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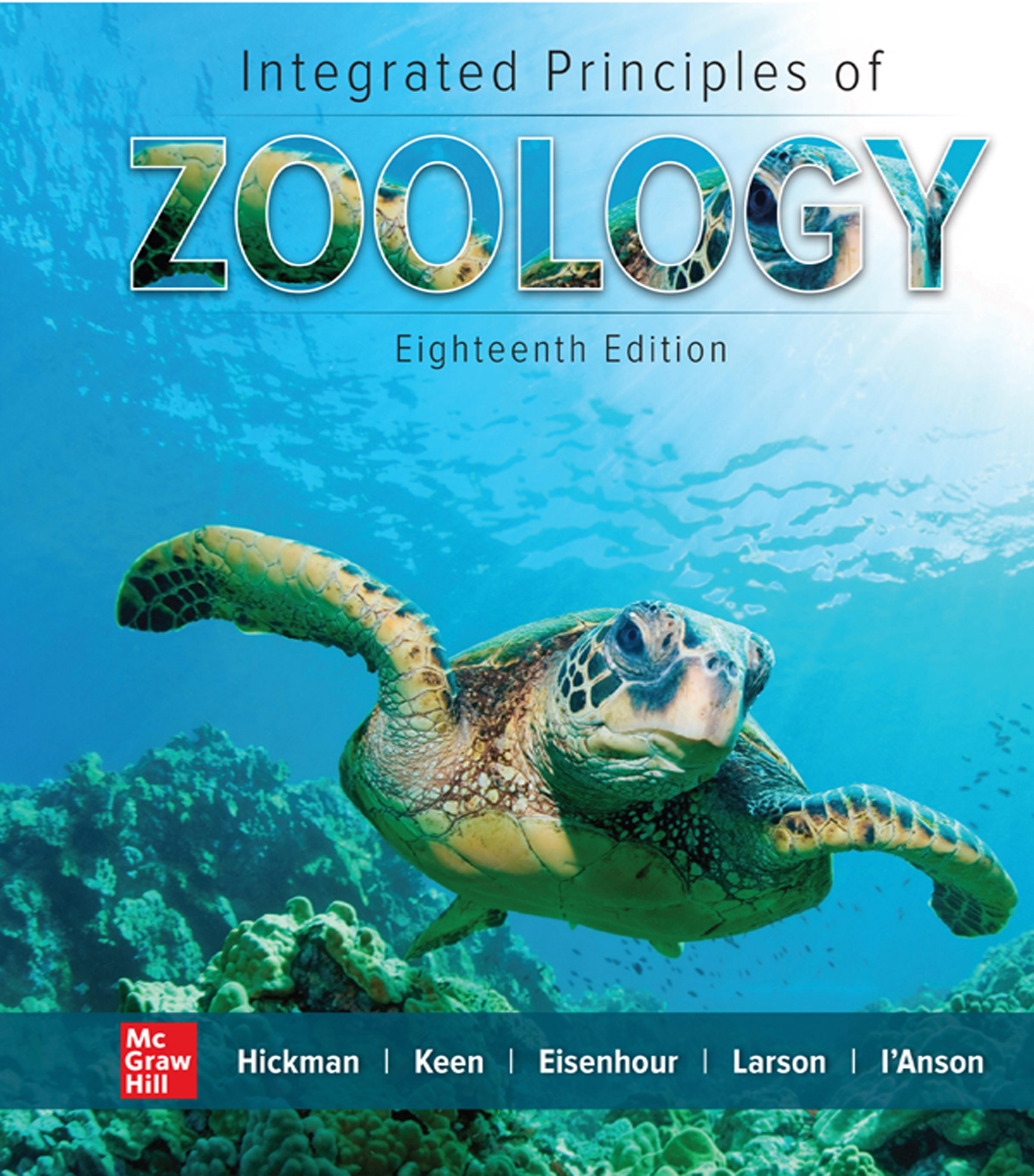

Integrated Principles of ZOOLOGY

Eighteenth Edition

McGraw Hill

Hickman | Keen | Eisenhour | Larson | I'Anson

INTEGRATED PRINCIPLES OF

ZOOLOGY

EIGHTEENTH EDITION

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INTEGRATED PRINCIPLES OF ZOOLOGY

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Over the years Dr. Hickman has led many field trips to the Galápagos Islands. His research is on intertidal zonation and marine invertebrate systematics in the Galápagos. He has published four field guides in the Galápagos Marine Life Series for the identification of echinoderms, marine molluscs, corals, and marine crustaceans.

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Dr. Keen is an invertebrate zoologist fascinated with sea jelly life histories, in particular those where both asexual and sexual phases of organisms are present, as in most jellies. Other research has included work on sessile marine invertebrate communities, spider populations, Andean potato evolution, and most recently how students learn.

Dr. Keen has been teaching evolution and animal diversity within the Introductory Biology series for 25 years. She enjoys all facets of the teaching process, from lectures and discussions to the design of effective laboratory exercises. In addition to her work with introductory biology, she works with an animator to create self-guided teaching modules on animal development. She attended the National Academies Summer Institute on Undergraduate Education in Biology, and was a National Academies Education Fellow in the Life Sciences for 2005–2006.

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Helen I'Anson, a native of England, is the John T. Perry Professor of Biology and Research Science at Washington and Lee University in Lexington, Virginia. She received her Ph.D. in physiology at the University of Kentucky, Lexington, and postdoctoral training at the University of Michigan, Ann Arbor. She teaches courses in animal physiology, microanatomy, neuroendocrinology, general biology, and reproductive physiology. She has an active research program that focuses on the mechanisms regulating the development of childhood obesity. Currently she is studying the role of snacking from weaning to adulthood in the onset of childhood obesity. In 2019 she was awarded the Outstanding Faculty Award for teaching, research, and service by the State Council of Higher Education for Virginia.

Her interests include gardening, hiking, fishing, aromatherapy, music, and participating in choral ensembles.

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PREFACE

Integrated Principles of Zoology continues to be the leading text for the introductory zoology course. With the eighteenth edition, the authors bring a wealth of real experience as they describe the diversity of animal life and the fascinating adaptations that enable animals to inhabit so many ecological niches.

The overall organization of this text has proven to work well to help students understand the content. Distinctive features, especially the emphasis on principles of evolution and zoological science, have been strengthened. To aid in student learning, several pedagogical features have been retained: opening chapter prologues drawn from the chapter's theme; chapter summaries and review questions to aid in comprehension and study; concise and visually appealing illustrations; chapter notes and essays that offer interesting sidelights to the narrative; literature citations; and an extensive glossary providing pronunciations, derivations, and definitions of terms used in the text.

NEW TO THE EIGHTEENTH EDITION

Starting with this edition, a list of Learning Objectives opens each chapter. These objectives are organized according to the chapter's main sections. Chapter summaries, many of which are expanded in content, are restructured in tabular form to list the main highlights of each section of the chapter. This correspondence between the learning objectives, chapter sections, and summary should help students to organize the main lessons of each chapter. Our extensive cross-referencing of material among the different parts of the book now uses section numbers, with live links available in electronic versions of the text.

Notes and essays separate from the main text are now numbered for reference and organized according to six Key Themes: (1) Adaptation and Physiology, (2) Ecology, (3) Evolution, (4) Genetics and Development, (5) Human Connections, and (6) Science Explained. Adaptation and Physiology connects the proximate and ultimate causes underlying organismal functioning. Ecology addresses the interactions of animal populations with their environments, including factors that influence their geographic distribution and abundance. Evolution highlights common descent of animal species and the historical processes that modify organismal characteristics in natural populations. Genetics and Development covers the mechanisms of heredity and the ways in which an organism uses genetic information to progress from a zygote ultimately to an adult animal. Human Connections highlights ways in which zoological findings influence human welfare, including medical applications and maintaining environmental health, or how human activities have affected animal species. Science Explained covers scientific methodology and the history of scientific discovery.

In addition to these organizational revisions, we have replaced many photographs and diagrams throughout the book to improve clarity and vibrancy.

We have updated geological periods on our phylogenetic trees throughout the book; for example, the former Tertiary period is replaced with the Paleogene and Neogene periods.

We highlight some major revisions in order by the book's five major parts.

Part One, Introduction to Living Animals

In Chapter 1, we introduce the microbiome as an important characteristic of animal life. It is often overlooked that animals typically harbor thousands of species of bacteria and archaea, primarily in the gut. These species typically exist in a harmless symbiosis with their animal hosts, with fewer than 100 species of bacteria being sources of infectious disease. As molecular genetic methods for identifying an animal's microbiome improve, this dimension is becoming an increasingly important part of zoology.

In Chapter 2, water as a solvent for respiratory gases is added to its important properties for supporting life. The introduction to proteins is made more specific in stating that a typical protein contains hundreds to thousands of amino acids of 20 standard kinds. Prions are described in a Key Theme essay. Atmospheric carbon dioxide is updated to 0.04%. The name Archaebacteria is updated to Archaea. In discussing endosymbiotic theory, cyanobacterial invaginations are introduced as a corresponding feature between cyanobacteria and plastids.

Chapter 3 includes more explicit labeling of some figures and color coordination among figures that incorporate the plasma membrane.

Part Two, Continuity and Evolution of Animal Life

In Chapter 5, single nucleotide polymorphism (SNP) is made a major concept and given a glossary entry. Key Themes include titles on chromosomes and the cell cycle, genic cloning, genome size, and junk or selfish DNA, and radiation and chemical mutagens. The chapter summary is expanded to cover more details of the chapter. Chapter 6 includes new material on neutral alleles and species selection in connection with the learning objectives. August Weismann's role in neo-Darwinian theory is elaborated. In Chapter 7, parthenogenesis has been moved from the section on sexual reproduction and presented instead as a separate condition intermediate between sexual and asexual reproduction. Chapter 8 includes a new short discussion of coelom function. Chapter 9 includes new material on the organizational level of flatworms, the status of the spongocoel as a gut cavity in sponges, junctional complexes found between epithelial cells, and properties of oblique striated muscle.

Part Three, Diversity of Animal Life

In Chapter 10, new information is added on the roles of the holotype and paratypes in taxonomy, with new glossary definitions of these terms. Contents of the major subdivisions of animal life are updated to reflect new phylogenetic hypotheses.

Chapter 11 includes three new glossary terms: ancoracyst, mixotrophy, and trogocytosis, plus a revised description of red tide in a Key Theme. New descriptions of clades Holomyota and Holozoa (within Opisthokonta) appear with an associated revised Figure 11.36. Chapter 12 has a new opening essay and a revised section on the origin of animals, with bioactive compounds now a Key Theme. Class Myxozoa has been added to Chapter 13 (full description) and to the associated cladogram in Figure 13.2. Phylum Xenacoelomorpha is now included in Chapter 14: Xenoturbellida, previously in Chapter 22, is now considered a protostome related to acoelomorph flatworms and not a deuterostome, so it has been allied with Acoelomorpha as Xenacoelomorpha. The figure from Chapter 22 is now Figure 14.2. The phylogeny section explains the revision of the group. Chapter 14 also contains a revised Key Theme on schistosomiasis.

In Chapter 15, clade Kryptrochozoa has been removed in favor of the more inclusive group Trochozoa, with an associated change in the cladogram, Figure 15.1. In Chapter 17, Phylum Sipuncula has been demoted and placed within Phylum Annelida; the cladogram in Figure 17.1 is revised to accommodate this change. Several new section numbers added to Chapter 17 make it easier to follow major topics. Chapter 18 contains a new Key Theme on cryptobiosis and its applications to storing blood. Chapter 21 contains a new Key Theme on *Varroa* mites and bee colony collapse disorder. The opening essay has updated statistics on locust outbreaks. Several new section numbers were added here to make it easier to follow major topics. Chapter 22 includes a revised Key Theme essay on Crown-of-Thorns sea-star outbreaks and one on *Diadema* sea urchin outbreaks. Figure 22.3 is revised to include new echinoderm fossil groups, which are discussed in the echinoderm phylogeny section. Several new section numbers make it easier to follow major topics.

Chapter 23 features consolidation of material on early chordate evolution into a single section, and improved art for the cladogram, chordate characters, and vertebrate innovations. New text is added to explain problems with using Linnean taxonomy in chordates, and why an unranked system is favored for higher chordate taxonomy. This material applies as well to the other vertebrate chapters. Taxonomy and species numbers are updated. The biology and ecology of amphioxus get increased treatment to match that of sea squirts and to introduce traits discussed in the vertebrate chapters. New material on early vertebrate evolution includes the early chordate *Metaspriggina*. In Chapter 24, the introduction is modestly revised to outline the contents of the chapter. A single table now consolidates characteristics of the four major fish groups, allowing easy comparison among groups. Teleost suction feeding is expanded to emphasize its importance and to contrast it with feeding in terrestrial vertebrates. Shark reproduction is rewritten to emphasize continuity of reproductive mechanisms.

Chapter 25 is reorganized into a greater number of sections with an expanded summary and some new information on temnospondyls as a source of modern amphibians. Numbers of species are updated to represent recent discoveries of cryptic species in many taxa. The introduction to Chapter 26 is reorganized to outline the chapter's contents. Changes to the section on amniote adaptations include revised coverage of respiration, circulation, and special sensory systems. Some material on limb positions was moved to the mammal chapter. New text on squamate reproduction complements coverage for turtles, crocodilians, and tuataras. Material on snake venom is rewritten for clarity. The section on dinosaur systematics is updated. Chapter 27 includes a new paragraph on early bird evolution in the Cretaceous and Paleogene, and an extensive rewrite on dinosaur ancestry of birds. We revised the sections on fluid dynamics of avian flight and the respiratory cycle. An expanded boxed essay now covers lead poisoning of condors. We reduce usage of the somewhat awkward term "nonavian reptile" for the traditional Class Reptilia. Chapter 28 features a substantial new section on early mammalian evolution and on the megafauna of the Pleistocene. Updates include mammalian dentition and feeding, migration of bats, and decline of caribou populations in North America. Coverage of mammalian population ecology was reduced to avoid redundancy with Chapter 38. Human evolution is revised to include new research on *Australopithecus, Homo heidelbergensis,* and Denisovans.

Part Four, Activity of Life

Chapter 30 includes new information on how mixing of freshwater and seawater at the ebbing of tides produces physiological challenges for aquatic animals. Oncotic pressure (colloid osmotic pressure) is added as a force opposing blood hydrostatic pressure and as a factor that produces edema in blood or interstitial fluid. New emphasis is placed on the relationship between surface area and volume in mammals' ability to withstand cold environmental temperatures. Chapter 31 includes a new Key Theme on hypertension and associated kidney disease. Chapter 32 adds breakdown of nucleic acids to the section on digestion. Chapter 33 features redrawn Figures 33.7 and 33.8, with channels shown as opening when the neurotransmitter binds. In Chapter 34 a new Key Theme lists the heart as an endocrine organ producing atrial natriuritic peptide. New information is added on the roles of oxytocin and vasopressin in social behavior and the use of oxytocin as a treatment for autism spectrum disorders. In Chapter 36, polyandry is now illustrated with the example of Galápagos hawks.

Part Five, Animals and Their Environments

In Chapter 37, a new Key Theme is added on the demand for fresh water and how global warming challenges our supply of fresh water. Information on the Peruvian anchoveta fishery is updated. Chapter 38 is restructured into more sections to coordinate the learning objectives and chapter summary. The growth of human populations and the taxonomic status of Galápagos finches are updated.

TEACHING AND LEARNING AIDS

To help students in **vocabulary development,** key words are boldfaced and derivations of technical and zoological terms are provided, along with generic names of animals where they first appear in the text. In this way students gradually become familiar with the more common roots that form many technical terms. An extensive **glossary** provides pronunciation, derivation, and definition for many terms, including new ones added to the glossary or existing ones rewritten for this edition.

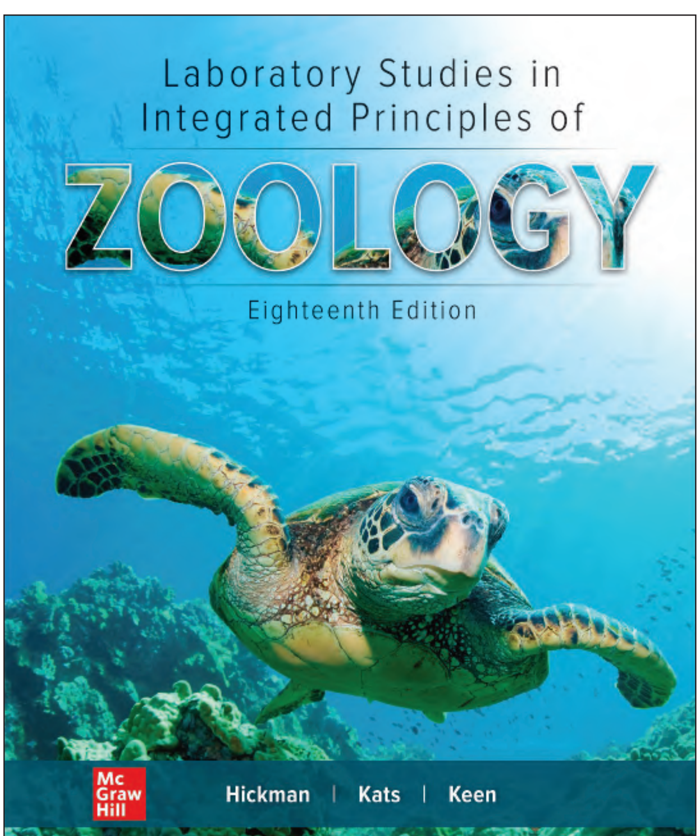
A distinctive feature of this text is a **prologue** for each chapter that highlights a theme or fact relating to the chapter. Some prologues present biological, particularly evolutionary, principles; those in Part Three on animal diversity illuminate distinguishing characteristics of the group presented in the chapter.

Again, William C. Ober and Claire W. Ober have strengthened the art program for this text with many new full-color paintings that replace older art, or that illustrate new material. Bill's artistic skills, knowledge of biology, and experience gained from an earlier career as a practicing physician have enriched this text through 10 of its editions. Claire practiced pediatric and obstetric nursing before turning to scientific illustration as a full-time career. Texts illustrated by Bill and Claire have received national recognition and won awards from the Association of Medical Illustrators, American Institute of Graphic Arts, Chicago Book Clinic, Printing Industries of America, and Bookbuilders West. They are also recipients of the Art Directors Award.

For the Zoology Lab

***Laboratory Studies in Integrated Principles of Zoology* by Cleveland Hickman, Jr., Susan Keen, and Lee B. Kats**

Now in its eighteenth edition, this lab manual was written to accompany *Integrated Principles of Zoology,* and can be easily adapted to fit a variety of course plans.



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We have received suggestions from faculty and students throughout the country. This is vital feedback that we rely on with each edition. Each person who has offered comments and suggestions has our thanks. The efforts of many people are needed to develop and improve a textbook. Among these people are the reviewers and consultants who point out areas of concern, cite areas of strength, and make recommendations for change. The following reviewers helped review the seventeenth edition to help with development of the eighteenth:

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Cleveland P. Hickman, Jr.
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Supplement	**Features**
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Chapter References	Listing of Selected References for each chapter (previously listed in the book)
Endsheets	• Cladogram • Timeline of Events
Conversion Guides	Spreadsheets detailing changes in each chapter between 17e and 18e
The Structure of Matter	PDF of Structure of Matter Appendix that appeared in earlier editions of the book
Additional Labs	• Lab Manual References (as noted in Appendix A of Lab Manual) • PDFs of Additional Labs that appeared in earlier editions of the lab manual

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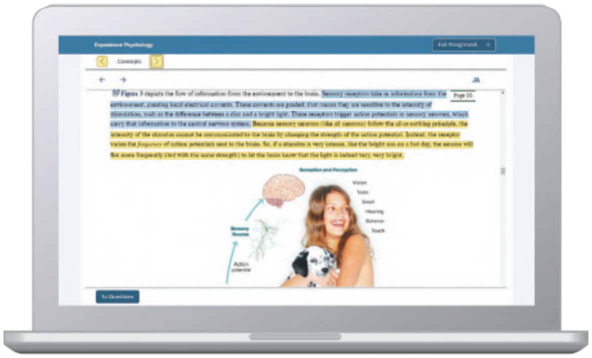

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PART ONE

1 Life: Biological Principles and the Science of Zoology

LEARNING OBJECTIVES

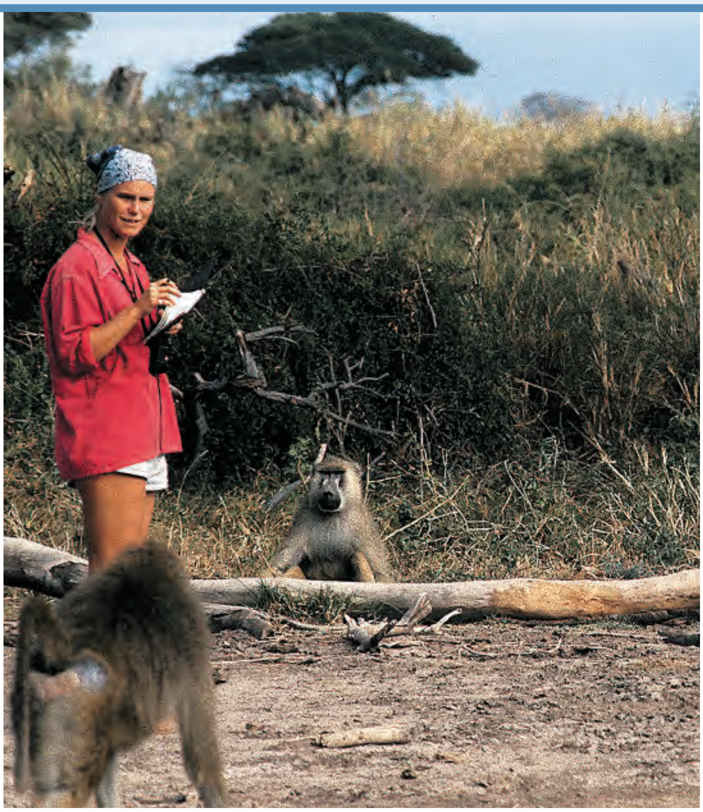
Readers will be able to:

1.1 Explain the unifying properties of living systems as outcomes of life's unique evolutionary history.

1.2 Explain the major features unique to the animal branch of the evolutionary tree of life.

1.3 Explain how science consists in testing, possibly rejecting, and improving our simplest and best explanations using data, not in proving the correctness of a conjecture.

1.4 Explain the five major conjectures of Darwin's evolutionary theory—perpetual change, common descent, multiplication of species, gradualism, and natural selection—and the roles of Mendelian genetics and the chromosomal theory of inheritance in animal evolution.



Zoologist studying the behavior of yellow baboons* (Papio cynocephalus) *in the Amboseli Reserve, Kenya.

The Uses of Principles

We explore the animal world by actively applying important guiding principles to our investigations. Just as the exploration of outer space is both guided and limited by such principles as the theories of gravitation and motion and their associated technologies, exploration of the animal world depends critically on the principles of evolution, genetics, and cellular organization, and the questions and methods derived from them. Zoology makes sense to us only when we understand the principles used to construct this knowledge.

The principles of modern zoology trace their long history to many sources. Some principles come from laws of physics and chemistry, which all living systems obey. Others come from the scientific method, which tells us that our hypothetical explanations of the animal world must guide us to gather data that potentially can refute these explanations. Many important principles come from previous studies of the living world, of which animals are one part.

Principles of heredity, variation, and organic evolution guide the study of life from the simplest unicellular forms to the most complex animals, fungi, and plants. Because life shares a common evolutionary origin, principles learned from the study of one group often provide insights into other groups as well. By tracing the origins of our operating principles, we see that zoologists are not an island unto themselves but part of a larger scientific community.

We begin our study of zoology by searching broadly through the history of science and biology for our most basic principles and their diverse sources. These principles simultaneously guide our studies of animals and integrate those studies into the broader context of human knowledge.

Zoology, the scientific study of animal life, builds on centuries of human observations of the animal world. Mythologies of nearly every human culture reveal early attempts to solve the mysteries of animal life and its origin. Zoologists now confront these same mysteries with the most advanced methods and technologies developed by all branches of science. We document the diversity of animal life and organize it in a systematic way. This complex and exciting process builds on the contributions of thousands of zoologists working in all dimensions of the biosphere (see Figure 1.1). We strive to explain how animal diversity originated and how animals perform the basic processes of life that permit them to inhabit diverse environments.

This chapter introduces the fundamental properties of animal life, the methodological principles that govern their study, and two important theories that guide our research: (1) the theory of evolution, which is the central organizing principle of biology, and (2) the chromosomal theory of inheritance, which explains heredity and variation in animals. These theories unify our knowledge of the animal world.

1.1 FUNDAMENTAL PROPERTIES OF LIFE

Historical Continuity of Life

We begin by asking, *What is life?* Our definition lies in the historical continuity of life on earth. Life's history of common descent with modification gives it an identity separate from the nonliving world. We trace this common history backward through time from the diverse forms observed today and in the fossil record to a common ancestor that must have arisen almost 4 billion years ago (see Chapter 2). There are no traces in the fossil record or on earth's surface of what we postulate to have been the incipient stages of life, those that predate cells. Replicating molecular systems, which could not have produced fossils, must have preceded and given rise to cellular life, whose history appears in the fossil record. All descendants of life's common ancestor, past and present, lie within our concept of life.

Life's most fundamental attribute is its reproduction of individuals with heredity and variation. Replication of large molecules that

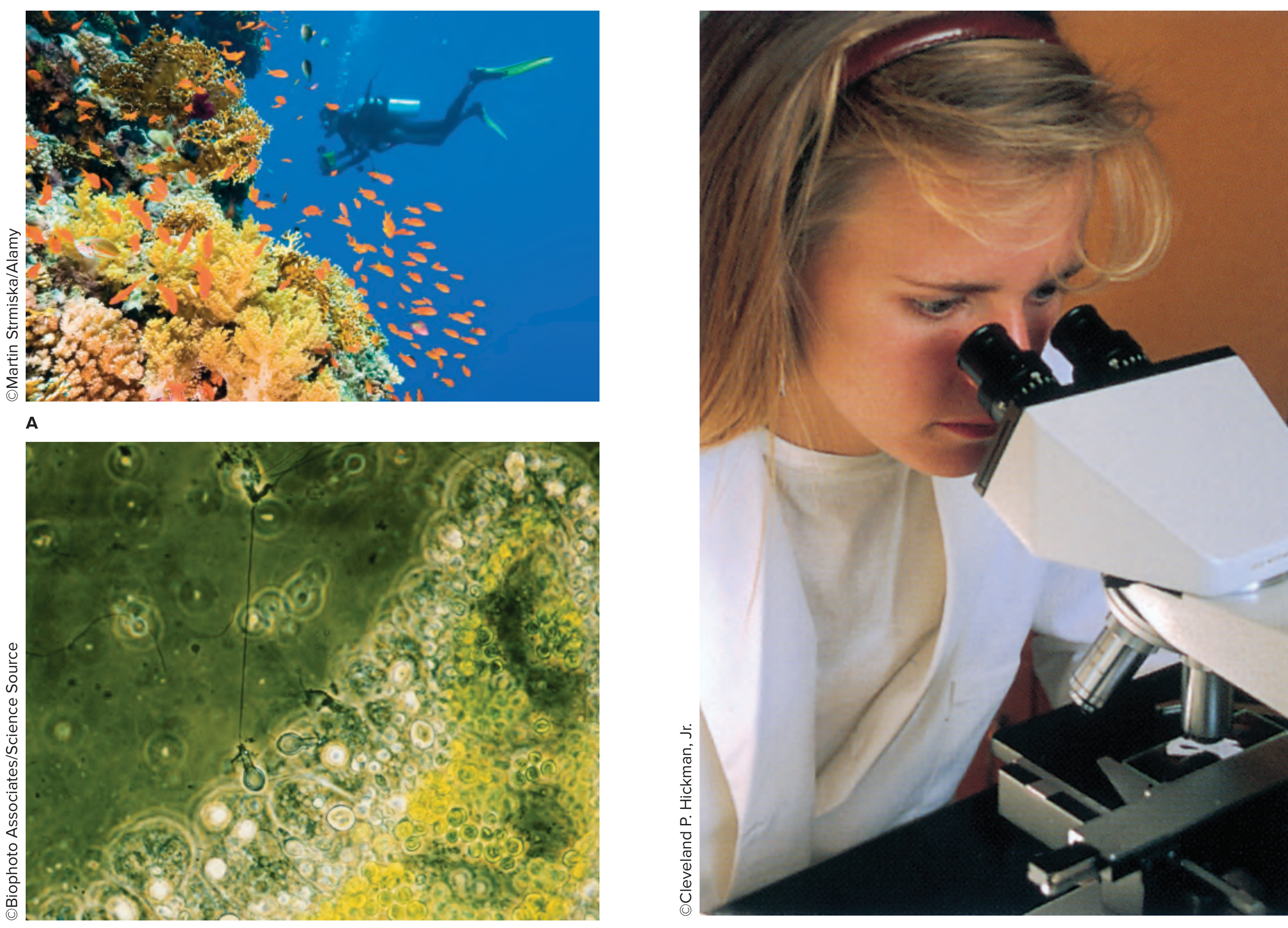


Figure 1.1 Examples of observation in zoological research. **A,** Observing a coral reef. **B,** Observing nematocyst discharge from cnidarian tentacles, as shown in **C,** (see Section 13.1).

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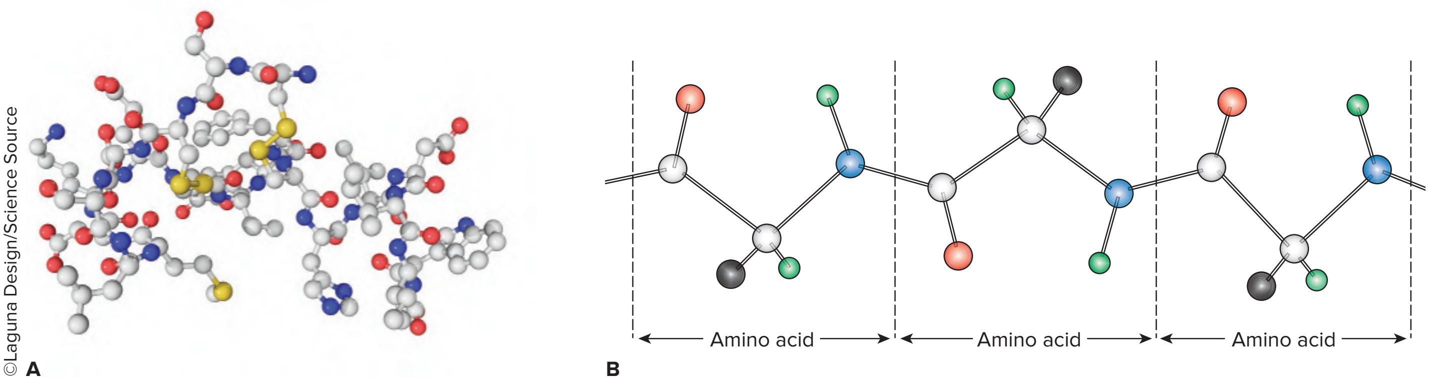

Figure 1.2 A computer simulation of the three-dimensional structure of the human endothelin-1 protein **(A),** which can constrict blood vessels to increase blood pressure. The protein is a linear string of molecular subunits called amino acids, connected as shown in **B,** which fold in a three-dimensional pattern to form the active protein. The white balls correspond to carbon atoms, the red balls to oxygen, the blue balls to nitrogen, the yellow balls to sulfur, the green balls to hydrogen, and the black balls **(B)** to molecular groups formed by various combinations of carbon, oxygen, nitrogen, hydrogen, and sulfur atoms that differ among amino acids. Hydrogen atoms are not shown in **A.**

store information is unique to life and must trace to life's origin. These properties establish a temporal continuity of ancestral and descendant populations showing extensive and ongoing change, which we call **evolution.** Through its evolution, life has generated many spectacular features that have no counterparts in the nonliving world. Novel properties emerge at all levels of life's hierarchical systems, from molecules and cells to organismal form and behavior.

We must resist giving life a definition based in essential characteristics that must occur in all living forms past and present. Such a definition would be particularly difficult for our theories of the origin of life from nonliving matter. Nonetheless, all living cells share metabolic processes and genetic information that reveal unmistakably their hereditary descent from life's common ancestor.

General Properties of Living Systems

Life's most outstanding general features include chemical uniqueness; complexity and hierarchical organization; reproduction (heredity and variation); possession of a genetic program; metabolism; development; environmental interaction; and movement.

1. **Chemical uniqueness.** *Living systems demonstrate a unique and complex molecular organization.* Living systems assemble large molecules, called macromolecules, that greatly exceed in complexity the small molecules of nonliving matter. Macromolecules contain the same kinds of atoms and chemical bonds that occur in nonliving matter and obey all fundamental laws of chemistry; it is only the complex organizational structure of these macromolecules that makes them unique to life. We recognize four major categories of biological macromolecules: nucleic acids, proteins, carbohydrates, and lipids (see Chapter 2). These categories differ in the structures of their component parts, the kinds of chemical bonds that link their subunits together, and their roles in living systems.

   The general structures of these macromolecules evolved and stabilized early in the history of life. With some modifications, these same general structures occur in every form of life today. Proteins, for example, are built from 20 specific kinds of amino acid subunits linked together by peptide bonds in a linear sequence (see Figure 1.2). Additional bonds occurring between amino acids that are not adjacent to each other in the protein chain give the protein a complex, three-dimensional structure (see Figures 1.2 and 2.15). A typical protein contains several hundred amino acid subunits. Despite the stability of this basic protein structure, the ordering of the different amino acids in a protein molecule shows enormous variation. This variation underlies much of the diversity that we observe among different kinds of living organisms. The nucleic acids, carbohydrates, and lipids likewise contain characteristic bonds that link variable subunits (see Chapter 2). This organization gives living systems a common biochemical theme with great potential diversity.
2. **Complexity and hierarchical organization.** *Living systems demonstrate a unique and complex hierarchical organization.* Nonliving matter is organized at least into atoms and molecules and often has a higher degree of organization as well. However, atoms and molecules are combined into patterns in the living world that do not exist in nonliving matter. In living systems, we find a hierarchy of levels that includes, in ascending order of complexity, macromolecules, cells, organisms, populations, and species (see Figure 1.3). Each level builds on

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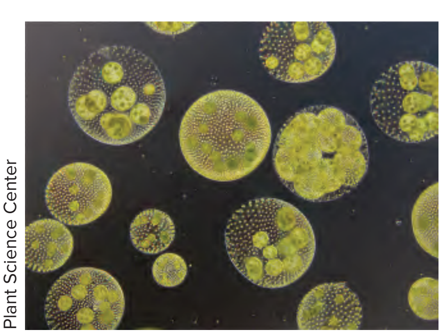


Figure 1.3 *Volvox carteri* (see Section 11.3: Viridiplantae) is a multicellular flagellate that illustrates three different levels of the biological hierarchy: cellular, organismal, and populational. Each individual spheroid (organism) contains cells embedded in a gelatinous matrix. The larger cells function in reproduction, and the smaller ones perform the general metabolic functions of the organism. The individual spheroids together form a population.

Figure 1.4 Electron micrograph of ciliated epithelial cells and mucus-secreting cells (see Section 9.3) lining the interior of a rat oviduct. Cells are the basic building blocks of living organisms.

the level below it and has its own internal structure, which is also often hierarchical. Within a cell, for example, macromolecules are assembled into structures such as ribosomes, chromosomes, and membranes, and these are likewise combined in various ways to form even more complex subcellular structures called organelles, such as mitochondria (see Chapter 3 and Chapter 4). The organismal level also has a hierarchical substructure; cells combine to form tissues, which combine to form organs, which likewise combine to form organ systems (see Chapter 9).

Cells (see Figure 1.4) are the smallest units of the biological hierarchy that are semiautonomous in their ability to conduct basic functions, including reproduction. Replication of molecules and subcellular components occurs only within a cellular context, not independently. Cells are therefore considered the basic units of living systems (see Chapter 3). We can isolate cells from an organism and cause them to grow and to multiply under laboratory conditions in the presence of nutrients alone. This semiautonomous replication cannot occur for any individual molecules or subcellular components, which require additional cellular constituents for their reproduction.

Each successively higher level of the biological hierarchy is composed of units of the preceding lower level in the hierarchy. An important consequence of this hierarchy is that we cannot infer the properties at any given level even from the most complete knowledge of the properties of its component parts. A physiological feature, such as blood pressure, is a property of the organismal level; it is impossible to predict someone's blood pressure simply by knowing the physical characteristics of individual cells of the body. Likewise, systems of social interaction, as seen in bees, appear at the populational level; one cannot infer properties of this social system by studying individual bees in isolation.

Appearance of new characteristics at a given level of organization is called **emergence,** and these characteristics are called **emergent properties.** These properties arise from interactions among the component parts of a system. For this reason, we must study all levels directly, each one being the focus of a different subfield of biology (molecular biology; cell biology; organismal anatomy, physiology, and genetics; population biology; see Table 1.1). Emergent properties expressed at a particular level of the biological hierarchy are certainly influenced and restricted by properties of the lower-level components. For example, a population of organisms that lack hearing could not develop a spoken language. Nonetheless, properties of parts of a living system do not rigidly determine properties of the whole. Many different spoken languages have

TABLE 1.1

Different Hierarchical Levels of Biological Complexity That Display Reproduction, Variation, and Heredity

Level	Timescale of Reproduction	Fields of Study	Methods of Study	Some Emergent Properties
Cell	Hours (mammalian cell = ~16 hours)	Cell biology, molecular biology	Microscopy (light, electron), biochemistry	Chromosomal replication (meiosis, mitosis), synthesis of macromolecules (DNA, RNA, proteins, lipids, polysaccharides)
Organism	Hours to days (unicellular); days to years (multicellular)	Organismal anatomy, physiology, genetics	Dissection, genetic crosses, clinical studies, physiological experimentation	Structure, functions and coordination of tissues, organs and organ systems (blood pressure, body temperature, sensory perception, feeding)
Population	Up to thousands of years	Population biology, population genetics, ecology	Statistical analysis of variation, abundance, geographical distribution	Social structures, systems of mating, age distribution of organisms, levels of variation, action of natural selection
Species	Thousands to millions of years	Systematics and evolutionary biology, community ecology	Study of reproductive barriers, phylogeny, paleontology, ecological interactions	Method of reproduction, reproductive barriers

emerged in human culture from the same basic anatomical structures that permit hearing and speech. The freedom of the parts to interact in different ways makes possible a great diversity of potential emergent properties at each level of the biological hierarchy.

Different levels of the biological hierarchy and their particular emergent properties are built by evolution. Before multicellular organisms evolved, there was no distinction between the organismal and cellular levels, and this distinction remains absent from single-celled organisms (see Chapter 11). The diversity of emergent properties that we see at all levels of the biological hierarchy contributes to the difficulty of giving life a simple definition or description.

3. **Reproduction.** *Living systems can reproduce themselves.* Life does not arise spontaneously but comes only from prior life, through reproduction. Although life certainly originated from nonliving matter at least once (see Chapter 2), this origin featured enormously long periods of time and conditions very different from the current biosphere. At each level of the biological hierarchy, living forms reproduce to generate others like themselves (see Figure 1.5). Genes replicate to produce new genes. Cells divide to produce new cells. Organisms reproduce, sexually or asexually, to produce new organisms (see Chapter 7). Populations reproduce themselves through time to form lineages of ancestral-descendant populations. Should a geographic barrier split a population into spatially isolated parts, multiple population lineages can emerge from a common ancestral one. Evolutionary divergence of character among separated population lineages can produce a multiplication of species, in a process called speciation. Reproduction at any hierarchical level usually features an increase in numbers. Individual genes, cells, organisms, populations, or species may fail to reproduce themselves, but reproduction is nonetheless an expected property of these individuals.

Reproduction at each of these levels shows the complementary, and yet apparently contradictory, phenomena of **heredity** and **variation.** Heredity is the faithful transmission of traits from parents to offspring, usually (but not necessarily)

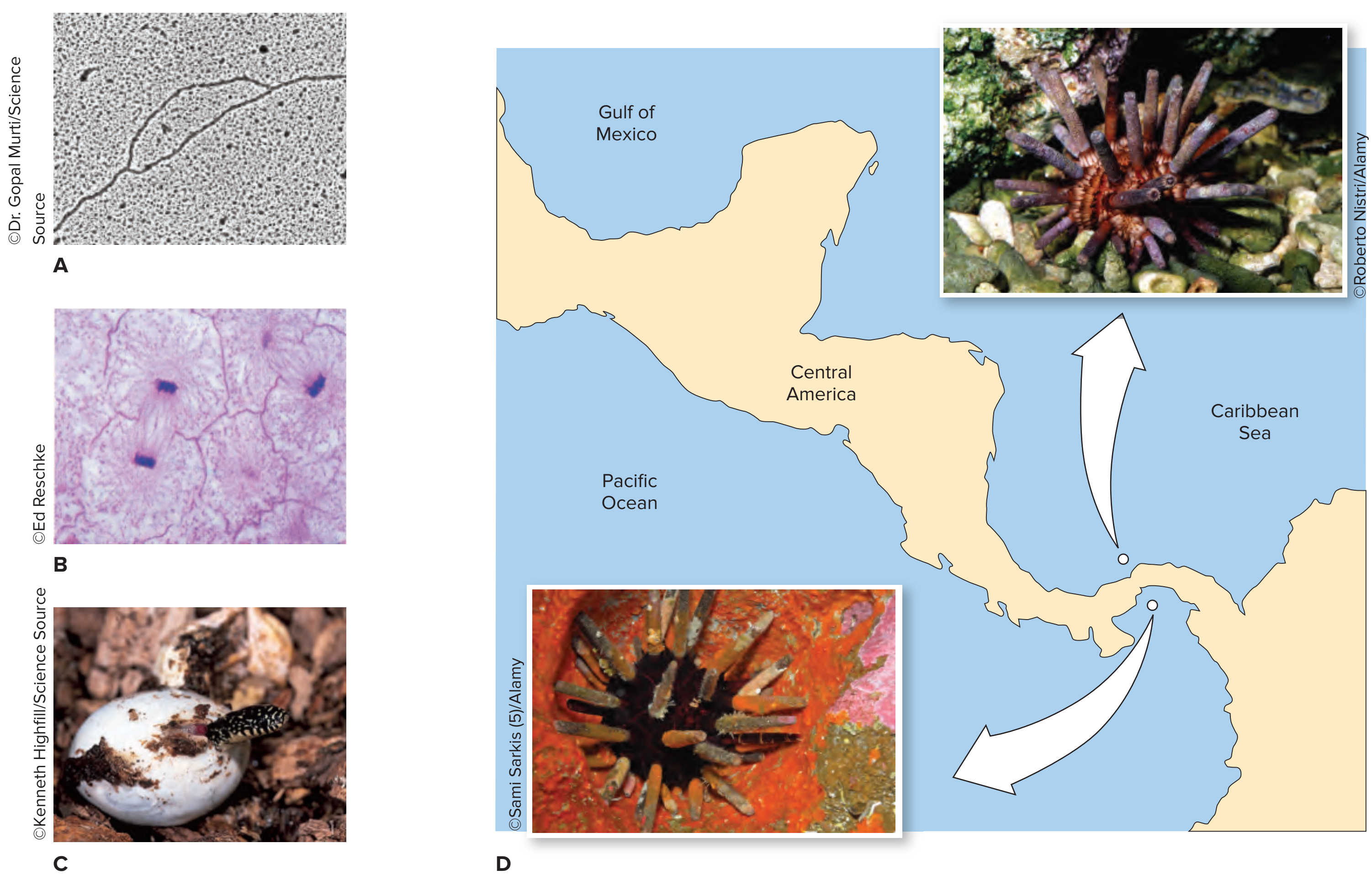


Figure 1.5 Reproductive processes observed at four different levels of biological complexity. **A,** Molecular level—electron micrograph of a replicating DNA molecule. **B,** Cellular level—micrograph of cell division at mitotic telophase. **C,** Organismal level—a king snake hatching. **D,** Species level—formation of new species in sea urchins (*Eucidaris*) after geographic separation of Caribbean (*E. tribuloides*) and Pacific (*E. thouarsi*) populations by a land bridge that formed approximately 3.5 million years ago.

observed at the organismal level. Variation is the production of *differences* among the traits of different individuals. In a reproductive process, properties of descendants resemble those of their parents to varying degrees but usually are not identical to them. Replication of deoxyribonucleic acid (DNA) occurs with high fidelity, but errors occur at repeatable rates. Cell division is exceptionally precise, especially with regard to nuclear material, but chromosomal changes occur nonetheless at measurable rates. Organismal reproduction likewise demonstrates both heredity and variation, the latter most obvious in sexually reproducing forms. Production of new populations and species also demonstrates conservation of some properties and changes of others. Two closely related frog species may have similar mating calls but differ in the rhythms of repeated sounds.

Interaction of heredity and variation in the reproductive process makes organic evolution possible and inevitable (see Chapter 6). If heredity were perfect, living systems would never change; if variation were uncontrolled by heredity, biological systems would lack the stability that allows them to persist through time.

4. **Possession of a genetic program.** *A genetic program provides fidelity of inheritance* (see Figure 1.6). **Nucleic acids** encode structures of the protein molecules needed for organismal development and functioning (see Chapter 5). For animals and most other organisms, **DNA** stores genetic information. DNA is a very long, linear chain of subunits called nucleotides, each of which contains a sugar phosphate (deoxyribose phosphate) and one of four nitrogenous bases (adenine, cytosine, guanine, or thymine, abbreviated A, C, G, and T, respectively). The sequence of nucleotide bases contains a code for the order of amino acids in the protein specified by the DNA molecule. The correspondence between the sequence of bases in DNA and the sequence of amino acids in a protein is the **genetic code.**

   The genetic code arose early in the evolutionary history of life, and the same code occurs in bacteria and in the nuclear genomes of almost all animals and plants. The near constancy of this code among living forms provides strong evidence for a single origin of life. The genetic code has undergone very little evolutionary change since its origin because an alteration would disrupt the structure of nearly every protein, which would in turn severely disrupt cellular functions that require very specific protein structures. Only in the rare instance that the altered protein structures maintained their cellular functions would such a change possibly survive and be reproduced. Evolutionary change in the genetic code has occurred in the DNA contained in animal mitochondria, the organelles that regulate cellular energy. The genetic code in animal mitochondrial DNA therefore is slightly different from the standard code of nuclear and bacterial DNA. Because mitochondrial DNA specifies far fewer proteins than does nuclear DNA, the likelihood of getting a change in the code that maintains cellular functions is greater there than in the nucleus.

5. **Metabolism.** *Living organisms maintain themselves by acquiring nutrients from their environments* (see Figure 1.7). Nutrients supply the chemical energy and molecular components for building and maintaining a living system (see Chapter 4). We call these essential chemical processes **metabolism.**

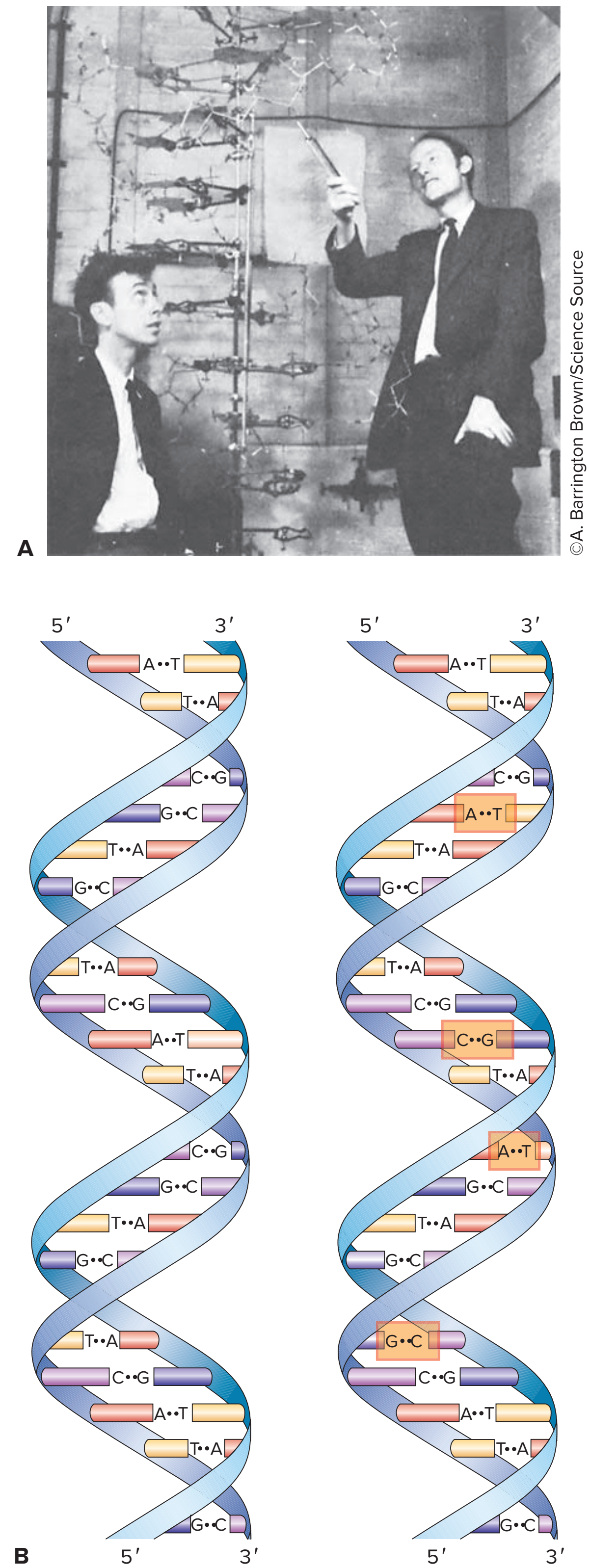
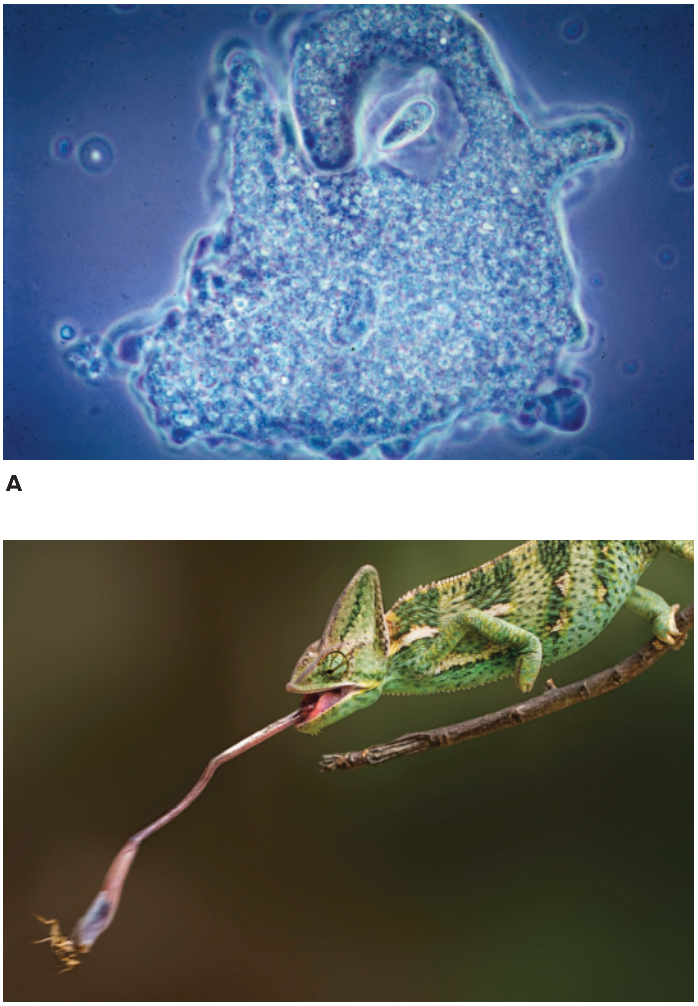


Figure 1.6 James Watson and Francis Crick with a model of the DNA double helix **(A).** The nucleotide base sequence inside the DNA molecule encodes genetic information. Genetic variation is shown **(B)** in DNA molecules that are similar in base sequence but differ from each other at four positions. Such differences can specify alternative traits, such as different eye colors.



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A

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B

Figure 1.7 Feeding processes illustrated by **(A)** an ameba surrounding food and **(B)** a chameleon capturing insect prey with its projectile tongue.

They include digestion, acquisition of energy (respiration), and synthesis of molecules and structures. Metabolism is an interaction of destructive (catabolic) and constructive (anabolic) reactions. The most fundamental anabolic and catabolic chemical processes used by living systems arose early in the evolutionary history of life, and all living forms share them. These reactions include synthesis of carbohydrates, lipids, nucleic acids, and proteins and their constituent parts and cleavage of chemical bonds to recover energy stored in them. In animals, many fundamental metabolic reactions occur at the cellular level, often in specific organelles present throughout the animal kingdom. Cellular respiration occurs, for example, in mitochondria. Cellular and nuclear membranes regulate metabolism by controlling the movement of molecules across the cellular and nuclear boundaries, respectively. The study of metabolic functions from the biochemical to the organismal levels is called **physiology.** We devote a large portion of this book to describing and comparing the diverse tissues, organs, and organ systems that different groups of animals have evolved to perform basic physiological functions of life (see Chapters 11 through Chapter 36).

6. **Development.** *All organisms pass through a characteristic life cycle.* Development describes the characteristic changes that an organism undergoes from its origin (usually the fertilization of an egg by sperm) to its final adult form (see Chapter 8). Development usually features changes in size and shape, and differentiation of structures within an organism. Even the simplest one-celled organisms grow in size and replicate their component parts until they divide into two or more cells. Multicellular organisms undergo more dramatic changes during their lives. Different developmental stages of some multicellular forms are so dissimilar that they are hardly recognizable as belonging to the same species. Embryos are distinctly different from juvenile and adult forms into which they develop. Even postembryonic development of some organisms includes stages dramatically different from each other. The transformation that occurs from one stage to another is called **metamorphosis.** There is little resemblance, for example, among the egg, larval, pupal, and adult stages of metamorphic insects (see Figure 1.8). Early stages of development are often more similar among organisms of different species than are later developmental stages. In our survey of animal diversity, we describe all stages of observed life histories but concentrate on adult stages, in which diversity tends to be most obvious.
7. **Environmental interaction.** *All animals interact with their environments.* The study of organismal interaction with an environment is called **ecology.** Of special interest are the factors that influence geographic distribution and abundance of animals (see Chapters 37 and 38). The science of ecology reveals how an organism perceives environmental stimuli and responds in appropriate ways by adjusting its metabolism and physiology (see Figure 1.9). All organisms respond to environmental stimuli, a property called **irritability.** The stimulus and response may be simple, such as a unicellular organism moving from or toward a light source or away from a noxious substance, or it

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A

B

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Figure 1.8 **A,** Adult monarch butterfly emerging from its pupal case. **B,** Fully formed adult monarch butterfly.

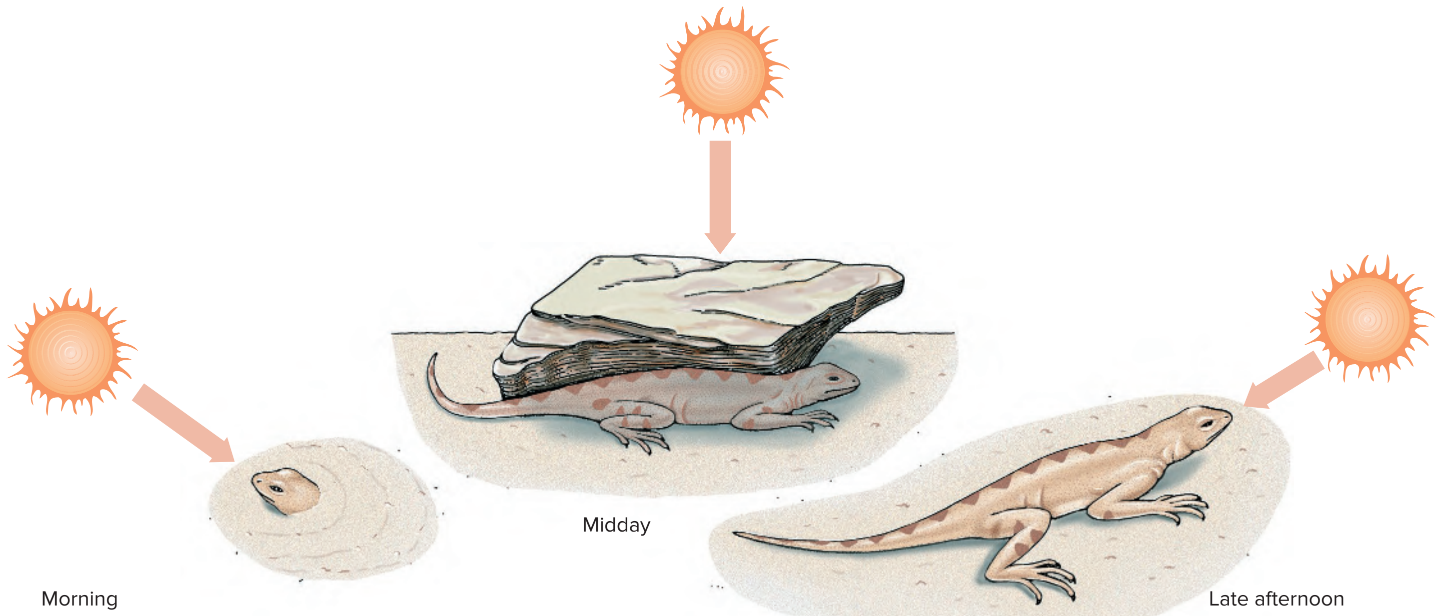

Figure 1.9 A lizard regulates its body temperature by choosing different locations (microhabitats) at different times of day.

may be quite complex, such as a bird responding to a complicated series of signals in a mating ritual (see Chapter 36). Life and environment are inseparable. We cannot isolate the evolutionary history of a lineage of populations from the environments in which it occurred.

8. **Movement.** *Living systems and their parts show precise and controlled movements arising from within the system.* The energy that living systems extract from their environments permits them to initiate controlled movements. Such movements at the cellular level are essential for reproduction, growth, and many responses to stimuli in all living forms and for development in multicellular ones. Semiautonomous movement occurs even in some biological macromolecules. An enzymatic protein undergoes characteristic and reversible changes in shape as it binds a substrate, catalyzes a reaction, and releases a product. These characteristic molecular movements occur even when the enzyme is removed from its cellular context and used as a reagent to catalyze reactions in a laboratory. Autonomous movement reaches great diversity in animals, and much of this book comprises descriptions of animal movement and the many adaptations that animals have evolved for locomotion. On a larger scale, entire populations or species may disperse from one geographic location to another one over time through their powers of movement. Movement characteristic of nonliving matter, such as that of particles in solution, radioactive decay of nuclei, and eruption of volcanoes is not precisely controlled by the moving objects themselves and often involves forces entirely external to them. The adaptive and often purposeful movements initiated by living systems are absent from the nonliving world.

Life Obeys Physical Laws

To untrained observers, these eight properties of life might appear to violate basic laws of physics. Vitalism, the idea that life has a mystical vital force that violates physical and chemical laws, was once widely advocated. Biological research has consistently rejected vitalism, showing instead that all living systems obey basic laws of physics and chemistry. Laws governing energy and its transformations (thermodynamics) are particularly important for understanding life (see Chapter 4). The **first law of thermodynamics** is the law of conservation of energy. Energy is neither created nor destroyed but can be transformed from one form to another. All aspects of life require energy and its transformation. The energy to support life on earth flows from the fusion reactions in our sun and reaches the earth as light and heat. Photosynthesis in green plants and cyanobacteria transforms energy captured as sunlight into chemical bonds. Energy in chemical bonds is a form of potential energy released when the bond is broken; the energy is used to perform numerous cellular tasks. Energy transformed and stored in plants is then used by animals that eat the plants, and these animals may in turn provide energy for predators.

The **second law of thermodynamics** states that physical systems tend to proceed toward a state of greater disorder, or **entropy.** Energy obtained and stored by plants is subsequently released by various mechanisms and finally dissipated as heat. Living cells maintain complex molecular organization only as long as energy fuels the organization. The ultimate fate of materials in the cells is degradation and dissipation of their chemical-bond energy as heat. An evolutionary increase over time in organismal complexity may appear at first to violate the second law of thermodynamics, but it does not. Organismal complexity is achieved and maintained only by the perpetual use and dissipation of energy flowing into the biosphere from the sun. Survival, growth, and reproduction of animals require energy that comes from breaking complex food molecules into simple organic waste. The processes by which animals acquire energy through nutrition and respiration reveal themselves to us through the many physiological sciences.

1.2 ZOOLOGY AS A PART OF BIOLOGY

Animals form a distinct branch on the evolutionary tree of life. It is a large and old branch that originated in the Precambrian seas over 600 million years ago. Animals form part of an even larger limb called **eukaryotes,** organisms whose cells contain membrane-enclosed nuclei. This larger limb includes plants, fungi, and numerous unicellular forms. Perhaps the most distinctive characteristic of animals as a group is their means of nutrition, which consists in eating other organisms. Animal evolution has elaborated this basic way of life through diverse systems for capturing and processing a wide array of food items and for locomotion.

We distinguish animals also by the absence of characteristics that have evolved in other eukaryotes but not in animals. Plants, for example, use light energy to produce organic compounds (photosynthesis), and they have evolved rigid cell walls that surround their cell membranes; photosynthesis and cell walls do not occur in animals. Fungi acquire nutrition by absorption of small organic molecules from their environments, and their body plan contains tubular filaments called *hyphae;* these structures do not occur in the animal kingdom.

Some organisms that are neither animals nor plants combine properties of animals and plants. For example, *Euglena* (see Figure 1.10) is a motile, single-celled organism that resembles plants in being photosynthetic, but resembles animals in its ability to eat food particles. *Euglena* is part of a separate eukaryotic lineage that diverged from those of plants and animals early in the evolutionary history of eukaryotes. *Euglena* and other unicellular eukaryotes formerly were grouped as the kingdom Protista, although this kingdom is an arbitrary grouping of taxa that are not each other's closest relatives and thus violates taxonomic principles (see Chapter 10).

The **microbiome** is a major characteristic of animal life that is often overlooked: animal bodies typically harbor thousands of species of bacteria and archaea, primarily in the gut. These species typically exist in a harmless symbiosis with their animal hosts, with fewer than 100 species of bacteria being sources of infectious disease. It is estimated that the microbial species in a human body collectively contain 500 times the number of genes present in our nuclear genomes. Because many of these microbes are hard to culture, their diversity was fully appreciated only after development of technology for sequencing DNA isolated from our symbiotic microbes. The microbiome influences our digestion of food, and variation in the content of the microbiome among individuals can influence our body weight and susceptibility to malnutrition. The microbiome is not essential for survival of humans or mice, but it is critical to the survival of other species. Cattle would be unable to digest food without the bacteria present in their foregut. Among insects, termites depend on bacteria to digest their food, and aphids and cicadas depend upon bacteria for nutrition. Corals become weak and decline in the absence of their symbiotic bacteria and algae. An animal's microbiome is not strictly constant in species diversity, and is subject to change as microbes are exchanged among animals of the same and different species. Studies of animal microbiology are still at an early stage and likely a source of interesting surprises ahead in our understanding of zoology.

We summarize in Chapters 8 and 9 the fundamental structural and developmental features evolved by the animal kingdom.

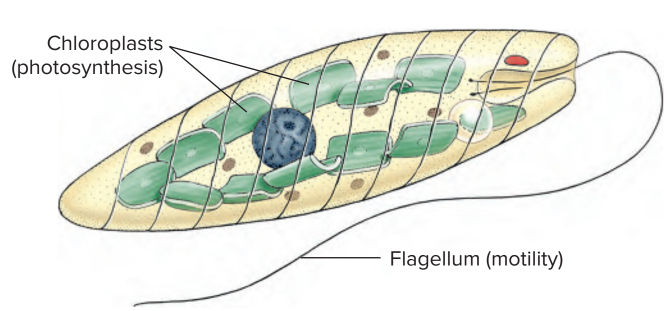

Figure 1.10 Some organisms that are neither animals nor plants, such as single-celled *Euglena* (shown here) and *Volvox* (see Figure 1.3), combine properties that distinguish animals (locomotion) from plants (photosynthetic ability).

1.3 PRINCIPLES OF SCIENCE

Nature of Science

A basic understanding of zoology requires understanding what science is, what it is not, and how we gain knowledge using the scientific method.

Science is a way of asking questions about the natural world and sometimes obtaining precise answers to them. Although science, in the modern sense, arose within the last 200 years or so, a tradition of asking questions about the natural world is ancient. In this section, we examine the methodology that zoology shares with science as a whole. These procedures for constructing data-based explanations of natural phenomena distinguish sciences from activities that we exclude from the realm of science, such as art and religion.

Despite an enormous impact of science on our lives, many people have only a minimal understanding of science. For example, on March 19, 1981, the governor of Arkansas signed into law the Balanced Treatment for Creation-Science and Evolution-Science Act (Act 590 of 1981). This act falsely presented "creation-science" as a valid scientific endeavor. "Creation-science" is instead a religious position advocated by a minority of the American religious community, and it does not qualify as science. Enactment of this law led to a historic lawsuit tried in December 1981 in the court of Judge William R. Overton, U.S. District Court, Eastern District of Arkansas. The American Civil Liberties Union brought this suit on behalf of 23 plaintiffs, including religious leaders and groups representing several denominations, individual parents, and educational associations. The plaintiffs contended that the law violated the First Amendment to the U.S. Constitution, which prohibits "establishment of religion" by government. This prohibition precludes passing a law that would aid one religion or prefer one religion over another. On January 5, 1982, Judge Overton permanently stopped the State of Arkansas from enforcing Act 590.

Considerable testimony during the trial described the process of science. Some witnesses defined science simply, if not very informatively, as "what is accepted by the scientific community" and