelial cells, such as those found in the upper layer of the skin, are so tightly bound to each other that strong mechanical forces are required to separate them. They are held together by structures called **desmosomes** (Fig. 5–23). Each desmosome includes parts of two adjacent cells. It is made up of regions of dense material associated with the cytosolic sides of the two plasma membranes, plus protein filaments that cross the 24 nanometer-wide intercellular space between them.

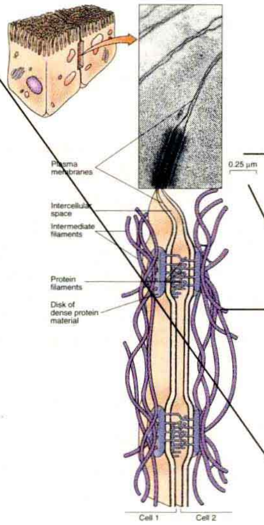



**FIGURE 5–23 Desmosomes may connect two animal cells.** The dense structure in the transmission electron micrograph is a desmosome. As can be seen in the interpretive drawing, each desmosome consists of a pair of button-like discs associated with the plasma membranes of adjacent cells, plus the intercellular protein filaments that connect them. Intracellular intermediate filaments attached to the discs are connected to other desmosomes. (D.W. Fawcett)

**Learning Objectives** at the beginning of each chapter indicate exactly what the student must be able to do in order to demonstrate mastery of the material in the chapter.

**Concept statement heads** formulated as complete statements, not as "disembodied" terminology, provide a clear preview and summary of conceptual discussion to follow. An innovation in the third edition, full-statement headings have remained popular with students.

Numerous **tables,** many of them illustrated, summarize and organize material presented in the text.



L E A R N I N G   O B J E C T I V E S

*After you have studied this chapter you should be able to*

1. Define a species and explain the limitations of the biological species concept.
2. Explain the significance of reproductive isolating mechanisms and distinguish among the different prezygotic and postzygotic isolating mechanisms.
3. Explain the mechanism of allopatric speciation and give an example.
4. Explain the mechanism of sympatric speciation and give an example.
5. Take either side in a debate on the pace of evolution, by representing the opposing views of gradualism and punctuated equilibrium.
6. Define macroevolution and distinguish among microevolution, speciation, and macroevolution.
7. Discuss macroevolution in the context of novel features, including preadaptations, allometric growth, and paedomorphosis.
8. Discuss the significance of evolutionary novelties, adaptive radiation, and extinction.

## SPECIES ACHIEVE REPRODUCTIVE ISOLATION IN VARIOUS WAYS

A number of **reproductive isolating mechanisms** prevent interbreeding between two different species whose ranges overlap. These mechanisms preserve the genetic integrity of each species because gene flow between species is prevented. To block a chance occurrence of individuals from two different species overcoming a single reproductive isolating mechanism, most species have two or more mechanisms. Many work before fertilization occurs (prezygotic), whereas others work after fertilization has taken place (postzygotic) (Table 19–1).

### Prezygotic barriers interfere with mating

Prezygotic barriers are reproductive isolating mechanisms that prevent fertilization from taking place. Because male and female gametes never come into contact, an interspecific zygote (fertilized egg formed by the union of an egg from one species and a sperm from another species) never forms. Prezygotic barriers include temporal isolation, behavioral isolation, mechanical isolation, and gametic isolation.

Sometimes genetic exchange between two groups is prevented because they reproduce at different times of the day, season, or year. Such examples demonstrate **tem-**

**Table 19–1** REPRODUCTIVE ISOLATING MECHANISMS

| *Mechanism* | *Type* | *How It Works* |
|---|---|---|
| Temporal isolation | Prezygotic | Similar species reproduce at different times |
| Behavioral isolation | Prezygotic | Similar species have distinctive courtship behaviors |
| Mechanical isolation | Prezygotic | Similar species have structural differences in their reproductive organs |
| Gametic isolation | Prezygotic | Gametes of similar species are chemically incompatible |
| Hybrid inviability | Postzygotic | Interspecific hybrid dies at early stage of embryonic development |
| Hybrid sterility | Postzygotic | Interspecific hybrid survives to adulthood but is unable to reproduce successfully |
| Hybrid breakdown | Postzygotic | Offspring of interspecific hybrid are unable to reproduce successfully |

**On the Cutting Edge** boxes highlight current, often controversial research; this feature complements the text's emphasis on the process of science and the influence of research applications on new thinking and future research.



ON THE CUTTING EDGE

## *Test-Tube Evolution*

**Objective:** To study bacterial evolution in the laboratory.

**Method:** Expose starving bacteria to a new food that they cannot metabolize.

**Results:** Mutations appear more frequently than would be expected in the starving cells, and some of these mutations are adaptive, allowing the bacteria to metabolize the new food. As a result, the bacteria survive and pass the ability to metabolize the new food on to their offspring.

**Conclusion:** Under conditions of starvation, adaptive mutation may occur in bacteria.

In 1988 a well-known British biologist, John Cairns, published the results of a study that indicated a different aspect of evolution known as **adaptive mutation.** By starving bacteria, Cairns found that they mutate in a nonrandom way and thus obtain the mutation they need to survive. His experiment startled many biologists because it seemed to support Lamarck's discredited idea that evolution is directed and purposeful. Like Lamarck's classical example of giraffes needing—and therefore evolving—longer necks to stretch into treetops, Cairn's starving bacteria needed—and seemed to evolve—a certain mutation that allowed them to use lactose for food.

The mutations produced by these bacteria did not appear to be the random mutations (that is, produced without regard for usefulness) characteristic of neo-Darwinian evolution. Adaptive mutation allowed the bacteria to obtain the needed mutation in a fraction of the number of cell divisions that "normal" random mutations would require.

Several other biologists repeated Cairn's experiment and reproduced his results, but the mechanism or mechanisms responsible for such apparently directed evolution remained unknown. Then in 1994 a group of researchers headed by Susan Rosenberg from the University of Alberta published two papers in the journal *Science** that reported a probable molecular mechanism for the variation produced by adaptive mutation. Certain proteins used during the recombination of bacterial DNA are necessary for adaptive mutation. The absence or inactivation of the genes encoding these proteins results in a strain of bacteria that cannot undergo rapid mutation when they are starving.

Many questions remain unanswered. Are these mutations occurring *because* they are needed? Why do the recombination genes cause adaptive mutation in starving bacteria but not in well-fed, rapidly growing cells? How important is adaptive mutation in bacterial evolution? Certain eukaryotic cells (yeasts) appear to have a process like adaptive mutation. Does it use a similar mechanism? Biologists disagree about the evolutionary implications of adaptive mutation, which will likely make this controversial phenomenon the target of investigation for many years.

*1. Harris, R.S., S. Longerich, and S.M. Rosenberg. "Recombination in adaptive mutation." *Science*, Vol. 264, 8 April 1994. 2. Rosenberg, S.M., S. Longerich, P. Gee, and R.S. Harris. "Adaptive mutation by deletions in small mononucleotide repeats." *Science*, Vol 265, 15 July 1994.

reasoning, Lamarck suggested that the long neck of the giraffe developed when a short-necked ancestor began browsing on the leaves of trees instead of on grass. Lamarck speculated that the ancestral giraffe, by reaching up, stretched and elongated its neck. Its offspring inherited the longer neck, which stretched still further. This process, repeated over many generations, supposedly resulted in the long necks of modern giraffes.

The proposed mechanism for Lamarckian evolution was an "inner drive" for self-improvement, a notion that was discredited when the actual basis of heredity was later discovered. (However, see *On the Cutting Edge: Test-Tube Evolution* for a possible example of "Lamarckian" evolution in bacteria.) Lamarck's contribution to science is important because he was the first to propose that organisms undergo change over time as a result of some natural phenomenon rather than divine intervention. It remained for Charles Darwin to discover the mechanism of evolution by natural selection.

### DARWIN WAS INFLUENCED BY HIS CONTEMPORARIES

Charles Darwin, the son of a prominent physician, was sent at the age of 15 to study medicine at the University of Edinburgh. Finding himself unsuited for medicine, he transferred to Cambridge University to study theology. Shortly after receiving his degree, Darwin embarked as a naturalist on the *H.M.S. Beagle*, which was taking a five-year exploratory cruise around the world to prepare navigation charts for the British Navy.

Career Visions

## Tissue Bank Director

MARTHA ANDERSON

*Martha Anderson originally planned to attend medical school after earning a biology degree at Colorado State University. But by the time she transferred to complete her biology studies at the University of Colorado, her focus had changed. Upon graduating, she began a career that enabled her to help many more patients and their families than a single doctor ever could. Martha is Vice President of Donor Services for the Musculoskeletal Transplant Foundation, a non-profit organization that "banks" human tissue for transplant use and conducts research to further develop transplantation techniques. The Foundation stores tissues and bone that are used in a variety of procedures, from periodontal reconstructive surgery to replacement of cancerous tissue. The Foundation is a membership organization composed of medical and academic institutions as well as other organ and tissue procurement agencies.*

**You had planned on going to medical school and decided against that profession. What did you do after college?**

I went to work in one of Denver's trauma hospitals where I took an administrative position. Eventually I was promoted into what was probably the best job of my life as a patient representative at St. Anthony's Hospital.

**What does a patient representative do?**

A patient representative acts as an advocate for patients. You resolve a lot of patient care related issues and are responsible for crisis intervention with many families. Sometimes you serve as a person to talk to for the patient who doesn't have any family or friends around. We had the first helicopter rescue system in the country at St. Anthony's, and as a result, we had a great deal of trauma victims. Often these patients arrived unconscious and without any identification. It was my job to find out who they were and contact their families. It was a very stressful job, but it was rewarding because we could help people negotiate the health care system. Many people don't know anything about health care, and if they are incapacitated by their illness or by grief it's difficult for them to know what questions to ask so they can get the help that they need. Through my work as a patient representative I became involved with the organ and tissue donation process.

**And that's how you got into your current position?**

Yes, I helped set up the largest donor program in Colorado. We had more donors from St. Anthony's in Denver than from any other hospital in the state.

**How did you do that?**

We were very pro-active in identifying potential donors and offering their families the opportunity to talk about donation and find out if they wanted to be donors.

**I suppose there are other organizations that "bank" bone or tissue. What's different about your organization?**

There are probably about 100 or 150 tissue banks in the country. Ours is the largest and we have a unique structure. Many organ and tissue banks are regional or local, but we're a national consortium of medical schools and other recovery agencies. When someone has the potential of being an organ or tissue donor the local organ procurement agency is usually contacted. There are over 25 locations around the country that recover tissue for us—the bones, tendons and ligaments—which we then provide to surgeons and hospitals throughout the U.S.

**Then you process them for storage so they can be transplanted?**

Yes, we have them processed in our New Jersey facility. The tissue is formed into different sorts of shapes depending on whatever the local need is. For example, there may be a hospital that does a lot of spine surgery so we would cut the bone into sizes for spine surgeons to use. Or there may be a need for an entire femur which would probably be used for someone who has cancer. In the past the only option for removing a cancerous tumor in a femur was to amputate the leg. Now we can take out the portion of bone that has the tumor in it and replace it with another that's the right size. Such a person can now keep their leg, and maintain an active lifestyle. This procedure is called limb salvage.

**Do you feel that you use your biology degree in your current job? And, if so, how do you use it?**

I used my biology degree when I was a patient representative because my studies focused on human physiology and anatomy. I had a very good basic understanding of how the human body works and that helped me a lot. One of the things that I do use every day are the critical thinking skills I developed as an undergraduate. I have to figure out answers to problems that have a basis in science. One of the things you learn in basic biology is that you have to think and figure out how things work. These are skills I use quite frequently.

**Is there a specific kind of science or education background required to work in your field?**

A lot of the people who work for me are either nurses or operating room technicians. A few people have bachelors degrees in biology. Having only a bachelor's degree in biology may not be enough anymore, and I think a graduate degree is probably required to advance in the field.



**Career Visions,** interviews with former biology majors who describe what they now do professionally, convey persuasive, practical information on the merits of studying biology, and the variety of opportunities open to biology majors.

## *Making the Connection*

### Evolution and Genetics

Can biologists make use of the fact that mutations in DNA sequences have been occurring throughout the course of evolution? Within a given taxonomic group, mutations appear to have occurred at a uniform rate over millions of years. From the number of alterations in the DNA nucleotide sequence of one organism compared with another, we can develop a **molecular clock** to estimate the time of divergence between two closely related species or higher taxonomic groups. Such molecular clocks can be used to complement geological estimates of the divergence of species or to assign tentative dates to evolutionary events that lack fossil evidence.

Molecular clocks must be developed and interpreted with care. The rates of mutation appear to vary among different genes and among different taxonomic groups. Therefore, although some mutations occur at a fairly uniform rate, a single molecular clock for all genes in all organisms cannot be elucidated. ▲

A **Chapter Summary** in outline form at the end of each chapter provides a review of the material presented.

### SUMMARY

I. Evolution, the genetic change in a population of organisms over time, is the unifying concept of biology.
II. Charles Darwin and Alfred Wallace independently proposed the theory of evolution by natural selection, which is based on four observations:
  A. Overproduction: Each species produces more offspring than will survive to maturity.
  B. Variation: Genetic variation exists among the individuals in a population.
  C. Limits on population growth: Organisms compete with one another for the resources needed for life, such as food, living space, water, light, and so on.
  D. Differential reproductive success: The offspring with the most favorable combination of characteristics are most likely to survive and reproduce, passing those genetic characteristics on to the next generation.
III. The synthetic theory of evolution combines Darwin's theory of evolution by natural selection with the genetic mechanisms to explain evolution.
  A. Mutation provides the genetic variability that natural selection acts on during evolution.
  B. The synthetic theory of evolution emphasizes genetics of populations rather than of individuals.
IV. The concept that evolution has occurred and is occurring is now well documented.
  A. Direct evidence of evolution comes from fossils, the remains or traces of ancient organisms.
  B. Evidence supporting evolution is derived from comparative anatomy.
    1. Homologous structures (those related by descent) have basic structural similarities, even though the structures may be used in different ways. Homologous structures indicate evolutionary ties among the organisms possessing them.
    2. Analogous organs (those not related by descent) have similar functions in quite different, genetically unrelated organisms. Analogous structures demonstrate that organisms with separate ancestries can adapt in similar ways to comparable environmental demands (convergent evolution).
    3. The occasional presence of a vestigial organ is to be expected as a species adapts to different modes of life.
  C. Developmental biology provides evidence of evolution.
    1. The embryos of related animals are more similar than the adults.
    2. The accumulation of genetic changes since organisms diverged in evolution modifies the pattern of development in more complex vertebrate embryos.
  D. Biogeography, the distribution of plants and animals, supports evolution.
    1. Each species originated only once (at its center of origin).
    2. From its center of origin, each species spread out until halted by a barrier of some kind.
    3. Areas that have been separated from the rest of the world for a long time have organisms that are unique to those areas.
  E. Molecular biology provides evidence of evolution.
    1. The universality of the genetic code is compelling evidence that all life is related.
    2. The sequence of amino acids in common proteins reveals greater similarities in closely related species.
    3. A greater proportion of the sequence of nucleotides in DNA is identical in closely related organisms.

### SELECTED KEY TERMS

| | | | |
|---|---|---|---|
| adaptation | DNA sequencing | index fossil | radioisotope |
| analogous structure | evolution | molecular clock | range |
| artificial selection | fossil | natural selection | synthetic theory of evolution |
| biogeography | gene pool | neo-Darwinism | vestigial organ |
| center of origin | half-life | phylogenetic tree | |
| convergent evolution | homologous structure | radioactive decay | |

**Selected Key Terms** at the end of every chapter direct students to important vocabulary explained in the chapter.

A **Post-Test** provides the opportunity to evaluate mastery of the material using new key terms from within the chapter; answers are provided.



### POST-TEST

1. The fact that all species developed from earlier forms by the accumulation of genetic changes over many successive generations is known as the theory of ________.
2. The genetic constitution of an entire population of a given species is termed its ________ ________.
3. Darwin proposed ________ ________ as the mechanism by which evolutionary change takes place.
4. The four premises of ________ ________ are overproduction, variation, limits on population growth, and differential reproductive success.
5. In natural selection, the selecting agent is the environment, whereas in ________ ________, the selecting agent is humans.
6. The modern theory of evolution in which Darwin's observation of variation is explained by mutation is known as the ________ ________ of evolution.
7. The synthetic theory of evolution is also called ________.
8. Geologists can identify specific layers of rock by the presence of certain key fossils, known as ________ ________.
9. Unstable isotopes that spontaneously emit radiation, known as ________, are used to date the rocks in which fossils appear.
10. An organ that appears to have little or no function, and is smaller than a similar, fully functional equivalent in the organism's ancestor or relatives, is known as a (an) ________ organ.
11. The wings of butterflies and bats have similar functions but are quite different in structure. This is an example of ________ structures.
12. The independent evolution of similar structures in two unrelated organisms is known as ________ ________.
13. The study of the distribution of plants and animals is called ________.
14. The portion of Earth over which a given species is found is its ________.
15. One type of molecular evidence for evolution is ________ ________, in which the order of nucleotide bases in a strand of DNA that codes for a gene shared by several organisms is determined.

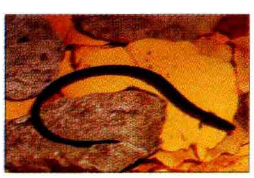
### REVIEW QUESTIONS

1. Explain briefly the concept of evolution by natural selection.
2. Why are only inherited variations important in the evolutionary process?
3. What part of Darwin's theory was he unable to explain? How does the synthetic theory of evolution explain this?
4. How do scientists date fossils? How do fossils provide evidence of evolution?
5. Distinguish among homologous, analogous, and vestigial structures. How does each provide evidence of evolution?
6. How does developmental biology provide evidence of a common ancestry for vertebrates as diverse as reptiles, birds, pigs, and humans?
7. Explain why marsupials are widespread in Australia and almost nonexistent elsewhere.
8. What is indicated if the DNA from two species is found to be almost identical?

**Review Questions** focus on mastery of chapter Learning Objectives.

### YOU MAKE THE CONNECTION

1. Although most salamanders have four legs, a few species that live in shallow water lack hindlimbs and have extremely tiny forelimbs. Explain how limbless salamanders came about according to Lamarck's concept of evolution. Then explain these amphibians using Darwin's mechanism of evolution by natural selection.
2. Based on what you have learned in this chapter, explain why such genetically different organisms as porpoises, which are mammals, and sharks, which are fish, are so similar in body form.
3. Discuss these statements:
   a. Natural selection chooses from among the individuals in a population those most suited to *current* environmental conditions. It does not guarantee survival under future conditions.
   b. Evolution is not hierarchical. For example, humans are not "better" or "more highly evolved" than the bacteria living in our intestines.
   c. Individuals do not evolve, but populations do.
   d. Evolution is not purposeful, but is based on chance.

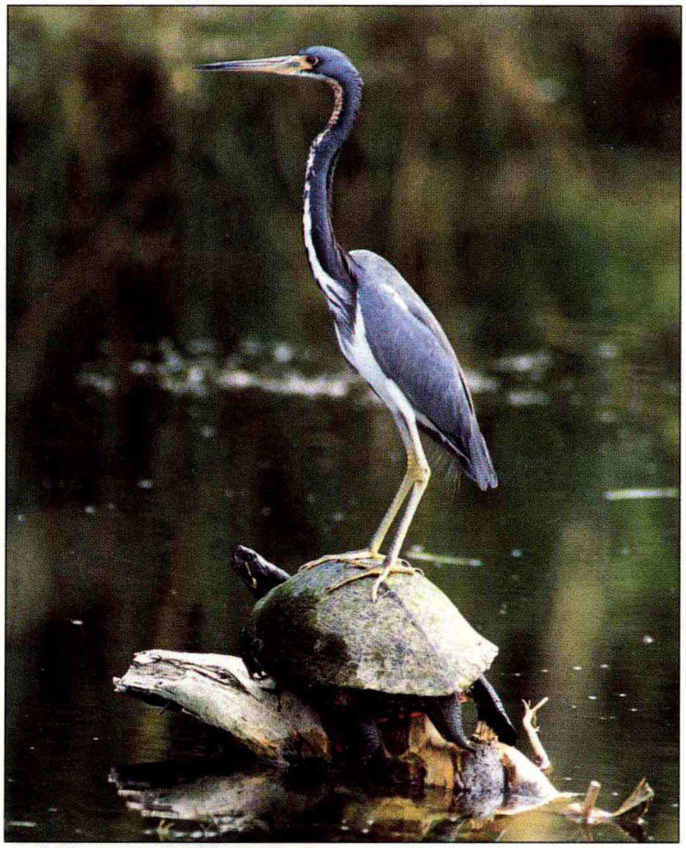


The narrow-striped dwarf siren (*Pseudobranchus striatus axanthus*) is an aquatic salamander that resembles an eel. It is native to Florida. (Suzanne L. Collins and Joseph T. Collins/Photo Researchers, Inc.)

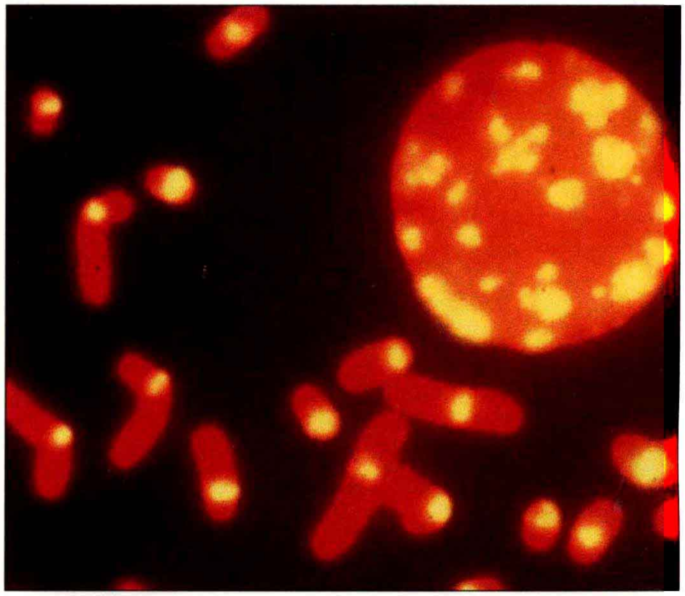
**You Make the Connection** questions, after every chapter, challenge students to synthesize material by applying concepts in the chapter to new situations.

# Contents Overview









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