

# Principles of Life

SECOND EDITION



Hillis  
Sadava  
Hill  
Price

Each chapter introduces essential biological concepts and the science that led to our understanding of them. Chapters are designed to help you focus on what's

## 33 Muscle and Movement

**KEY CONCEPTS**

33.1 Muscle Cells Develop Forces by Means of Cycles of Protein-Protein Interaction

33.2 Skeletal Muscles Pull on Skeletal Elements to Produce Useful Movements

33.3 Skeletal Muscle Performance Depends on ATP Supply, Cell Type, and Training

33.4 Many Distinctive Types of Muscle Have Evolved



A sphinx moth (*Hemaris thysbe*) uses its flight muscles to hover at a flower, collecting nectar with its long proboscis.

This moth, a type of sphinx or hawk moth, is sometimes mistaken for a hummingbird, accounting for its name, the hummingbird clearwing moth (*Hemaris thysbe*). Common in several parts of the United States and Canada, it feeds during daylight by hovering at flowers using rapid wingstrokes driven by the flight muscles in its thorax. It has frequency whining wingstrokes of mosquitoes. Today, engineers are studying insects to learn more about the aerodynamics of flight. Sphinx moths are of particular interest because they are powerful fliers that can quickly alternate between hovering and flying straight ahead at high speeds.

Muscle cells—one of the defining draw the interest of muscle physiologists because they are among the animals that have the highest frequencies of muscle contraction during flight while retaining this 1:1 ratio. Their wingstrokes can number more than 30 per second (30 Hz). Per gram, insect flight muscle stands out as one of the tissues that attain the

## OPENING STORY & QUESTION

Chapters begin with an **OPENING STORY** designed to show you how the biology relates to historical, medical, or social issues. Each story ends with an intriguing question.

**Q** Why is it likely that available space inside cells has limited the contents of contractile proteins and mitochondria in high-performance muscles?

You will find the answer to this question on page 697.

**Q** Why is it likely that available space inside cells has limited the contents of contractile proteins and mitochondria in high-performance muscles?

**ANSWER** **FIGURE 33.17** is a highly magnified image of an insect flight muscle cell, obtained by electron microscopy. The inside of the cell is filled almost completely by mitochondria and contractile proteins. Open space is thus a scarce resource. Put simply, a high-performance muscle cell needs as large a set of contractile proteins as possible and as many mitochondria as possible—meaning there is a sort of “competition” for space in which the amounts of contractile proteins and mitochondria are each limited by space shortage. If, over evolutionary time, natural selection started to favor larger numbers of contractile protein molecules, the contractile proteins could edge out some of the mitochondria—jeopardizing the ability of the contractile proteins to get enough ATP. If natural selection started to favor more mitochondria, the mitochondria would edge out contractile proteins—jeopardizing the ability of the cell to use the ATP it could produce. The fact that space is limited has resulted in a sort of compromise in the use of space inside a high-performance muscle cell.

The **ANSWER** comes at the chapter's conclusion, with references to relevant information and illustrations in the chapter.

## KEY CONCEPTS & CHECKPOINTS

**KEY CONCEPTS**

33.1 Muscle Cells Develop Forces by Means of Cycles of Protein-Protein Interaction

33.2 Skeletal Muscles Pull on Skeletal Elements to Produce Useful Movements

33.3 Skeletal Muscle Performance Depends

**CHECKPOINT CONCEPT 33.1**

- ✓ Imagine planting your feet and trying to push through a concrete wall that's far too heavy to move. As you push, would you describe the associated muscles in your back, arms, and legs as contracting, shortening, lengthening, or a combination of these words? Explain.
- ✓ In a muscle fiber, how is force development aided by the interdigitated arrangement of actin and myosin filaments?
- ✓ Describe how the concentration of  $Ca^{2+}$  in the sarcoplasmic reticulum of a muscle cell changes before, during, and after the cell is excited by a nerve impulse (action potential).

**KEY CONCEPTS** begin each chapter.

**CHECKPOINTS** revisit the Key Concepts at the end of each section.

## APPLY THE CONCEPT

**APPLY THE CONCEPT**

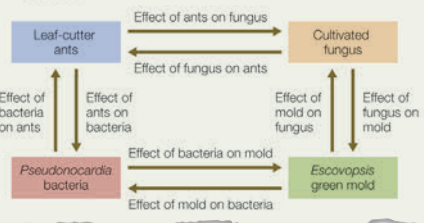
**Interactions within and among species affect population dynamics and species distributions**

A leaf-cutter ant nest can be considered a community—an ecological system (see Concepts 1.2 and 41.1) in which the species are components that interact with one another. Major components of the system are shown as labeled boxes, and their interactions as arrows between those boxes.

Use the description of interactions within leaf-cutter ant nests in the opening story of this chapter to answer the following questions:

- What is the sign of the following direct effects of each species on another?
 

Ants on fungus	Fungus on ants
Fungus on mold	Mold on fungus
Mold on bacteria	Bacteria on mold
Bacteria on ants	Ants on bacteria
- Explain for each interaction the mechanism by which the fitness of interacting individuals is affected.
- To which of the five categories of interspecific interactions does each pairwise interaction belong?
- Explain how the spatial distribution of the green mold *Escovopsis* might affect the spatial distribution of leaf-cutter ant colonies.



**APPLY THE CONCEPT** exercises ask you to use a concept in a real-world setting to interpret actual research data and draw your own conclusions.

## LINKS

to both partners. Mutualisms take many forms and involve many kinds of organisms. They also vary in how essential the interaction is to the partners.

**LINK**

We have seen several examples of mutualisms in this book, including interactions between mycorrhizal fungi and plants (see [Concepts 22.2 and 25.2](#)); between fungi, algae, and cyanobacteria in lichens (see [Concept 22.2](#)); and between corals and dinoflagellates (see [Concept 20.4](#)).

Competition, consumer-resource interactions, and mutualism all affect the fitness of both participants. The other two defined types of interactions affect only one of the participants.

In-text **LINKS** point you to additional discussion of a concept or key term elsewhere in the book.

# Works for You...

important, and they offer a number of ways to analyze and review what you've read as you prepare for class or exams.

**INVESTIGATION**

**FIGURE 6.11 An Experiment Demonstrates the Chemiosmotic Mechanism** The chemiosmosis hypothesis was a bold departure from the conventional scientific thinking of the time. It required an intact compartment separated by a membrane. Could a proton gradient drive the synthesis of ATP? The first experiments to answer this question used chloroplasts, plant organelles that use the same mechanism as mitochondria to synthesize ATP.<sup>9</sup>

**HYPOTHESIS**  
A H<sup>+</sup> gradient across a membrane that contains ATP synthase is sufficient to drive ATP synthesis.

**METHOD**  
Chloroplasts are isolated from cells and broken to expose their thylakoids (internal compartments). The broken chloroplasts are preincubated in an acidic medium (pH 3.8).  
The broken chloroplasts are moved quickly to an alkaline medium (pH 8). This lowers the H<sup>+</sup> concentration outside the thylakoids and creates a H<sup>+</sup> gradient across the thylakoid membrane (high inside, low outside).

**RESULTS**  
H<sup>+</sup> movement out of the thylakoids drives the synthesis of ATP from ADP and P<sub>i</sub>.

**CONCLUSION**  
A H<sup>+</sup> gradient across an ATP synthase-containing membrane is sufficient for ATP synthesis by organelles.

**ANALYZE THE DATA**  
The formation of ATP from ADP and P<sub>i</sub> was measured using luciferase, which catalyzes the formation of a luminescent (light-emitting) molecule if ATP is present. The experiment was performed under different conditions, with the following results:

Experiment	Preincubation pH	ATP synthase mixture (pH 8)	ATP formation (nmoles/mg chlorophyll)
1	3.8	Complete mixture	144
2	7.0	Complete mixture	12
3	3.8	P <sub>i</sub> omitted	12
4	3.8	ADP omitted	4
5	3.8	Thylakoids omitted	7

A. Which experiments show that a proton gradient is necessary to stimulate ATP formation?  
B. Why was there less ATP production in the absence of P<sub>i</sub>?

Go to **ANIMATED TUTORIAL 6.2**  
**Two Experiments Demonstrate the Chemiosmotic Mechanism**  
[PoL2e.com/at6.2](http://PoL2e.com/at6.2)

Go to **LaunchPad** for discussion and relevant links for all **INVESTIGATION** figures.

\*A. T. Jagendorf and E. Uribe. 1966. *Proceedings of the National Academy of Sciences USA* 55: 170-177.

## INVESTIGATION

**INVESTIGATION** figures emphasize the process of scientific inquiry to give you a realistic sense of how science is done. Each Investigation figure is organized in order of **hypothesis, method, results, and conclusion** and cites the original research paper(s).

## ANALYZE THE DATA

Most **INVESTIGATION** figures are followed by **ANALYZE THE DATA** problems, which ask you to work with data from published biological research and make your own connections between observations, analyses, hypotheses, and conclusions.

## INSTANT ACCESS CODES

**QUICK RESPONSE (QR) CODES** and **DIRECT WEB ADDRESSES** integrated into the text link you immediately to engaging animations, media clips, and activities. Just scan the code with your smartphone or tablet, or type the short Web address into any browser. (Free QR reader apps are available from your mobile device's app store.)



Go to **MEDIA CLIP 23.7**  
**Octopuses Can Pass through Small Openings**  
[PoL2e.com/mc23.7](http://PoL2e.com/mc23.7)

## CHAPTER SUMMARY

### SUMMARY

#### CONCEPT 19.1 Life Consists of Three Domains That Share a Common Ancestor

- Two of life's three **domains**, Bacteria and Archaea, are **prokaryotic**. They are distinguished from Eukarya in several ways, including their lack of a nucleus and of membrane-enclosed organelles. **Review Table 19.1**
- Eukaryotes are related to both Archaea and Bacteria and appear to have formed through endosymbiosis between members of these two lineages. The last common ancestor of all three domains probably lived about 3 billion years ago. **Review Figure 19.1 and ANIMATED TUTORIAL 19.1**

**CHAPTER SUMMARIES** provide a thorough review of chapter content, including key figures, and references to supporting online resources, including Animated Tutorials and Activities.

## HELPFUL ART WITH BALLOON CAPTIONS

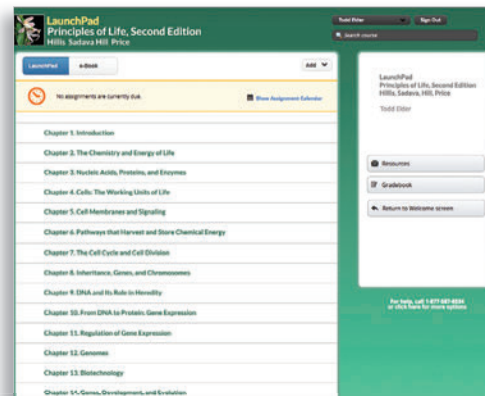
**FIGURE 14.13 A Gene Cascade Controls Pattern Formation in the *Drosophila* Embryo** Maternal effect genes induce gap, pair rule, and segment polarity genes—collectively referred to as segmentation genes. By the end of this cascade, a group of nuclei at the anterior of the embryo, for example, is determined to become the first head segment in the adult fly. In the micrographs at left, various staining methods have been used to highlight the different gene products.

- Maternal effect genes determine the anterior-posterior axis and induce gap genes.
- Gap genes define several broad areas and regulate...
- ...pair rule genes, which refine the segment locations and regulate...
- ...segment polarity genes, which determine the boundaries and anterior-posterior orientation of each segment.
- Together, the gap, pair rule, and segment polarity genes control expression of the **Hox genes**, which define the identity of each segment.

Go to **ANIMATED TUTORIAL 14.4**  
**Pattern Formation in the *Drosophila* Embryo**  
[PoL2e.com/at14.4](http://PoL2e.com/at14.4)

Numbered **BALLOON CAPTIONS** in the illustrations make it easy to follow key processes step by step.

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**Concept 16.1 All of Life Is Connected through Its Evolutionary History**

The sequencing of complete genomes from many diverse species has confirmed what biologists have long suspected: all of life is related through a common ancestor. The common ancestry of life explains why the general principles of biology apply to all organisms. Thus, we can learn much about how the human genome works by studying the biology of model organisms because we share a common evolutionary history with those organisms. The evolutionary history of these relationships is known as **phylogeny**, and a **phylogenetic tree** is a diagrammatic reconstruction of that history.

Phylogenetic trees are commonly used to depict the evolutionary relationships among populations and genes. For many plants such trees have been used to reconstruct the evolutionary history of a particular group of organisms or their genes. A **phylogenetic tree** is a diagrammatic reconstruction of these lines of evolutionary descent.

In Chapter 15 we discussed why we expect populations of organisms to evolve over time. Such a series of ancestor and descendant populations forms a **lineage**, which we can depict as a line drawn on a time axis.

What happens when a single lineage divides into two? For example, a geographic barrier (such as a new mountain range) may divide an ancestral population into two descendant populations that no longer interact with one another. This event is known as a **split** or **node**. In a phylogenetic tree, each of the descendant populations gives rise to a new lineage, and as these independent lineages evolve, new traits arise in each.

## INTERACTIVE e-BOOK

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**Chapter 16. Reconstructing and Using Phylogenies**

In this chapter we examine the field of systematics, the scientific study of the diversity of life. We see how phylogenetic methods are used to reconstruct evolutionary history and to study diversity across genes, populations, species, and larger groups of organisms. We see how systematists reconstruct the past and use phylogenies to make predictions in biology. We end the chapter with a look at taxonomy, the theory and practice of classifying organisms.

- Chapter Introduction e-Book
- 16.1 All of Life Is Connected through Its Evolutionary History e-Book
- 16.2 Phylogeny Can Be Reconstructed from Traits of Organisms e-Book
  - Activity 16.1 Constructing a Phylogenetic Tree
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  - Animated Tutorial 16.2 Using Phylogenetic Analysis to Reconstruct Evolutionary History
  - 16.3 Phylogeny Makes Biology Comparative and Predictive
  - 16.4 Phylogeny Is the Basis of Biological Classification
- Chapter Summary e-Book
- Chapter 16 LearningCurve: Reconstructing and Using Phylogenies
- Summative Quiz for Chapter 16
- Chapter 22 Lecture Notebook
- Instructor Resources

Browse more resources for this unit...

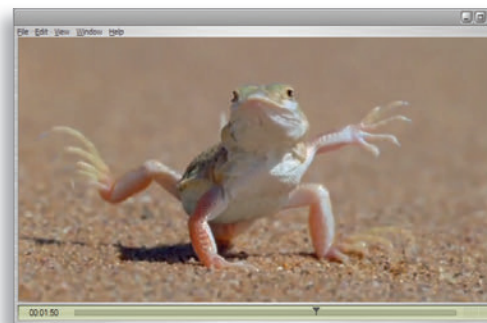
## MEDIA RESOURCES

LaunchPad features a wealth of study and review resources for each chapter of the textbook. These include Animated Tutorials, Activities, Media Clips, Flashcards and Key Terms, Investigation Links, Analyze the Data exercises, and more, all designed to help you learn and apply the material.

**An Ant-Plant Mutualism**

The ants have a full banquet and residence on the bull's horn acacia. They nest in the enlarged hollow thorns, entering and exiting from a hole near the tip. They consume energy-rich nectar from specialized extrafloral nectaries at the base of the leaves. The ants also take the oil and protein packets at the ends of some leaflets back to the nest for their young. The food-producing structures on the plant have no apparent purpose other than to provide for the ants. Did the ants just get lucky, or are they providing the tree with something that it needs in return?

Textbook Reference: Concept 43.4 Interactions within and among Species Can Result in Evolution



**LEARNINGCurve** 15.1.2 Derived traits provide evidence of evolutionary relationships

Refer to the figure below. (Click image to enlarge.)

What synapomorphies are shared by lizards and salamanders?

- Lungs only
- Lungs and claws/nails
- Jaws, lungs, and scales
- Lungs and jaws
- Lungs, jaws, and claws/nails

## LEARNINGCURVE SELF-ASSESSMENT

LEARNINGCurve is a dynamic quizzing system that helps you learn the material in each chapter. By adapting to your responses, it presents questions at appropriate difficulty levels within each topic area and across the chapter. With its game-like format, direct links to the e-Book, and instant feedback, LEARNINGCurve is a great way to understand the concepts and master the content.

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Principles of

# Life

SECOND EDITION





# Principles of Life

SECOND EDITION

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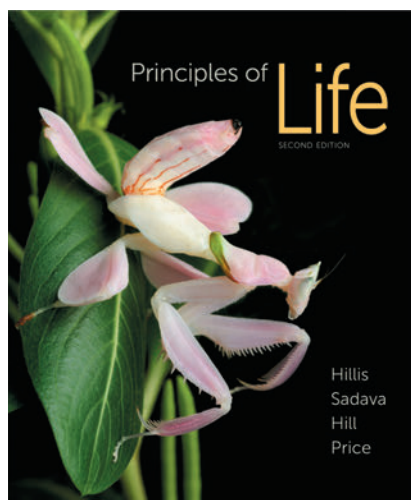
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## About the Cover

A juvenile pink orchid mantis (*Hymenopus coronatus*) looks, at first glance, like an orchid flower. Its abdomen, head, and four walking legs look like the petals of the flower, and the small black dot at the posterior tip of the abdomen resembles a small fly investigating the flower. This mimicry is advantageous to the mantid for two reasons. The mantis is concealed from potential predators, which mistake the mantis for a flower. At the same time, insects looking for nectar become prey for the mantis, which captures visiting insects with its front pair of toothed, grasping legs. As a result of these advantages, natural selection favored the evolution of this spectacular example of an insect that resembles an orchid flower. © Ch'ien Lee/Minden Pictures.

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*To all our students. You have taught us, too, and inspired us to write this book.*

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# Preface

Since the First Edition of *Principles of Life* was published, the surge in biology education research and the availability of resources for teachers continues to create excitement among the teaching community. Just as the First Edition appeared, the American Association for the Advancement of Science (supported by the National Science Foundation) published *Vision and Change in Undergraduate Biology Education: A Call to Action*. This report endorsed teaching core concepts and core competencies, and promoted the active involvement of students in problem-solving activities. When the First Edition of *Principles of Life* was published, it offered a radically new approach to teaching introductory biology that aligns with the goals put forward in the *Vision and Change* report (see below).

*Principles of Life* emphasizes mastering major concepts in biology through active learning, problem solving in realistic scenarios, and understanding rather than memorization. Now other textbook authors are beginning to follow our lead. We are proud that *Principles of Life* has helped to usher in this change in the way biology courses are taught, and we intend to continue to develop our book as the leading vehicle for this new approach to biology education.

## Leading the Change in Undergraduate Biology Education

We are standing at an important crossroads in biology education, and many recent efforts have converged to produce an opportunity for lasting change in the way that instructors teach introductory biology. The validity of our approach in *Principles of Life* is supported by numerous reports and studies published by education agencies and national study groups since the turn of the millennium. In particular, two major reports have encouraged this change: the *Vision and Change* report mentioned above and *BIO2010: Transforming Undergraduate Education for Future Research Biologists*, sponsored by the National Institutes of Health and the Howard Hughes Medical Institute. These reports recommended focusing on core concepts and competencies, teaching students through active learning rather than memorization, and improving the integration of statistical and computational approaches. At about the same time, the College Board was redesigning the Advanced Placement Biology course with the same objectives. In *Principles of Life*, we have used our experience as authors and educators to implement these recommendations in a new approach to teaching introductory biology.

The *Vision and Change* report (2011) identified five “core concepts for biological literacy” that should be integrated throughout the curriculum. These core concepts center around the themes of:

- evolution
- the relationship between structure and function

- information flow, exchange, and storage
- pathways and transformations of energy and matter
- biological systems

In the Second Edition of *Principles of Life*, we have worked to ensure that these five core concepts are stressed and reinforced throughout the text, problems, media links, and other activities. To help students build bridges between different portions of the course and areas of knowledge, we have provided **Links** throughout the book. Using these *Links*, students can see, for example, that information they learn about molecular or cell biology is connected to topics in evolution, diversity, physiology, and ecology.

In addition to urging a focus on core concepts, the *Vision and Change* report argued that students need to cultivate certain core competencies to become successful scientists. Students should be able to:

- apply the process of science
- use quantitative reasoning
- use modeling and simulation
- tap into the interdisciplinary nature of science
- communicate and collaborate with other disciplines
- understand the relationship between science and society

Students are encouraged to practice these core competencies throughout the Second Edition of *Principles of Life*. Every chapter contains *Apply the Concept* exercises, which give students opportunities to practice working with data. These problems tie in with our *Making Sense of Data: A Statistics Primer* (Appendix B), which helps students understand why and how biologists draw conclusions from biological data, and thus helps them develop quantitative reasoning skills. We have also added more online *Animated Tutorials* and *Activities*, which include opportunities for students to use modeling and simulation modules to further reinforce their understanding of concepts. By engaging in these activities, students also learn about the importance of biological concepts and analyses for addressing societal issues and challenges.

## The *Principles of Life* Story

Prior to our launch of the First Edition of *Principles of Life*, introductory biology textbooks for science majors presented encyclopedic summaries of biological knowledge. We believe that students who spend their time diligently memorizing myriad details and vast terminology actually retain fewer of the concepts that are the foundation for further study in advanced courses. In *Principles of Life*, we take the opposite approach: we promote understanding over memorization. Details are important, but no modern biology textbook can



begin to cover all the information biologists have learned to date, and students today have many other ways to access the details as they need them.

To help us create this new breed of biology textbook, in 2009 our publishers Sinauer Associates and W. H. Freeman brought together an Advisory Board of 20 leading biology educators and instructors in introductory biology from throughout North America. During an intensive meeting of the authors and the Board, dynamic discussions led to the solidification of the core concepts we believe are essential for teaching introductory biology. The book took shape, and the Advisory Board members then reviewed the emerging chapters and provided considerable feedback at every stage of the book's development. The result was a book that showcased the logical structure of scientific investigation, including lab, field, and computer modeling approaches. *Principles of Life* helped students apply the concepts they learn by providing opportunities for them to analyze original data in every chapter. In this and many other ways *Principles of Life* incorporated inquiry-based approaches that encourage active learning.

The First Edition of *Principles of Life* was widely adopted and well received. Adopters and reviewers praised the approach, and encouraged us to expand the effort to include even more problem-solving opportunities for students and more examples of the experiments that have formed the basis of our understanding. For the Second Edition, all chapters underwent extensive between-edition review by experts in each respective subdiscipline, and the chapters were revised accordingly. We now provide more references to original data and analyses so that students and instructors can easily explore the original experiments in greater depth. Moreover, we have expanded opportunities for students to apply what they have learned by using real data and examples, and have better integrated and explained the concepts of statistical analysis of data. We have included links to online videos (the new Media Clips) that help students to appreciate the relevance of what they have learned and to enjoy the excitement of biology.

### How Is *Principles of Life* Different?

Each chapter of *Principles of Life* is organized into a series of **Concepts** that are important for mastering introductory biology. We have carefully chosen these concepts in light of feedback from our colleagues, from the Advisory Board, and from the numerous reports examining introductory biology. Concepts are elaborated upon, but not with the extensive detail found in most introductory texts. *Principles of Life* is focused; it is not meant to be encyclopedic.

Students learn concepts best when they apply them to practical problems. Each chapter of *Principles of Life* contains exercises, called **Apply the Concept**, that present data for students to analyze. Each of these exercises reinforces a concept that is central to that chapter. Science students need to understand basic methods for data presentation and analysis, so many of these problems ask students about statistical significance of the results. To help students understand issues in data presentation and interpretation, we have provided a short introduction to the reasoning behind biological statistics in Appendix B.

Although this Appendix is not meant to replace a more formal introduction to statistics, we believe that statistical thinking is an important skill that should be developed in all introductory science courses. We have kept the problems and examples straightforward to emphasize the concepts of statistical analysis rather than the details of any particular statistical test. Some of the *Apply the Concept* exercises are simple enough that they can be presented, analyzed, and discussed in class; others are better suited for homework assignments.

Our **Investigation** figures let students see *how* we know *what* we know. These figures present a Hypothesis, Method, Results, and Conclusion. Most of these *Investigation* figures now include a section titled **Analyze the Data**, in which we have extracted a subset of data from the published experiment. Students are asked to analyze these data and to make connections between observations, analyses, hypotheses, and conclusions. As with *Apply the Concept* problems, students are asked to apply basic statistical approaches to understand the results and draw conclusions. We have also provided original references and extensive online resources for each *Investigation* figure. The online resources are available in LaunchPad, *Principles of Life's* new online platform. These resources include expanded discussions of the original research, links to the original publications, and discussion and links for any follow-up investigations that have been published.

Each chapter begins with an application of a major concept—a story that illustrates and provides a motivation for understanding the chapter's content, and provides a social, medical, scientific, or historical context for the material. Each of these vignettes ends with an open-ended question that students can keep in mind as they read and study the rest of the chapter. We return to this opening question at the close of the chapter to show how information presented throughout the chapter illuminates the question and helps provide an answer. By pondering these questions as they read and study, students can begin to think like scientists.

At the end of each conceptual discussion we provide **Checkpoints** designed to help students self-evaluate their understanding of the material. These *Checkpoints* span the incremental levels of Bloom's Taxonomy of Cognitive Domains: factual knowledge, comprehension, application, analysis, synthesis, and evaluation.

Another important element for student success is reinforcement and application of concepts through online **Animated Tutorials**, **Activities**, and **Media Clips**. Each chapter contains instant access codes (in the form of both a direct URL and a Quick Response, or QR, code, a barcode students can scan with a smartphone or tablet) that allow students to quickly access these online resources while reading. For many concepts, students can conduct their own simulations, explore a concept in greater depth, and understand concepts through active discovery. Using the *Media Clips*, they can also watch videos that help explain concepts or introduce students to the wonders of biological diversity.

Students need to learn about some of the major **Research Tools** that are used in biology, including major laboratory, computational, and field methods. Our *Research Tools* figures

explain these tools and provide a context for how they are used by biologists.

Our art program for *Principles of Life* continues to build on our success from *Life: The Science of Biology*. We pioneered the use of balloon captions to help students understand and interpret the biological processes illustrated in figures without repeatedly going back and forth between a figure, its legend, and the text. These guides help students connect critical points of figures to the concepts that are developed in the text.

## Media and Supplements

The Second Edition of *Principles of Life* features an expanded collection of online resources to support and reinforce the material covered in the textbook. In an effort to more closely link the printed book to the online resources, you will find references with instant access (QR) codes and direct Web addresses for all of the new Media Clips, Animated Tutorials, Activities, and Interactive Summaries throughout the book. These allow students to link instantly to these resources from any device—computer, smartphone, or tablet—while reading the book.

The new **LaunchPad** online platform integrates all of the student resources, instructor resources, the complete eBook, and all assessment tools within a streamlined interface that groups essential content into easily assignable learning units. LaunchPad features a range of assessment tools including the new **LearningCurve** adaptive quizzing engine, and pre-built summative quizzes for each chapter. To support course preparation, classroom sessions, and assessment programs, there is a wide range of instructor resources available, including multiple versions of all textbook figures, a wealth of PowerPoint resources, multiple banks of assessment questions, a large collection of videos, and in-class active learning exercises.

For a complete list of all the media and supplements available for *Principles of Life*, please refer to “Media and Supplements to accompany *Principles of Life*” following this Preface. Also, please refer to the inside front cover for a full list of the student media resources referenced in the text.

## Special Contributions

Many people contributed to the creation of the Second Edition of *Principles of Life* (see below). However, two individuals deserve special mention for their contributions. Susan D. Hill did a masterful job in writing Chapter 38 on Animal Development. Nickolas Waser worked extensively with Mary Price on the Ecology section (Part 7), and was otherwise intimately involved in discussions of the book’s planning and execution.

## Many People to Thank

In addition to the many biologists listed on the next page who provided formal reviews, each of us benefitted enormously from personal contacts with colleagues who helped us resolve issues and made critical suggestions for new material. They are: Walter Arnold, University of Veterinary Medicine (Vienna);

Harry Greene, Cornell University; Will Petry, University of California, Irvine; David Sleboda, Brown University; Thomas Ruf, University of Veterinary Medicine (Vienna); Andrew Zanella, The Claremont Colleges; Edward McCabe, University of Colorado and the March of Dimes Foundation; and Frank Price, Utica College.

Our editor and publisher, Andy Sinauer, embraced the need for change in introductory biology textbooks and has helped make our vision into a reality. Bill Purves, Gordon Orians, and Craig Heller, our co-authors on earlier editions of *Life: The Science of Biology* and/or *Principles of Life*, were instrumental in articulating the concepts developed in this Second Edition of *Principles of Life*, and many aspects of this book can be traced back to their critical contributions.

For this new Edition, Sinauer Associates assembled a talented duo, Laura Green and Danna Niedzwiecki, who coordinated the editorial team and did much of the developmental editing. Annie Reid and Carol Pritchard-Martinez worked to ensure that the level and terminology are appropriate for beginning undergraduate students. Jane Murfett also contributed to developmental editing. Laura and Danna worked closely with a top-notch copyeditor, Liz Pierson. Carol Wigg was the principle production editor on previous editions of *Principles of Life* and *Life: The Science of Biology* and her mark endures. Elizabeth Morales, our artist, again worked with each of us to create effective and beautiful line art. She also revised many figures to make them more effective for people with common forms of color blindness. David McIntyre again rose to the challenge of finding new, even better photographs. Designer Joan Gemme brought a fresh look to the book and did a fine job of assembling all of the book’s elements into clear and attractive pages. Chris Small coordinated production and imposed his exacting standards on keeping the myriad components consistent. Johannah Walkowicz organized and commissioned the many expert academic reviews. Jason Dirks coordinated the team that created the vast array of online media and supplements. Dean Scudder, Director of Sales and Marketing, and Azelie Fortier, Biology Acquisitions Editor, participated in every stage of the book’s development.

At W. H. Freeman, we continue to benefit from the long-term input of Biology Publisher Susan Winslow. John Britch, Director of Marketing, in collaboration with the Regional Specialists, Regional Sales Managers, and the Market Development team, coordinated all the stages of informing Freeman’s skilled sales force of our book’s story. We also wish to thank the Freeman media group for their expertise in producing LaunchPad.

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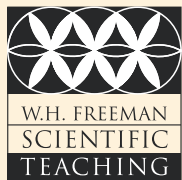
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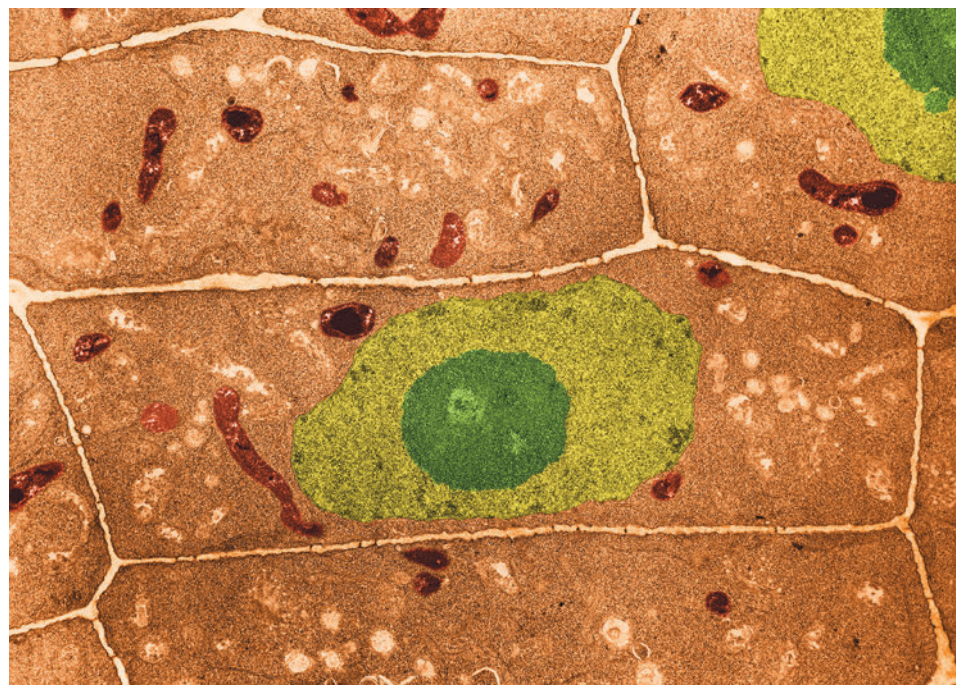
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 Many groups of organisms that arose during the Cambrian later diversified 372  
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Hadobacteria live in extreme environments 385



Cyanobacteria were the first photosynthesizers 385

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- The sexual structures of angiosperms are flowers 439

- Flower structure has evolved over time 440
- Angiosperms have coevolved with animals 441
- The angiosperm life cycle produces diploid zygotes nourished by triploid endosperms 442
- Fruits aid angiosperm seed dispersal 443
- Recent analyses have revealed the phylogenetic relationships of angiosperms 445

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- Segmentation improves control of movement 473
- Appendages have many uses 474
- Nervous systems coordinate movement and allow sensory processing 474

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 Chelicerates are characterized by pointed, nonchewing mouthparts 491  
 Mandibles and antennae characterize the remaining arthropod groups 492  
 More than half of all described species are insects 494

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 Hemichordates are wormlike marine deuterostomes 499  
 Chordate characteristics are most evident in larvae 500  
 Adults of most lancelets and tunicates are sessile 500  
 The vertebrate body plan can support large, active animals 501  
 There are two groups of living jawless fishes 501  
 Jaws and teeth improved feeding efficiency 503  
 Fins and swim bladders improved stability and control over locomotion 503

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 Amphibians adapted to life on land 506  
 Amniotes colonized dry environments 508  
 Reptiles adapted to life in many habitats 508  
 Crocodylians and birds share their ancestry with the dinosaurs 510  
 The evolution of feathers allowed birds to fly 511  
 Mammals radiated as non-avian dinosaurs declined in diversity 511  
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## PART 5 Plant Form and Function

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 The plant body has an apical–basal axis and a radial axis 523  
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 The products of the root's primary meristems become root tissues 528  
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 Ion exchange makes nutrients available to plants 540  
 Fertilizers can be used to add nutrients to soil 541

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 Rhizobia capture nitrogen from the air and make it available to plant cells 543  
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Differences in water potential govern the direction of water movement 545  
 Water and ions move across the root cell's cell membrane 546  
 Water and ions pass to the xylem by way of the apoplast and symplast 547  
 Water moves through the xylem by the transpiration–cohesion–tension mechanism 548  
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Brassinosteroids are plant steroid hormones 566

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Angiosperms have microscopic gametophytes 575

Angiosperms have mechanisms to prevent inbreeding 576

A pollen tube delivers sperm cells to the embryo sac 576

Angiosperms perform double fertilization 577

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A cascade of gene expression leads to flowering 580

Photoperiodic cues can initiate flowering 580

Plants vary in their responses to photoperiodic cues 580

Night length is the key photoperiodic cue that determines flowering 581

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Some plants can tolerate heavy metals 601

## PART 6 Animal Form and Function

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Animals need chemical building blocks to grow and to replace chemical constituents throughout life 606

Animals need inputs of chemical-bond energy to maintain their organized state throughout life 606

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We quantify an animal's metabolic rate by measuring heat production or O<sub>2</sub> consumption 607

Physical activity increases an animal's metabolic rate 608

Among related animals, metabolic rate usually varies in a regular way with body size 609

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Animals are classed as regulators and conformers 609

Regulation is more expensive than conformity 610

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Animals are classed as homeotherms or poikilotherms based on their thermal relationships with their external environment 610

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Fluid compartments are separated from one another by physiologically active epithelia and cell membranes 615

Animals exhibit a high degree of division of labor 616

Division of labor requires a rapid transport system 617

Each cell must make its own ATP 617

Animal cells have aerobic and anaerobic processes for making ATP 617

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Positive feedback occurs in some cases 620

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Food provides chemical building blocks 627

Some nutrients in foods are essential 627

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Processing of food starts in the foregut 636

Food processing continues in the midgut and hindgut 637

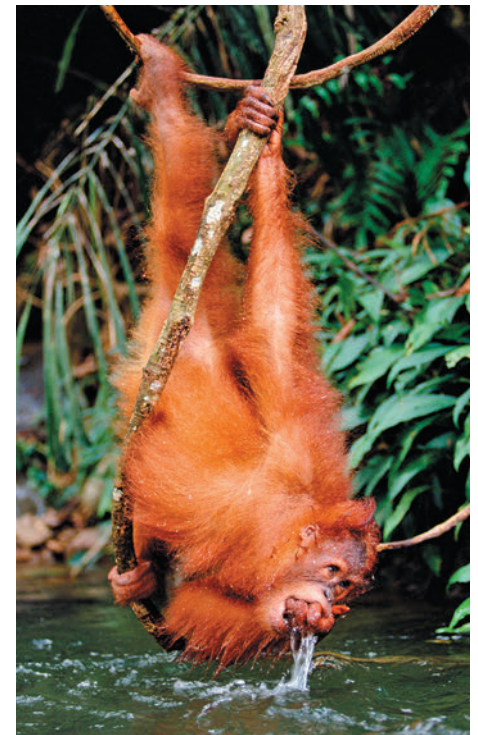
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 Gas transport in animals often occurs by alternating diffusion and bulk flow 646  
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 Air and water are very different respiratory environments 647

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Specialized breathing organs have large surface areas of thin membranes 649  
 The directions of ventilation and perfusion can greatly affect the efficiency of gas exchange 649  
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 Birds have rigid lungs ventilated unidirectionally by air sacs 652  
 Insects have airways throughout their bodies 653

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 The lungs are ventilated by expansion and contraction of the thoracic cavity 656  
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# 1

## Principles of Life

### KEY CONCEPTS

- 1.1 Living Organisms Share Common Aspects of Structure, Function, and Energy Flow
- 1.2 Life Depends on Organization and Energy
- 1.3 Genetic Systems Control the Flow, Exchange, Storage, and Use of Information
- 1.4 Evolution Explains the Diversity as Well as the Unity of Life
- 1.5 Science Is Based on Quantitative Observations, Experiments, and Reasoning



What principles of life are illustrated in this scene?

When you take a walk through the woods and fields or a park near your home, what do you see? Like most people, you probably notice the trees, colorful flowers, and some animals. But do you spend more than a little time thinking about how these living things survive, reproduce, interact with one another, or affect their environment? With the introduction to biology in this book, we would like to inspire you to ask questions about what life is, how living systems work, and how the living world came to be as we observe it today.

Biologists have amassed a huge amount of information about the living world, and some introductory biology classes focus on memorizing these details. In this book we take a different approach, focusing on the major principles of life that underlie everything in biology.

What do we mean by “principles of life”? Look at the photograph. Why is the view so overwhelmingly green? A fundamental principle of life, namely that all living organisms require energy to grow,

move, reproduce, and maintain their bodies, can explain the color. Ultimately, most of that energy comes from the sun. The leaves of plants contain chlorophyll, a green pigment that captures energy from the sun and uses it to transform water and carbon dioxide into sugar and oxygen (in the process called photosynthesis). That sugar stores some of the energy from the sun in its chemical bonds. The plant, or other organisms that eat the plant, can then obtain energy by breaking down the sugar. The frog in the photo used energy to climb up the tree. That energy came from molecules in the bodies of insects eaten by the frog. The insects, in turn, had built up their bodies by ingesting tissues of plant leaves, which grew by using some of the sun’s energy captured through photosynthesis. The frog, like the plants, is ultimately solar-powered, as is the human observer who took this photograph.

The photograph also illustrates other principles of biology. One is that living organisms often survive and thrive by

interacting with one another in complex ways. You probably noticed the frog and the trees. But did you notice the patches of growth on the trunk of the tree? Most of those are lichens, a complex interaction between a fungus and a photosynthetic organism (in this case, a kind of alga). In lichens, the fungus and the alga depend on each other for survival. Many other organisms in this scene are too small to be seen, but they are critical components for keeping this living system functioning over time.

After reading this book, you should understand the main principles of life. You’ll be able to describe how organisms capture and transform energy; pass genetic information to their offspring in reproduction; grow, develop, and behave; and interact with other organisms and with their physical environment. You will also have learned how this system of life on Earth evolved, and how it continues to change. May a walk in the park never be the same for you again!

## CONCEPT 1.1 Living Organisms Share Common Aspects of Structure, Function, and Energy Flow

Biology is the scientific study of life, which encompasses all living things, or **organisms**. The living things we know about are all descended from a single-celled ancestor that lived on Earth almost 4 billion years ago. We can imagine that something with some similarities to life as we know it might have originated differently, perhaps on other planets. But the evidence suggests that all of life on Earth today has a single origin—a single common ancestor—and we consider all the organisms that descended from that common ancestor to be a part of life.

### Life as we know it had a single origin

The overwhelming evidence for the common ancestry of life lies in the many characteristics that are shared among living organisms. Typically, living organisms

- are composed of a common set of chemical parts, such as nucleic acids (one example is DNA, which is the important molecule that carries our genetic information) and amino acids (the chemical building blocks that make up proteins), and similar structures, such as cells enclosed within membranes
- depend on intricate interactions among structurally complex parts to maintain the living state
- contain genetic information that uses a nearly universal code to specify how proteins are assembled
- convert molecules obtained from their environment into new biological molecules
- extract energy from the environment and use it to carry out life functions
- replicate their genetic information in the same manner when reproducing themselves
- share structural similarities among a fundamental set of genes
- evolve through gradual changes in their genetic information

Taken together, these shared characteristics logically lead to the conclusion that all life has a common ancestry, and that the diverse organisms that exist today originated from one life form. If life had multiple origins, there would be little reason to expect a nearly universal genetic code, or the similarities among many genes, or a common set of amino acids. If we were to discover something similar to life, such as a self-replicating system that originated independently on another planet, we would expect it to be fundamentally different in these aspects. It might be similar in some ways to life on Earth, such as using genetic information to reproduce. But we would not expect the details of its genetic code, for example, to be like ours.

The simple list of shared characteristics above, however, does not describe the incredible complexity and diversity of life. Some forms of life may not even display all of these

characteristics all of the time. For example, the seed of a desert plant may exist for many years in a dormant state in which it doesn't extract energy from the environment, convert molecules, or reproduce. Yet the seed is alive.

And then there are viruses, which are not composed of cells and cannot carry out physiological functions on their own. Instead they use the cells they invade to perform these functions for them. Yet viruses contain genetic information, and they mutate and evolve. So even though viruses are not independent cellular organisms, their existence depends on cells, and there is strong evidence that viruses evolved from cellular life forms. For these reasons, most biologists consider viruses to be a part of life. But as viruses illustrate, the boundaries between "living" and "nonliving" are not always clear, and all biologists do not agree exactly on where we should draw the lines.

### Major steps in the history of life are compatible with known physical and chemical processes

Geologists estimate that Earth formed between 4.6 and 4.5 billion years ago. At first the planet was not a very hospitable place. It was some 600 million years or more before the earliest life evolved. If we picture the history of Earth as a 30-day month, with each day representing about 150 million years, life first appeared somewhere toward the end of the first week (**FIGURE 1.1**).

How might life have arisen from nonliving matter? In thinking about this question, we must take into account that the young Earth's atmosphere, oceans, and climate all were very different than they are today. Biologists have conducted many experiments that simulate the conditions on early Earth. These experiments have confirmed that the formation of complex organic molecules under such conditions is possible, even probable.

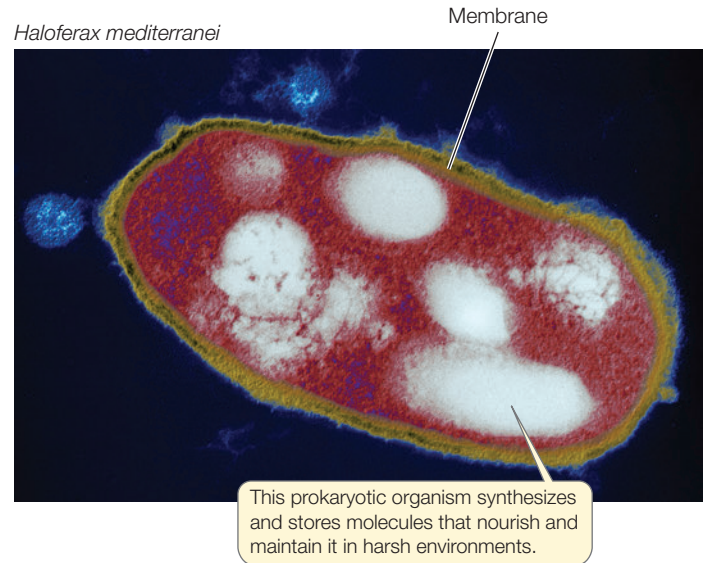
The critical step for the evolution of life, however, was the appearance of **nucleic acids**—molecules that could reproduce themselves and also contain the information for the synthesis, or manufacture, of large molecules with complex but stable shapes. These large, complex molecules were proteins. Their shapes varied enough to enable them to participate in increasing numbers and kinds of chemical reactions with other molecules.

### CELLULAR STRUCTURE EVOLVED IN THE COMMON ANCESTOR OF LIFE

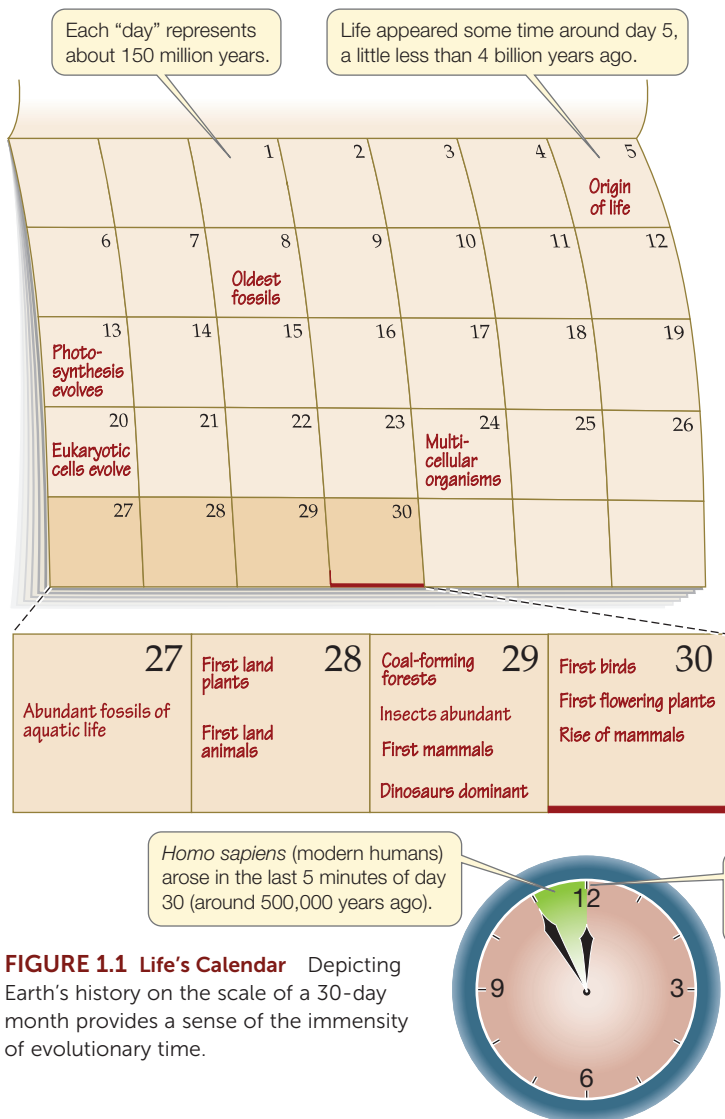
In the next big step in the origin of life, a membrane surrounded and enclosed complex proteins and other biological molecules, forming a tiny **cell**. This membrane kept the enclosed components separate from the surrounding external environment. Molecules called fatty acids played a critical role because these molecules form membrane-like films instead of dissolving in water. When agitated, these films can form hollow spheres, which could have enveloped assemblages of biological molecules. The creation of a cell interior, separate from the external environment, allowed the reactants and products of chemical reactions to be concentrated, opening up the possibility that those reactions could be integrated and controlled. This natural process of membrane formation likely resulted in the first cells with the ability to reproduce—the evolution of the first cellular organisms.

For more than 2 billion years after cells originated, every organism consisted of only one cell. These first organisms were **prokaryotes**, which are made up of single cells containing genetic material and other biochemical structures enclosed in a membrane (FIGURE 1.2). Vast numbers of their descendants, such as bacteria, exist in similar form today. Early prokaryotes were confined to the oceans, which had an abundance of complex molecules they could use as raw materials and sources of energy. The oceans also shielded them from the damaging effects of ultraviolet (UV) light, which was intense at that time because there was little or no oxygen (O<sub>2</sub>) in the atmosphere, and for that reason, no protective ozone (O<sub>3</sub>) layer in the upper atmosphere.

**PHOTOSYNTHESIS ALLOWED LIVING ORGANISMS TO CAPTURE THE SUN'S ENERGY** To fuel the chemical reactions inside them, the earliest prokaryotes took in molecules directly from their environment and broke down these small molecules to release and use the energy contained in their chemical bonds. Many modern prokaryotes still function this way, and very successfully.



**FIGURE 1.2 The Basic Unit of Life Is the Cell** The concentration of reactions within the enclosing membrane of a cell allowed the evolution of integrated organisms. Today all organisms, even the largest and most complex, are made up of cells. Single-celled organisms such as this one, however, remain the most abundant living organisms (in absolute numbers) on Earth.



**FIGURE 1.1 Life's Calendar** Depicting Earth's history on the scale of a 30-day month provides a sense of the immensity of evolutionary time.

About 2.7 billion years ago, or on day 13 of our imaginary month-long calendar of life, the emergence of photosynthesis changed the nature of life on Earth (see Figure 1.1). **Photosynthesis** is a set of chemical reactions that transforms the energy of sunlight into chemical-bond energy of the sugar glucose and other relatively small biological molecules. In turn, the chemical-bond energy of these small molecules can be tapped to power other chemical reactions inside cells, including the synthesis of large molecules, such as proteins, that are the building blocks of cells.

Photosynthesis is the basis of much of life on Earth today because its energy-capturing processes provide food for other organisms. Photosynthetic organisms use solar energy to build their tissues, and then other organisms use those tissues as food. Early photosynthetic cells were probably similar to the present-day prokaryotes called cyanobacteria (FIGURE 1.3). Over time, photosynthetic prokaryotes became so abundant that they produced vast quantities of O<sub>2</sub> as a by-product of photosynthesis.

During the early eons of life on Earth, there was no O<sub>2</sub> in the atmosphere. In fact, O<sub>2</sub> was poisonous to many of the prokaryotes that lived at that time. But those organisms that tolerated O<sub>2</sub> were able to proliferate as O<sub>2</sub> slowly began to accumulate in the atmosphere. The presence of O<sub>2</sub> opened up vast new avenues of evolution. **Aerobic metabolism**, a set of chemical reactions that releases energy from life's molecules by using O<sub>2</sub>, proved to be more efficient than **anaerobic metabolism**, a set of reactions that extracts energy without using O<sub>2</sub>. For this reason, O<sub>2</sub> allowed organisms to live more intensely and grow larger. The majority of living organisms today use O<sub>2</sub> in extracting energy from molecules.

(A)



(B)



**FIGURE 1.3 Photosynthetic Organisms Changed Earth's Atmosphere** Cyanobacteria were the first photosynthetic organisms on Earth. (A) Colonies of cyanobacteria called stromatolites are known from the ancient fossil record. (B) Living stromatolites are still found in suitable environments on Earth today.

Oxygen in the atmosphere also made it possible for life to move onto land. For most of life's history, UV radiation falling on Earth's surface was so intense that it destroyed any living cell that was not well shielded by water. But as a result of photosynthesis,  $O_2$  accumulated in the atmosphere for more than 2 billion years and gradually resulted in a layer of ozone in the upper atmosphere. By about 500 million years ago, or about day 28 on our imaginary calendar of life, the ozone layer was sufficiently dense and absorbed enough of the sun's UV radiation to make it possible for organisms to leave the protection of the water and live on land (see Figure 1.1).

#### EUKARYOTIC CELLS AROSE THROUGH ENDOSYMBIOSIS

Another important, earlier step in the history of life was the evolution of cells with membrane-enclosed compartments called **organelles**. Organelles were—and are—important because specialized cellular functions could be performed inside them, separated from the rest of the cell. The first organelles probably appeared about 2.5 billion years after life first appeared on Earth, or about day 20 on Figure 1.1.

One of these organelles, the **nucleus**, came to contain the cell's genetic information. The nucleus (Latin *nux*, “nut” or “core”) gives these cells their name: **eukaryotes** (Greek *eu*, “true”; *karyon*, “kernel” or “core”). The eukaryotic cell is distinct from the cells of prokaryotes (*pro*, “before”), which lack nuclei and other internal compartments.

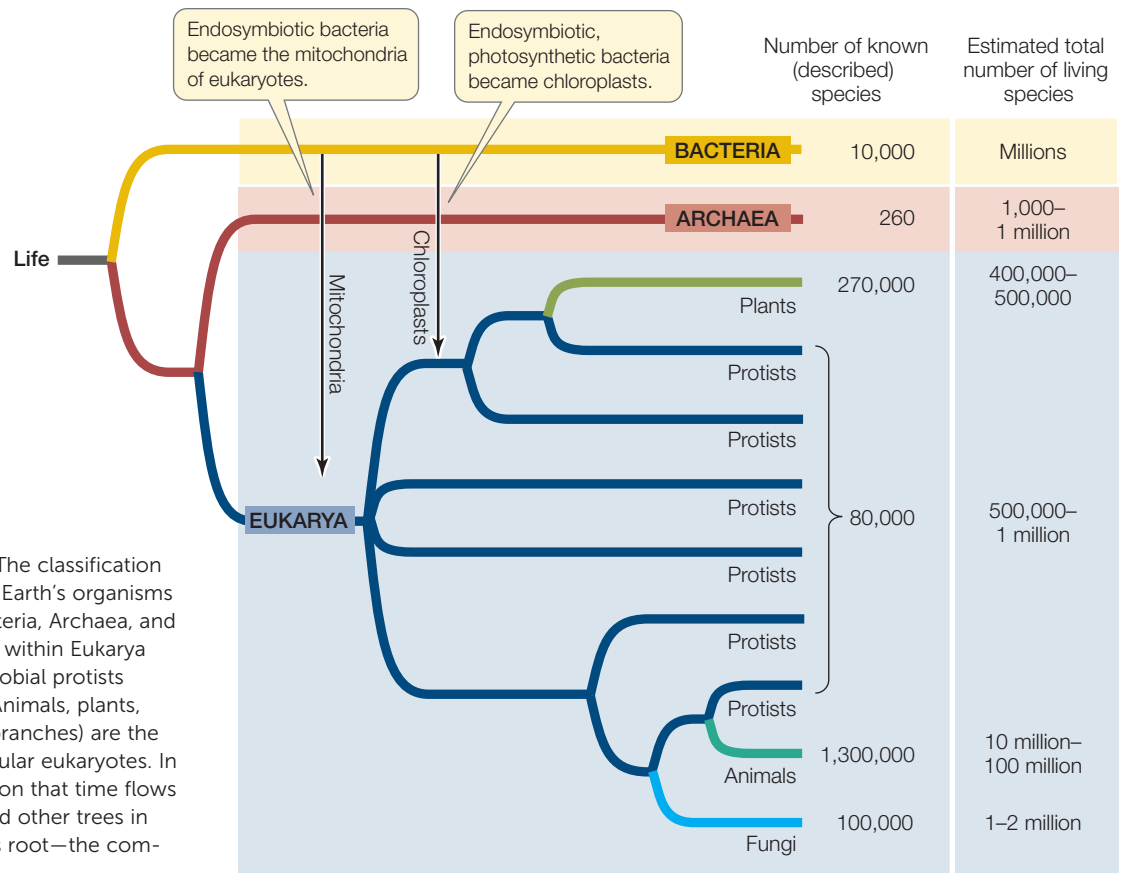
Some organelles are hypothesized to have originated by **endosymbiosis**, which means “living inside another” and may have occurred when larger cells ingested smaller ones. The **mitochondria** that release energy for use by a eukaryotic cell probably evolved from engulfed prokaryotic organisms. And **chloroplasts**—the organelles specialized to conduct photosynthesis in eukaryotic photosynthetic organisms—could have originated when larger eukaryotes ingested photosynthetic prokaryotes. If the larger cell failed to break down this intended food object, a partnership could have evolved in which the ingested prokaryote provided sugars from photosynthesis and the host cell provided a good environment for its smaller partner.

**MULTICELLULARITY ALLOWED SPECIALIZATION OF TISSUES AND FUNCTIONS** For the first few billion years of life, all organisms—whether prokaryotic or eukaryotic—were single-celled. At some point, the cells of some eukaryotes failed to separate after cell division and remained attached to each other. These groupings of cells made it possible for some cells in the group to specialize in certain functions, such as reproduction, while other cells specialized in other functions, such as absorbing nutrients. **Cellular specialization** enabled multicellular eukaryotes to increase in size and become more efficient at gathering resources and living in specific environments.

#### Biologists can trace the evolutionary tree of life

If all the organisms on Earth today are the descendants of a single kind of unicellular organism that lived almost 4 billion years ago, how have they become so different? An organism reproduces by replicating its **genome**, which is the sum total of its genetic material, as we will discuss shortly. This replication process is not perfect, however, and changes, called **mutations**, are introduced almost every time a genome is replicated. Some mutations give rise to structural and functional changes in organisms. As individuals mate with one another, these changes can spread within a population, but the population continues to be made up of one kind, or species, of organism. However, if something happens to isolate some members of a population from the others, structural and functional differences between the two groups will accumulate over time. The two groups may eventually differ enough that their members no longer regularly reproduce with one another. In this way the two populations become two different species.

Tens of millions of species exist on Earth today. Many times that number lived in the past but are now extinct. As biologists discover species, they give each one a scientific name called a **binomial** (because it is made up of two Latinized words). The first word identifies the species' genus—a group of species that share a recent common ancestor. The second word indicates the species. For example, the scientific name for the



**FIGURE 1.4 The Tree of Life** The classification system used in this book divides Earth’s organisms into three primary domains: Bacteria, Archaea, and Eukarya. The dark blue branches within Eukarya represent various groups of microbial protists (mostly unicellular eukaryotes). Animals, plants, and fungi (green and turquoise branches) are the most familiar groups of multicellular eukaryotes. In this book we adopt the convention that time flows from left to right, so this tree (and other trees in this book) lies on its side, with its root—the common ancestor—at the left.

human species is *Homo sapiens*: *Homo* is our genus and *sapiens* our species. *Homo* is Latin for “man,” and *sapiens* is from the Latin word for “wise” or “rational.” Our closest relatives in the genus *Homo* are the Neanderthals (*Homo neanderthalensis*), which are now extinct and are known only from fossil remains.

Much of biology is based on comparisons among species. Our ability to make relevant comparisons has improved greatly in recent decades as a result of our relatively newfound ability to study and compare the genomes of different species. We do this by sequencing a genome (in whole or in part), which means we can determine the order of the nucleotides that serve as the building blocks of the organism’s DNA. Genome sequencing and other molecular techniques have allowed biologists to add a vast array of molecular evidence to existing evolutionary knowledge based on the fossil record. The result is the ongoing compilation of **phylogenetic trees** that document and diagram evolutionary relationships as part of an overarching **tree of life**. The broadest categories of this tree are shown in **FIGURE 1.4**. (The tree is expanded in Appendix A, and you can also explore the tree interactively online.)

Many details remain to be clarified, but the broad outlines of the tree of life have been determined. Its branching patterns are based on a rich array of evidence from fossils, structures, chemical processes, behavior, and molecular analyses of genomes. Molecular data in particular have been used to separate the tree into three major branches called **domains**: Archaea, Bacteria, and Eukarya. The organisms of each domain have been

evolving separately from those in the other domains for more than a billion years. Note that all organisms that are alive today descended from common ancestors in the past. In other words, living species did not evolve from other species living today. Rather, all living organisms evolved from now-extinct common ancestors. For example, humans did not evolve from our close relatives, the chimpanzees, but humans and chimpanzees both evolved from a common (now extinct) ancestral species.

Organisms in the domains **Archaea** and **Bacteria** are single-celled prokaryotes. However, members of these two groups differ so fundamentally that they are thought to have separated into distinct evolutionary lineages very early. Species belonging to the third domain—**Eukarya**—have eukaryotic cells whose mitochondria and chloroplasts originated from endosymbioses with bacteria, as we have described.

Plants, fungi, and animals are examples of familiar multicellular eukaryotes. We know that multicellularity arose independently in each of these three multicellular groups because they are each most closely related to different groups of unicellular eukaryotes (commonly called protists), as you can see from the branching pattern of Figure 1.4.

### Life’s unity allows discoveries in biology to be generalized

Knowledge gained from investigations of one kind of organism can, with care, be generalized to other organisms because all life is related by descent from a common ancestor, shares a genetic

code, and consists of similar molecular building blocks. Biologists use certain **model organisms** for research, knowing they can extend their findings to other organisms, including humans.

Our basic understanding of the chemical reactions in cells came from research on bacteria but is applicable to all cells, including those of humans. Similarly, the biochemistry of photosynthesis—the process by which plants use sunlight to produce sugars—was largely worked out from experiments on *Chlorella*, a unicellular green alga. Much of what we know about the genes that control plant development is the result of work on *Arabidopsis thaliana*, a member of the mustard family. Knowledge about how animals develop has come from work on sea urchins, frogs, chickens, roundworms, and fruit flies. And recently, the discovery of a major gene controlling human skin color came from work on zebrafish. Being able to generalize from model systems is a powerful tool in biology.

### CONCEPT Life Depends on Organization 1.2 and Energy

All of life depends on organization. Physics gives us the second law of thermodynamics, which states that, left to themselves, organized entities tend to become more random. Any loss of organization threatens the well-being of organisms. Cells, for example, must combat the thermodynamic tendency for their molecules, structures, and systems to lose organization—to become disorganized. Energy is required to maintain organization. For this reason, cells require energy throughout their lives.

#### Organization is apparent in a hierarchy of levels from molecules to ecosystems

Cells synthesize, or manufacture, proteins and other complex molecules by assembling atoms into new, highly organized configurations. Such complex molecules give cells their structure and enable them to function. For example, a fatty acid molecule that the cell synthesizes may become part of a membrane that structures the inside of the cell by dividing it into compartments. Or a protein made by a cell may enable a specific chemical reaction to take place in the cell by helping start or speed up the reaction—that is, by acting as a catalyst for the reaction.

Organization is also essential for many cells to function together in a multicellular organism. As we have seen,

multicellularity allows individual cells to specialize and depend on other cells for functions they themselves do not perform. But the different specialized cells also work together. For example, division of labor in a multicellular organism usually requires a circulatory system so that the functions of specialized cells in one part of the body are of use to cells in other, distant parts of the body.

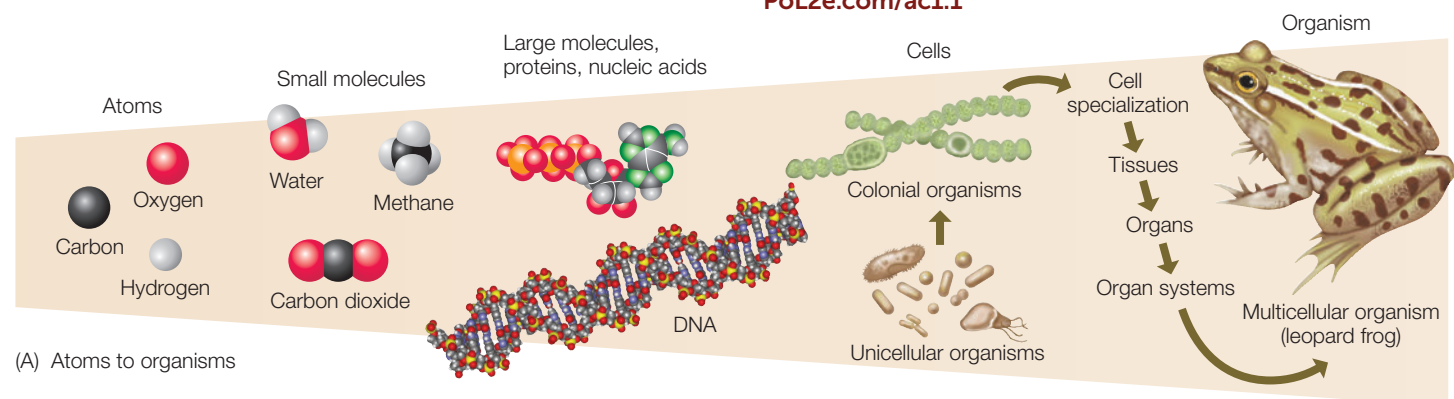
Overall, a multicellular organism exhibits many hierarchical levels of organization (**FIGURE 1.5A**). Small molecules are organized into larger ones, such as DNA and proteins. Large molecules are organized into cells, and assemblages of differentiated cells are organized into **tissues**. For example, a single muscle cell cannot generate much force, but when many cells combine to form the tissue of a working muscle, considerable force and movement can be generated. Different tissue types are organized to form **organs** that accomplish specific functions. The heart, brain, and stomach are each constructed of several types of tissues, as are the roots, stems, and leaves of plants. Organs whose functions are interrelated can be grouped into **organ systems**; the esophagus, stomach, and intestines, for example, are all part of the digestive system. Because all these levels of organization are subject to the second law of thermodynamics, they all tend to degrade unless energy is applied to the system. This is why an organism must use energy to maintain its functions.

Matching the internal hierarchy of an individual organism is an external hierarchy in the larger biological world where organisms interact with their physical environment—an **ecological system**, often shortened to **ecosystem** (**FIGURE 1.5B**). Individual organisms interacting with their immediate

#### FIGURE 1.5 Life Consists of Organized Systems at a Hierarchy of Scales

(A) The hierarchy of systems within a multicellular organism. DNA—a molecule—encodes the information for cells—a higher level of organization. Cells, in turn, are the components of still higher levels of organization: tissues, organs, and the organism itself. (B) Organisms interacting with their external environment form ecological systems on a hierarchy of scales. Individual organisms form the smallest ecological system. Individuals of a species form populations, which interact with other populations to form communities. Multiple communities in turn interact within landscapes at progressively larger scales until they include all the landscapes and organisms of Earth: the entire biosphere.

#### Go to ACTIVITY 1.1 The Hierarchy of Life [PoL2e.com/ac1.1](http://PoL2e.com/ac1.1)





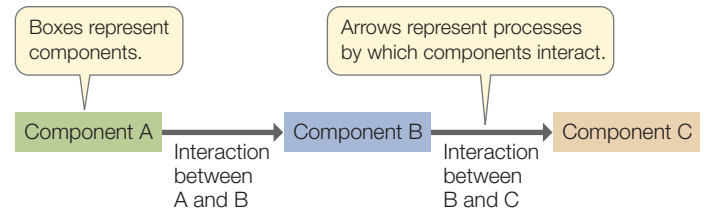
environment form the smallest ecological system. Groups of individuals of any one species live together and interact in **populations**, and populations of different species that live and interact in a single area form ecological **communities**. Multiple communities interact within **landscapes**. The landscape of the entire Earth and all its life is known as the **biosphere**.

But there are some important differences between biological systems at the organismal level and these larger scales. All the hierarchical levels of organization within an individual organism are encoded by its single genome, so that these levels generally interact harmoniously. By contrast, the external hierarchy of populations, communities, and landscapes involves interactions among multiple species with multiple genomes, so that interactions are not always harmonious. For example, individuals often prevent others of their own species from exploiting a necessary resource such as food, or they exploit members of their own or different species as food.

### Each level of biological organization consists of systems

We have already discussed organ systems and ecological systems. More generally, a **system** is a set of interacting parts in which neither the parts nor the whole can be understood without taking into account the interactions. A simple biological system might consist of a few **components** (e.g., proteins, pools of nutrients, or organisms) and the **processes** by which the components interact (e.g., protein synthesis, nutrient metabolism, or grazing) (**FIGURE 1.6**).

Consider, for example, the system within a cell that synthesizes and controls the quantity of a particular protein, which we'll call Protein T (**FIGURE 1.7A**). The components of the system are the amino acids from which Protein T is made, Protein T, and the breakdown products of Protein T. The processes are the biochemical pathways that synthesize and break down Protein T. To understand how the cell controls the amount of Protein T, we must understand how all the other components and processes in this system function.



**FIGURE 1.6 A Generalized System** Systems in cells, whole organisms, and ecosystems can be represented with boxes and arrows.

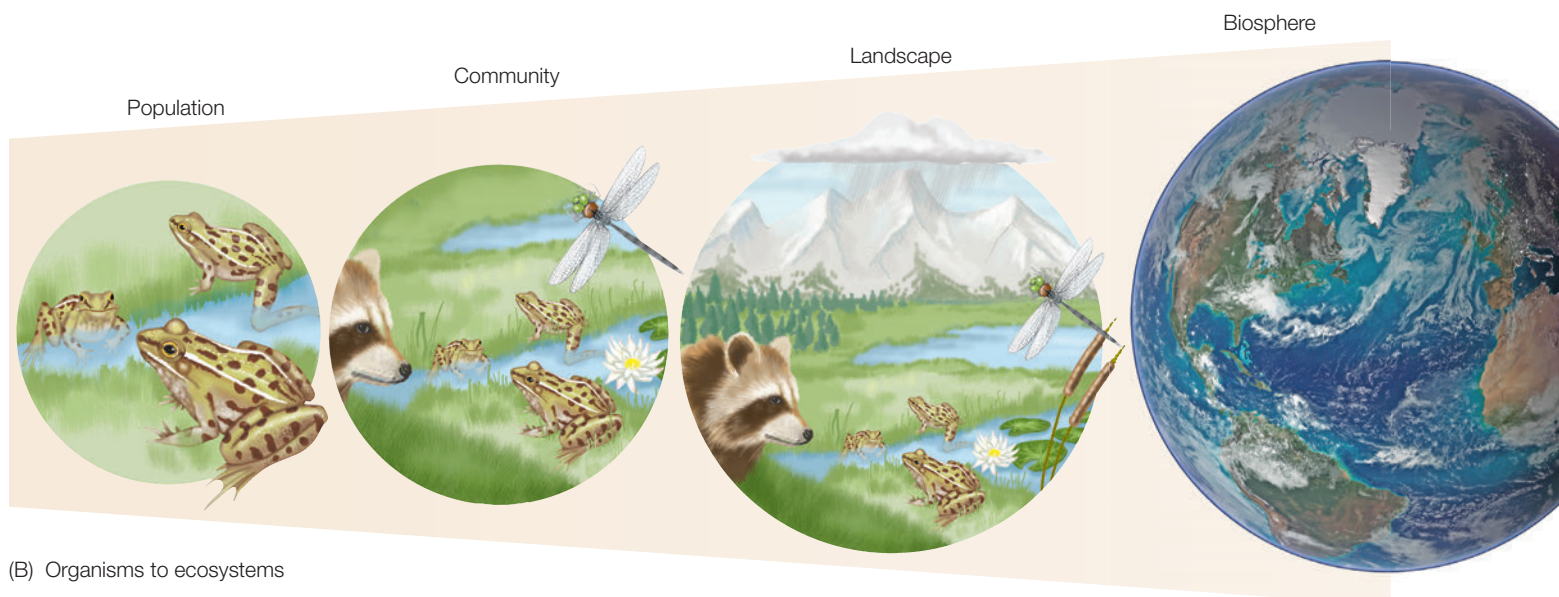
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System Simulation  
[Pol2e.com/at1.1](https://pol2e.com/at1.1)

Systems are found at every level of biological organization. For example, our bodies have a physiological system that controls the amount of sodium ( $\text{Na}^+$ ) in our body fluids (**FIGURE 1.7B**). Grass, voles, and predators (foxes and owls) are components of a community-level system (**FIGURE 1.7C**).

### Biological systems are highly dynamic even as they maintain their essential organization

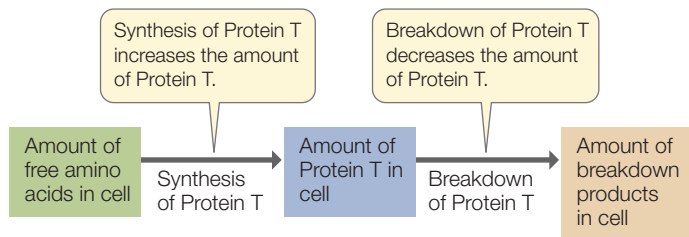
Given the central importance of organization, you might think that biological systems are inflexible and static. Actually, they are often incredibly dynamic—characterized by rapid flows of matter and energy. On average, for example, a cell in your body breaks down and rebuilds 2–3 percent of its protein molecules per day. Each day it also makes and uses more than 100,000 trillion ( $10^{14}$ ) molecules of adenosine triphosphate (ATP), the molecule responsible for shuttling energy from sources to uses. Collectively, all the cells in your body liberate more than 90 grams of hydrogen every day from the foods they break down to obtain energy. Your cells also combine that hydrogen with oxygen ( $\text{O}_2$ ) to make almost a liter of water every day.

This dynamic aspect of biological systems means that they constantly exchange energy and matter with their surroundings. For example, even after a single-celled or multicellular

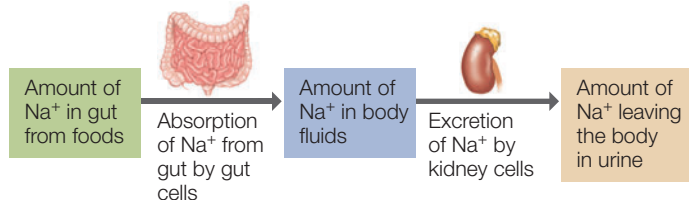


(B) Organisms to ecosystems

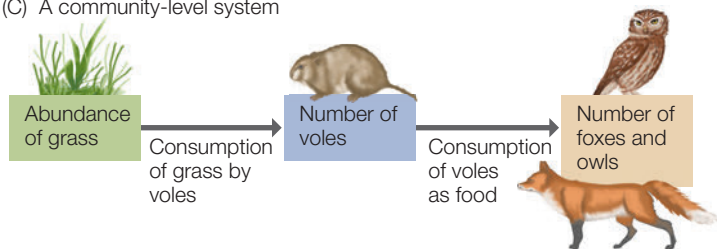
(A) A cellular-level system



(B) An organismal-level system



(C) A community-level system



**FIGURE 1.7 Organized Systems Exist at Many Levels** (A) This cellular-level system synthesizes and breaks down a cell protein called Protein T. (B) This organismal-level system determines the amount (and thus the concentration) of sodium ( $\text{Na}^+$ ) in the blood plasma and other extracellular body fluids of a human. (C) This community-level system helps determine the number of meadow voles (*Microtus pennsylvanicus*) in a field in the spring.

organism has reached maturity, most of its molecules are steadily replaced. In this ceaseless, dynamic process, atoms are lost from the cells in the organism to the surrounding soil, air, or water, and they are replaced with atoms from the soil, air, or water. Yet as the atomic building blocks of any particular cell come and go, the organization of the molecules, structures, and systems in the cell persists. This fact emphasizes the central importance of organization.

### Positive and negative feedback are common in biological systems

Often, the amount of one of the components of a system, such as component C in **FIGURE 1.8**, affects the rate of one of the earlier processes in the system. This effect is called **feedback** and may be described as positive or negative. Feedback is often diagrammed simply with a line and symbol, but its actual mechanism may be complex.

**Positive feedback** occurs in a system when a product of the system *speeds up* an earlier process. The effect of positive feedback is to cause the product to be produced faster and faster. To return to one of our earlier examples, if the breakdown products of Protein T sped up synthesis of Protein T, this would lead to more breakdown products, then even more Protein T, then even more breakdown products, and so on. Positive

feedback tends to destabilize a system, but destabilization can sometimes be advantageous, provided it is ultimately brought under control.

**Negative feedback** occurs when a product of a system *slows down* an earlier process in the system. Often, as the product increases in amount or concentration, it exerts more and more of a slowing effect. Negative feedback stabilizes the amount of the product in this way: if a high amount of the product accumulates, that accumulation tends to reduce further production of the product. For example, if an increase in the amount of breakdown products of Protein T slowed down synthesis of Protein T, this would lead to a decreased amount of breakdown products and a return to the previous rate of Protein T synthesis. Negative feedback is very common in **regulatory systems**, which are systems that tend to stabilize amounts or concentrations.

### Systems analysis is a conceptual tool for understanding all levels of organization

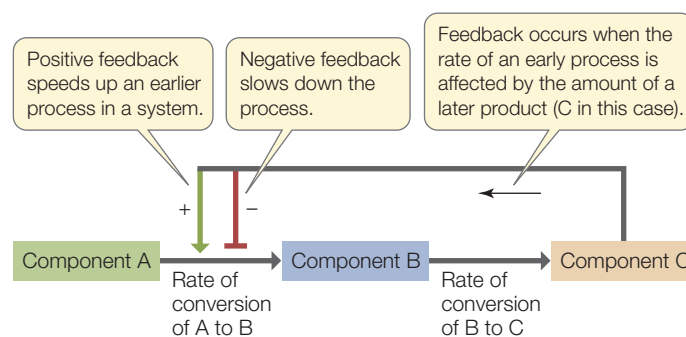
Biologists today employ an approach known as **systems analysis** to understand how biological systems function. In systems analysis, we identify the parts or components of a biological system and specify the processes by which the components interact (see Figure 1.6). We may also be able to specify the *rates* of these interactions and how the rates are affected by feedback. What we can do then is analyze how the system will change through time. Will the amounts of different components increase or decrease, and how quickly, and how will this depend on the rates of the interactions? Will there be any stable balance, or equilibrium, that the system eventually reaches?

To do the analysis we write out mathematical equations that express the amounts of the different components and that include the processes and their rates. Expressed in words, such an equation for component B in Figure 1.6 has the following form:

$$\begin{aligned} \text{The amount of B present at some time in the future} = \\ \text{the amount of B now} + \text{the amount of A converted into B} \\ - \text{the amount of B converted into C} \end{aligned}$$

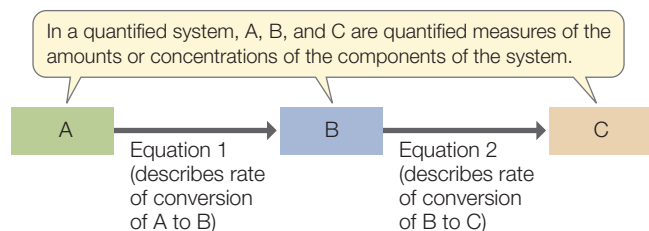
We write out a similar equation for each component in the system.

We can analyze the relatively simple biological systems in Figure 1.7 by hand, but the analysis of larger systems quickly



**FIGURE 1.8 Feedback Can Be Positive or Negative** Positive feedback tends to destabilize a system, whereas negative feedback typically stabilizes a system.

becomes very complicated and is typically carried out using computers. The approach, however, is the same: We express the rates of all processes as mathematical equations.



After this analysis is done, we have a **computational model** of the biological system. If the computational model is well grounded in factual knowledge of the biological system, the model will mimic the biological system.

An important use of computational models is prediction. For instance, if atmospheric temperature affects a biological system, we can use a computational model to develop a hypothetical prediction of the future behavior of the system in a warming world by adjusting the model to take into account the expected increases in temperature.

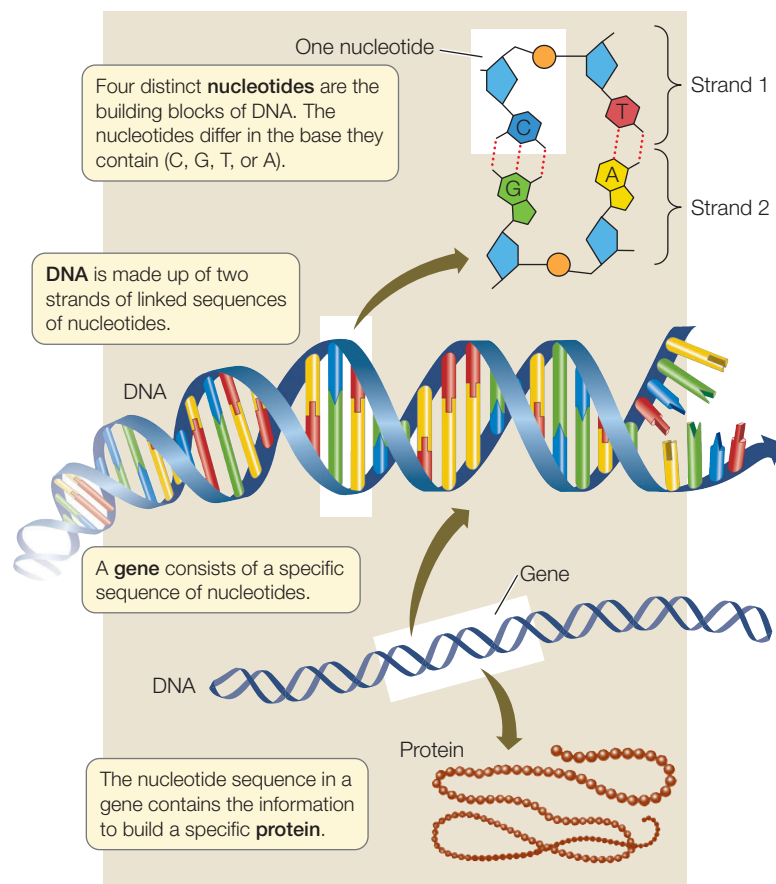
### CONCEPT 1.3 Genetic Systems Control the Flow, Exchange, Storage, and Use of Information

The information required for an organism to function—the “blueprint” for its existence—is contained in the organism’s genome, which as we noted earlier is the sum total of all the information encoded by its genes. The presence of genetic information and the processes by which organisms “decode” and use it to build the proteins that underlie a body’s structure and function involve fundamental principles that we will discuss and expand on throughout the book, especially in Chapters 10–14.

#### Genomes encode the proteins that govern an organism’s structure

Early in the chapter we noted the importance of self-replicating nucleic acids in the origin of life. Nucleic acid molecules contain long sequences of four subunits called **nucleotides**. The sequence of these nucleotides in **deoxyribonucleic acid**, or **DNA**, allows the organism to assemble **proteins**. Each **gene** is a specific segment of DNA whose sequence carries the information for building, or controlling the building of, one or more proteins (**FIGURE 1.9**). Proteins, in turn, are the molecules that govern the chemical reactions within cells and form much of an organism’s structure. For these reasons, in biology we often say that genes “encode” proteins.

By analogy with a book, the nucleotides of DNA are like the letters of an alphabet. The sentences in the book are genes that encode proteins, which means that the genes provide instructions for making the proteins at a particular time or place. If you were to write out your own genome using four letters to represent the four DNA nucleotides, you would write more



**FIGURE 1.9 DNA Is Life’s Blueprint** The instructions for life are contained in the sequences of nucleotides in DNA molecules. Specific DNA nucleotide sequences comprise genes. The average length of a single human gene is 27,000 nucleotides. The information in each gene provides the cell with the information it needs to manufacture molecules of a specific protein.

than 3 billion letters. Using the size type you are reading now, your genome would fill more than 1,000 books the size of this one.

All the cells of a given multicellular organism contain the same genome, yet the different cells have different functions and form different proteins. For example, oxygen-carrying hemoglobin occurs in red blood cells, gut cells produce digestive proteins, and so on. Therefore different types of cells in an organism must express, or use, different parts of the genome. How any given cell controls which genes it expresses, or uses (and which genes it suppresses, or doesn’t use), is a major focus of current biological research.

The genome of an organism contains thousands of genes. If mutations alter the nucleotide sequence of a gene, the protein that the gene encodes is often altered as well. Mutations may occur spontaneously, as happens when mistakes take place during replication of DNA. Mutations can also be caused by certain chemicals (such as those in cigarette smoke) and radiation (including UV radiation from the sun). Most mutations either are harmful or have no effect. Occasionally a mutation improves the functioning of the organism under the environmental conditions the individual encounters. Mutations are the raw material of evolution.